Трансформация экосистем
Ecosystem Transformation

ISSN 2619-0931 Online
www.ecosysttrans.com

DOI: https://doi.org/10.23859/estr-240405
EDN: https://elibrary.ru/opxmxx
UDC 631.466.1*630*114

Article

Fungi of forest litter in experimental plantations of lodgepole pine (*Pinus contorta* Dougl.)

V.A. Kovaleva, Yu.A. Vinogradova, T.A. Pristova

Institute of Biology, Komi Science Centre of the Ural Branch of the Russian Academy of Sciences, Kommunisticheskaya St. 28, Syktyvkar, 167000 Russia

**pristova@ib.komisc.ru*

Abstract. The paper deals with the community of soil fungi of forest litter in experimental plantations of the Krasnozatonsky forestry in the Komi Republic, created in a clear-cut area using an introduced species, i.e. lodgepole pine (*Pinus contorta* Dougl.), during the growing season of 2023. The species composition of fungi is shown to include 34 species from 8 genera, 7 orders and 2 divisions, including sterile mycelium. Most species belong to ascomycetes (88.2% of the total species diversity). Representatives of the genus *Penicillium* dominate by species number, frequency of occurrence and abundance. The litter fungal community is subject to significant seasonal dynamics with the microbial abundance increasing from May (17.1 ± 7.5 × 10^3 CFU/g) to September (60.9 ± 19.2 × 10^3 CFU/g) and the number of species increasing from 12 to 25. The biomass of fungi during the growing season ranges from 1.04 ± 0.17 to 7.68 ± 3.31 mg/g. The results obtained can be further used in assessing the impact of forest crops grown with the use of introduced species on the forming forest litter.

Keywords: pine forests, experimental plantations, introduced species, fungi, microbial biomass

Funding. The work was carried out with the financial support of the state tasks of the Institute of Biology, Komi Science Centre of the Ural Branch of the Russian Academy of Sciences titled “Environment-forming role and productivity of forest and peatland ecosystems of the European North-East of Russia” (№ 125020501547–8) and “Microbial communities of ecosystems in the North, their biotechnological potential and its realisation technologies” (№ 125021201993–3).

ORCID:
V.A. Kovaleva, https://orcid.org/0000-0001-5465-6134
Yu.A. Vinogradova, https://orcid.org/0000-0003-4891-4904
T.A. Pristova, https://orcid.org/0000-0002-8266-8113

To cite this article: Kovaleva, V.A. et al., 2025. Fungi of forest litter in experimental plantations of lodgepole pine (*Pinus contorta* Dougl.). *Ecosystem Transformation* **8** (3), 82–98. https://doi.org/10.23859/estr-240405

Received: 05.04.2024
Accepted: 02.08.2024
Published online: 01.08.2025

DOI: https://doi.org/10.23859/estr-240405
EDN: https://elibrary.ru/opxmxx
УДК 631.466.1*630*114

Научная статья

Микромицеты лесной подстилки в опытных культурах сосны скрученной (*Pinus contorta* Dougl.)

В.А. Ковалева, Ю.А. Виноградова, Т.А. Пристова*

Институт биологии Коми научного центра Уральского отделения РАН, 167000, Россия, г. Сыктывкар, ул. Коммунистическая, д. 28

**pristova@ib.komisc.ru*

Аннотация. В течение вегетационного периода 2023 г. изучено сообщество почвенных микромицетов лесной подстилки в экспериментальных культурах Краснозатонского лесничества Республики Коми, созданных на вырубке с применением вида-интродуцента – сосны скрученной (*Pinus contorta* Dougl.). Показано, что видовой состав микромицетов насчитывает 34 вида из 8 родов, 7 порядков и 2 отделов, включая стерильный мицелий. Большинство видов относится к аскомицетам (88.2% от всего видового разнообразия). Представители рода *Penicillium* доминируют по количеству видов, частоте встречаемости и обилию. Микоценоз подстилки подвержен значительной сезонной динамике, численность микромицетов возрастает с мая (17.1 ± 7.5 × 10^3 КОЕ/г) по сентябрь (60.9 ± 19.2 × 10^3 КОЕ/г), количество видов увеличивается с 12 до 25. Биомасса микромицетов за вегетационный период варьирует от 1.04 ± 0.17 до 7.68 ± 3.31 мг/г. Полученные результаты в дальнейшем могут быть использованы при оценке влияния лесных культур, созданных с применением интродуцентов, на формирующуюся лесную подстилку.

Ключевые слова: сосновые леса, экспериментальные культуры, интродуцент, микоценоз, микробная биомасса

Финансирование. Работа выполнена при финансовой поддержке тем госзадания Института биологии Коми НЦ УрО РАН «Средообразующая роль и продуктивность лесных и болотных экосистеме европейского северо-востока России», 2025–2029 гг. (№ 125020501547-8) и «Микробные сообщества экосистем Севера, их биотехнологический потенциал и технологии его реализации» регистрационный номер (№ 125021201993-3).

ORCID:
В.А. Ковалева, https://orcid.org/0000-0001-5465-6134
Ю.А. Виноградова, https://orcid.org/0000-0003-4891-4904
Т.А. Пристова, https://orcid.org/0000-0002-8266-8113

Для цитирования: Ковалева, В.А. и др., 2025. Микромицеты лесной подстилки в опытных культурах сосны скрученной (*Pinus contorta* Dougl.). *Трансформация экосистем* **8** (3), 82–98. https://doi.org/10.23859/estr-240405

Поступила в редакцию: 05.04.2024
Принята к печати: 02.08.2024
Опубликована онлайн: 01.08.2025

Introduction

Intensive use and reproduction of forests requires an accelerated timber growing that implies, among other things, the use of fast-growing tree species. One of such species for the taiga zone of the Russian Federation is lodgepole pine (*Pinus contorta* Dougl.) (Melekhov, 1984). The natural range of this species is the western part of North America (Elias, 2014). Lodgepole pine is known to be superior to Scots pine by the growth rate (Fedorkov and Gutiy, 2017; Feklistov et al., 2008; Elfving et al., 2001; Raevsky, 2015). The use of introduced species can lead not only to their naturalisation and introduction into natural communities (Zagurskaya, 2022), but also to changes in the quality of leaf waste and litter during artificial forest restoration. This, in turn, can cause changes in ecosystem processes (decomposition and nutrient cycling rates), as well as in ecosystem properties (changes in soil carbon pool values) (McIntosh et al., 2012). Even if introduced and native species are functionally similar but differ by their growth rate and, consequently, by input of organic material from leaf fall into the litter, this will still result in changes in ecosystem properties and processes (McIntosh et al., 2012).

The process of forest ecosystem restoration affects the intensity of biological processes and organic matter accumulation. Soil microorganisms determine the direction and rate of plant waste transformation (Dobrovolskaya et al., 2015). Soil fungi possess a wide range of extracellular enzymes, produce acids, antibiotics, toxins, phytohormones, pigments, etc. (Berestetsky, 2008; Dobrovolsky and Nikitin, 2006; Karlovsky, 2008; Looby and Treseder, 2018). Due to this, they are actively involved in the processes of humus formation, immobilisation and mobilisation of nutrients and so maintain the homeostasis and recovery under anthropogenic disturbances in forest ecosystems (Aleksandrova et al., 2006a; Bakhmet and Medvedeva, 2022; Dobrovolskaya et al., 2015; Habibullina et al., 2018). Forest litter has optimal conditions for the development of different groups of fungi: high organic matter content, favourable physic-chemical and hydrothermal parameters (Dobrovolskaya et al., 2015; Kitikidou, 2012). The fungal community of forest litter includes fungal species of phyllosphere and just soil fungus, which determines high diversity and changes in taxonomic structure of fungi during the decomposition of plant waste (Habibullina and Tvorozhnikova, 2007; Kurakov and Semenova, 2016; Pristova et al., 2012; Semenova, 2002; Terekhova et al., 1998; Voříšková and Baldrian, 2013). The fungal communities of forest plantations differ from those of natural stands qualitatively and quantitatively, which roots in the characteristic features of forest litter between these communities (Shebalova, 2008; Shebalova and Zalesov, 2006). Litter fungi in pine plantations, as well as in forest plantations created using introduced species, are rarely studied (Bakhmet and Medvedeva, 2022; McIntosh et al., 2012; Shebalova and Zalesov, 2006). We did not find the study results on soil fungal community in lodgepole pine plantations in the literature.

The aim of the research was to assess the species diversity of fungi, their number and biomass in experimental plantations of lodgepole pine.

Materials and methods

The study materials were experimental plantations of lodgepole pine located on the territory of the Krasnozatonsky district forestry (Division 34) of the Syktyvkar forestry in the Komi Republic (N 61°40' E 51°03') (Fig. 1). Forest litter fungi were studied during the growing season of 2023.

Forest plantations were planted as two-year-old bare-root seedlings, grown from seeds of Swedish reproduction, instead of logged cowberry-lichen pine forest in 2006. The soil was prepared by the tractor-mounted plow TK-1 in summer 2005. The site area is 1.0 ha, total number of seedlings – 2531 units. The soil type is illuvial-iron podzol. The average litter thickness is 3.9 cm. The site hosts 36 plant species: 8 species of trees, 7 species of shrubs and dwarf shrubs, 16 species of herbs, 5 species of mosses, and 3 species of lichens. Tree and shrub species include *Betula pendula* Roth., *B. pubescens* Ehrh. and single specimens of *Salix caprea* L., *Sorbus aucuparia* L., *Populus tremula* L., and *Picea obovata* Ledeb. of seed origin.

The total projective cover (TPC) of ground cover plants at the site averages 90%, varying from 60 to 100%. The projective cover of moss cover is 55% dominated by *Polytrichum commune* Hedw.; *Pleurozium schreberi* (Willd ex Brid.) Mitt.; *Dicranum polysetum* Sw. The dominating position of mosses, in particular polytrichum mosses, is related to the microrelief specificity: a combination of rows with pine plantings and inter-rows (depressions). Moist inter-rows favours the development of moss cover. The projective cover of the herbaceous-dwarf shrub layer averages 45%, varying from 15 to 80%. Dwarf shrubs play a leading role in formation of the herbaceous-dwarf shrub layer, their projective cover can reach 55% of TPC, averaging 30% with dominating *Vaccinium vitis-idaea*L. Among herbs, *Calamagrostis epigeios* (L.) Roth.; *Chamerion angustifolium* (L.). Scop.; *Luzula pilosa* (L.) Willd; *Agrostis gigantea* Roth. are common species. In the living soil ground cover, ferns, lycopods, and lichens are rare or single with projective cover of less than 1%.

Fig. 1. Experimental crops of lodgepole pine in the Krasnozatonsky forestry.

The litter fungal community under lodgepole plantations was analysed in the beginning (May) and the end (August and September) of the vegetation period. Forest litter samples were collected from the entire area of experimental cultures: 12 samples in May, 12 samples in August, and 15 samples in September. The material was sampled according to the generally accepted methods (Kurakov, 2001). Prior to microbiological analyses, collected litter samples were stored in a freezer at –18...–20 °C. Isolation of fungi and their number calculation (in colony-forming units per gram of absolutely dry soil – CFU/g a.d.s.) were done by sowing from serial dilutions onto the agar Chapek's medium (pH = 4.5) in fivefold repetition for each sample. Calculation of fungal colonies was carried out 5–7 days later (Kazeev et al., 2003). Taxonomic affiliation of fungal isolates was identified to species using identification guides of fungi (Alexandrova et al., 2006b; Domsch et al., 2007; Egorova, 1986; Ellis, 1971; Pitt, 1991; Ramirez, 1982, etc.). Name and systematic position of taxa were unified using the database – Index Fungorum[1]. To characterise the complex of cultivated soil fungi, we applied the Shannon species diversity index (H), the Pielou index of evenness (E), the Simpson domination index (D), as well as the spatial frequency and the relative abundance indices of species (Kurakov, 2001). Spatial frequency was estimated as the proportion of samples, where the particular species was found, to the total number of collected samples.

Spore number, length and viability of fungal mycelium, the fungal biomass value was estimated by the luminescence microscopy (Metody..., 1991; Polyanskaya, 1996) using fluorescein diacetate (FDA) dye (Gaspar et al., 2001).

Statistical processing of the obtained data was carried out using Microsoft Excel 2010 programme.

Results and discussion

Number and species diversity of fungi

The number of fungi in the studied samples differed significantly in May and September. The fungal number was $17.1 \pm 7.5 \times 10^3$ CFU/g in May but $25.4 \pm 14.3 \times 10^3$ and $60.9 \pm 19.2 \times 10^3$ CFU/g in August and September, respectively. The number of estimated fungi is a relatively low value as compared to natural pine forests on the Kola Peninsula where the number of fungi varies from 46×10^3 to 216×10^3 CFU/g (Korneikova et al., 2018).

The litter samples of the studied pine plantation were isolated for 34 species of fungi from 8 genera, 7 orders and 2 divisions, including sterile mycelium (Table 1).

By the taxonomic structure analysis of the fungal community, the species diversity of fungi in litter under experimental lodgepole pine plantation exceeds the results we obtained earlier for the lodgepole pine plantations in the Storozhevsk forestry – 17 species from 9 genera (Kovaleva et al., 2023) and for the pine forests on the Kola Peninsula – 12 species from 5 orders (Korneikova et al., 2018).

The Mucoromycota division is not numerous and includes three species as *Mortierella alpina*, *Mucor hiemalis*, and *Umbelopsis vinacea* that make 8.8% of the total species composition. These species are widely distributed and are common soil representatives not only in the middle taiga of the Komi Republic (Khabibullina and Tvorozhnikova, 2007; Khabibullina et al., 2018), but also in higher latitudes (Vinogradova et al., 2019, 2023). *M. hiemalis*, like other representatives of the *Mucoromycota* division, belongs to the group of saprotrophic fungi that first utilise readily-available sugars (Domsh et al., 2007). For this reason, it is normally found in litter towards the end of the growing season at the fresh leaf fall stage (Table 1). The species prefers plant waste from the herb-dwarf shrub layer.

The main part of fungal species belong to anamorphic ascomycetes (from the Ascomycota division) – 30 species from 5 genera that make 88.2% of the total species composition. Fungi of the *Penicillium* genus, which is dominant in soils of the Komi Republic (Khabibullina et al., 2018; Kovaleva et al., 2023; Sizonenko et al., 2010; Vinogradova et al., 2019, 2023), account for 51% of the total number of isolated species (Fig. 2).

Fungi of the *Penicillium* genus belong mainly to typical hydrolytics that can develop on poor-available nutrients and assimilate difficult-to-decompose polymeric substrates at places with low rate mineralisation processes (Domssh et al., 2007; Osono, 2007; Vinogradova et al., 2023). In this connection, the litter micromycete complex in the early vegetation period is mostly composed of fungi of the *Penicillium* genus that participate in mineralisation of the previous year's fall.

[1] Index Fungorum. Web page. URL: https://www.indexfungarum.org (accessed: 14.03.2024).

Table 1. Species diversity, relative abundance of species and spatial frequency of occurrence (SFO) of soil fungi species. Frequency of occurrence categories: > 60% dominant (D), 30–60% – often-met (OM), 10–30% – rare (R), < 10% – occasional (O).

Species	May		August		September	
	Abundance, %	SFO	Abundance, %	SFO	Abundance, %	SFO
Division Mucoromycota						
Order Mortierellales						
Mortierella alpina Peyron	–	–	1.1	O	–	–
Order Mucorales						
Mucor hiemalis Wehmer	–	–	0.5	O	2.5	R
Order Umbelopsidales						
Umbelopsis vinacea (Dixon.) W. Gams	–	–	0.5	O	0.3	O
Division Ascomycota						
Order Capnodiales						
Cladosporium herbarum (Pers.) Link	–	–	–	–	0.5	O
Order Eurotiales						
Penicillium aurantiogriseum Dierckx	–	–	5.3	R	0.3	O
P. brevicompactum Dierckx	–	–	–	–	0.3	O
P. canescens Sopp	–	–	5.3	OM	15.4	OM
P. camemberti Thom	–	–	–	–	0.3	O
P. commune Thom	–	–	–	–	0.5	R
P. citreonigrum Dierckx	–	–	0.5	O	2.2	OM
P. expansum Link	1.6	O	2.1	O	–	–
P. decumbens Thom	1.6	O	4.3	OM	8.0	Д
P. dierckxii Biourge	–	–	1.1	O	1.1	R
P. granulatum Bainier	–	–	6.9	R	–	–
P. glabrum (Wehmer) Westling	–	–	0.5	O	–	–
P. jensenii K.W. Zaleski	6.3	R	0.5	O	6.3	OM
P. lanosum Westling	–	–	0.5	O	3.3	R
P. lividum Westling	3.2	R	2.7	R	5.5	D
P. raistrickii G. Sm.	–	–	0.5	O	1.4	R
P. simplicissimum (Oudem.) Thom	–	–	2.1	O	2.7	R

Species	May		August		September	
	Abundance, %	SFO	Abundance, %	SFO	Abundance, %	SFO
P. thomii Maire	15.9	OM	36.2	D	28.6	D
P. vulpinum (Cooke & Massee) Seifert & Samso	1.6	O	6.9	R	–	–
P. waksmanii K.M. Zaleski	1.6	O	–	–	–	–
Penicillium sp.	3.2	R	1.1	R	1.9	R
Talaromyces diversus (Raper & Fennell) Samson, N. Yilmaz & Frisvad	–	–	0.5	O	-	-
T. funiculosus (Thom) Samson, N. Yilmaz, Frisvad & Seifert	–	–	–	–	3.0	OM
T. rugulosus (Thom) Samson, N. Yilmaz, Frisvad & Seifert	6.3	R	1.6	R	–	–
T. variabilis (Sopp) Samson, N. Yilmaz, Frisvad & Seifert	–	–	0.5	O	0.3	O
Order Hypocreales						
Trichoderma koningii Oudemans	1.6	O	–	–	–	–
T. hamatum (Bonord.) Bainier	–	–	2.7	R	–	–
T. polysporum (Link) Rifai	–	–	–	–	1.4	O
T. viride Pers.	1.6	O	0.5	O	0.5	O
Order Thelebolales						
Pseudogymnoascus pannorum (Link) Minnis & D.L. Lindner	–	–	–	–	14.0	R
Sterile mycelium						
Mycelia sterilia	55.6	D	15.4	OM	0.3	O

The *Trichoderma* and *Talaromyces* genera are represented by 4 species. The other genera are represented by single species. Fungi of the *Talaromyces* genus are normally soil saprotrophs, widely distributed (Domssh et al., 2007; Kurakov and Semenova, 2016). Species of the *Trichoderma* genus occur in various substrates (Alexandrova et al., 2006b) and secrete cellulases, which make them part of the group of cellulose-destroying fungi involved in the mineralisation of difficult-to-decompose organic compounds (Rakhleeva et al., 2011; Osono and Takeda, 2001; Osono et al., 2003). Species of the *Trichoderma* genus were isolated from litter samples at any sampling dates: in May – *T. koningii*, in August – *T. hamatum*, in September – *T. polysporum* and at any year time – *T. viride*.

Penicillium thomii dominates by the frequency of occurrence and abundance in litter samples at any sampling dates. The abundance of this species increases from May to September (Table 1). In addition to *P. thomii*, the species *Penicillium jensenii*, *P. lividum*, *Trichoderma viride* and *Mycelia sterilia* are common at any sampling dates. The relative abundance towards the end of the growing season increases for the *Penicillium decumbens* and *Penicillium lividum* species, whereas the abundance of the *Trichoderma viride* and *Mycelia sterilia* species decreases by September (Table 1). The latter actively

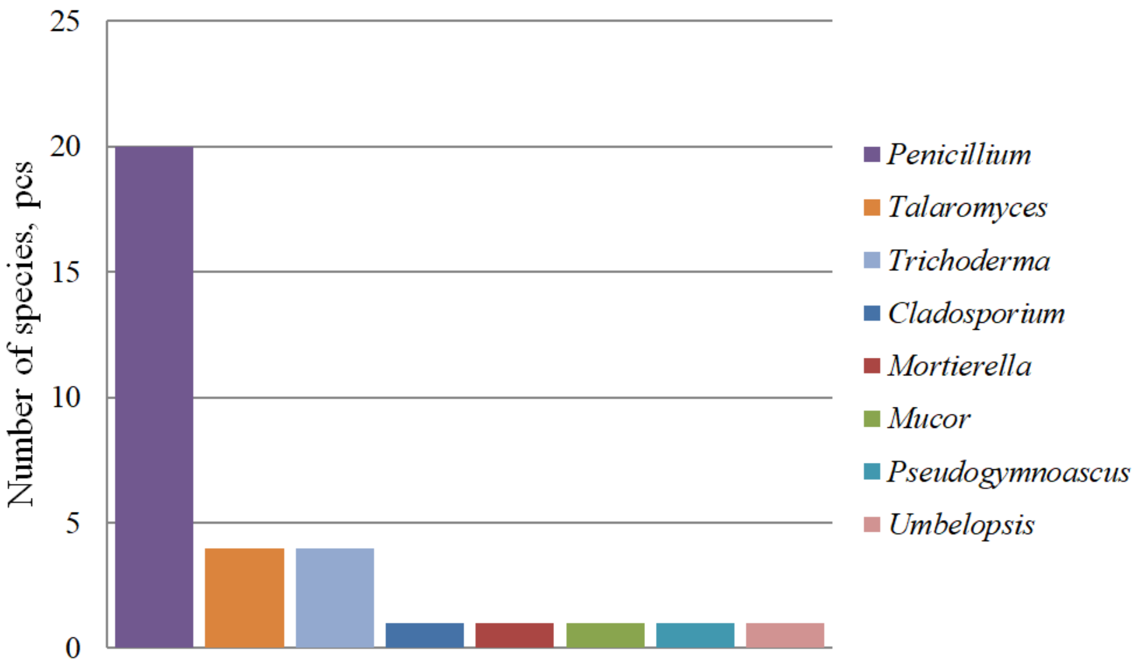

Fig. 2. Number of micromycete species of the main genera.

develop at the final stages of organic matter mineralisation and play an important role in decomposition of the previous year's fall (Rakhleeva et al., 2011; Osono, 2005; Osono et al., 2003). Sterile mycelium was isolated throughout the whole growing season with different frequency of occurrence and relative abundance values (Table 1). The formation of sterile mycelium results from the loss of the spore formation capacity on every nutrition medium used. The presence of various forms of sterile mycelium is a characteristic feature of soil micromycete communities in natural pine forests (Evdokimova and Mozgova, 2001; Korneikova et al., 2018).

Thus, the micromycete complex of the forest litter under lodgepole pine plantation consists of widely distributed species that inhabit both soils of the middle taiga of the Komi Republic (Khabibullina et al., 2018; Sizonenko et al., 2010) and far northward soils of higher latitudes (Vinogradova et al., 2019, 2023).

According to the seasonal observations of changes in the abundance and species diversity of soil fungi from lodgepole pine litter, the micromycete community had relatively low quantitative and qualitative indices in May. Twelve species of fungi from 3 genera, including sterile mycelium, were isolated from litter samples in May. The isolated species were ascomycetes, among them 8 species belonged to the *Penicillium* genus. *Penicillium thomii* and sterile mycelium dominated by the frequency of occurrence. Sterile mycelium demonstrated high values of relative abundance in May (Fig. 3).

The other species, according to the frequency of occurrence value, compose the group of rare and occasional species, the relative abundance of which varies from 1.6 to 6.3%. The processes of organic matter decomposition and transformation, in which fungi play a key role, are slowed down at the beginning of the vegetation period when the amount of fresh plant fall is low and the litter is not warm enough. The high abundance value of sterile mycelium also indicates unfavourable conditions for the development of litter fungi in May. Therefore, this period has a small group of fungi, represented by species of the *Penicillium* genus, participating in mineralisation of the last year's fall.

Towards the end of the vegetation period, the number of fungi and simultaneously the species diversity of mycocenosis increases. 24–25 species of fungi, including sterile mycelium, were isolated from the litter in August–September (Table 1). The group of dominant and frequently occurring species includes *Penicillium canescens*, *P. decumbens*, *P. thomii* and sterile mycelium in August. In September, the group of dominant and frequently occurring species increases significantly but mainly by the species of the *Penicillium* genus such as *Penicillium citreonigrum*, *P. jensenii*, *P. lividum* and additionally by *Talaromyces funiculosus*.

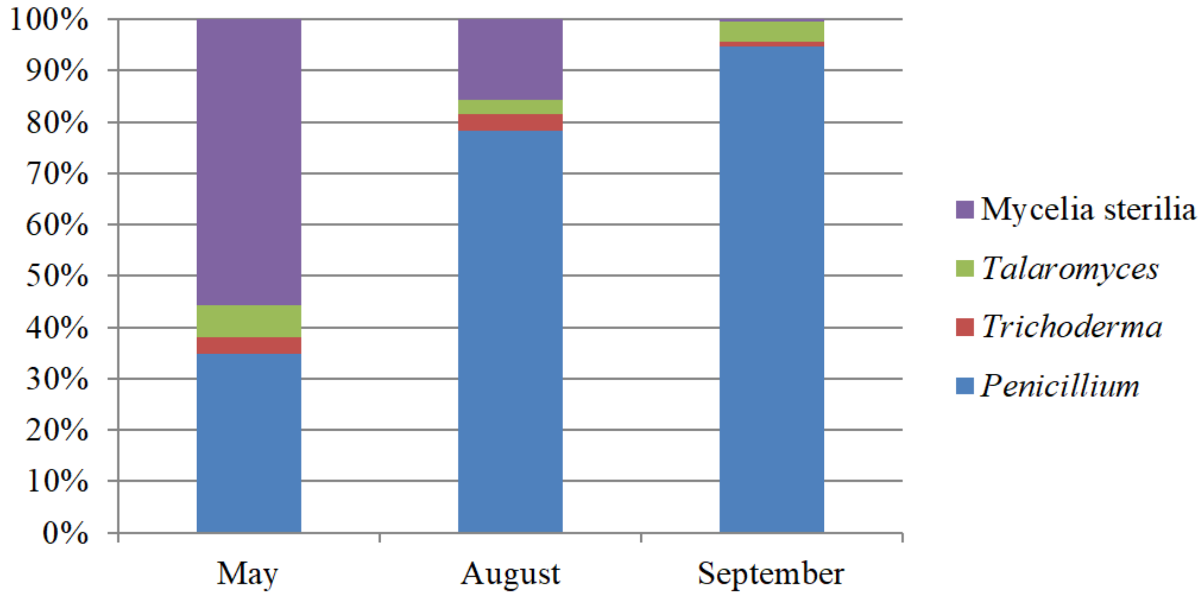

Fig. 3. Seasonal dynamics of relative abundance of sterile mycelium and the main fungal genera in litter.

In contrast to the early vegetation period, sterile mycelium disappears from the group of dominants at the end of the vegetation period. Its number and abundance sharply decrease (Fig. 3). At the same time, the majority of species also belong to the group of rare and occasional species (Table 1). Their development is associated with changes in the trophic structure of the micromycete community. The fresh plant fall stimulates the development of fungi and increases their species diversity by new species as *Penicillium aurantiogriseum*, *P. canescens*, *P. citreonigrum*, *P. dierckxii*, *P. lanosum*, *P. raistrickii*, *P. simplicissimum*, *Talaromyces funiculosus*, *T. variabilis*, *Trichoderma hamatum*, *T. polysporum*, *Umbelopsis vinacea* and others. Moreover, the number and species diversity of litter fungi in the studied artificial plantation increases at the late vegetation period both by soil species and plant species that attained the litter together with the fall (*Cladosporium herbarum*, *Mucor hiemalis*).

The end of the vegetation period is characterised by the maximum high values of the Shannon species diversity index (H = 2.37), which is associated with an increase in the number of dominant species and their relative abundance (Table 2).

The obtained data on the relative abundance of species are also confirmed by the Simpson index. The Simpson index has its minimum value in September when the micromycete community is reorganised and increases in number of species dominating by relative abundance. At the same time, the evenness of the micromycete community increases.

Biomass of fungi

The fungal biomass in the litter of experimental plantation of lodgepole pine during the growing season decreases from to 7.68 ± 3.31 in May to 1.04 ± 0.17 mg/g in September. This is due to the fact that the main contribution to the biomass structure is made by fungal mycelium. Its length in May attains the maximum values, 1963 ± 865 m/g a.d.s., and decreases to 139.22 ± 21.56 m/g a.d.s. by the end of the growing season in September. The share of spores in fungal biomass structure increases in September, as compared to May (Fig. 4). In general, the observed biomass values of microscopic fungi are higher than our previously obtained data on fungal biomass in the litter of lodgepole pine from the Storozhevsk forestry (Kovaleva et al., 2023). In podzols of the Kola Peninsula, fungal biomass in natural pine forest ranges from 1.2 to 2.1 mg/g soil (Korneikova et al., 2018).

Table 2. Values of diversity, dominance and evenness indices for complexes of microscopic fungi.

Sampling month	Index		
	Shannon	Simpson	Pielou
May	1.58	0.33	0.73
August	2.32	0.17	0.78
September	2.37	0.14	0.81

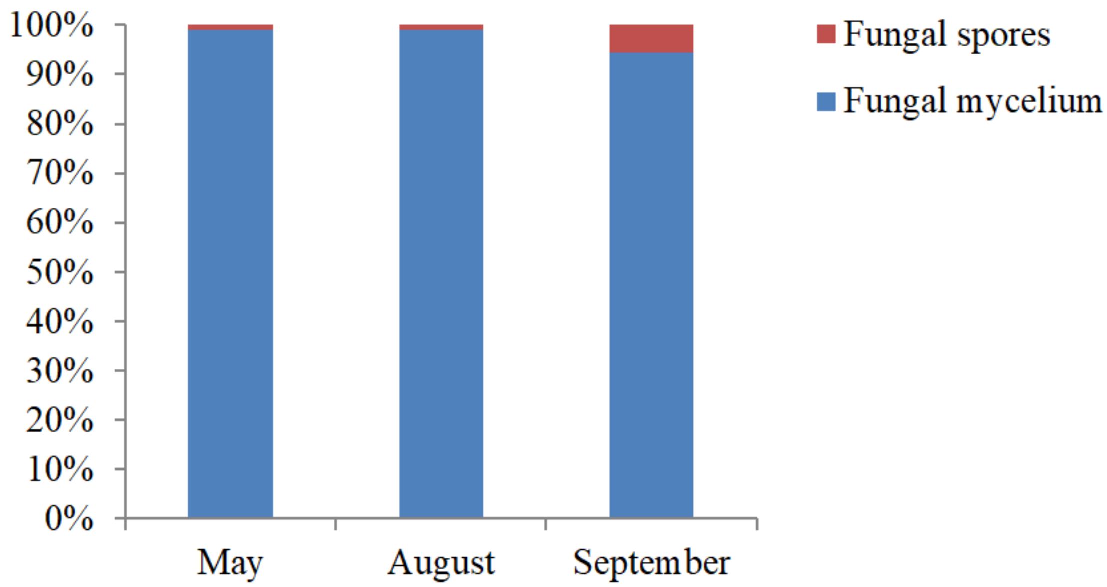

Fig. 4. Ratio of fungal mycelium and spore biomass during the growing season.

Conclusion

The experimental site under study is a result of numerous transformations: from natural forest ecosystem (pine forest) and subsequent cutting to ploughing and planting of seedlings of native Scotch pine and introduced lodgepole pine. The destruction of forest litter followed by its restoration in the artificially created forest phytocenosis affects the mycocenosis. In general, the number of microscopic fungi in artificial forest is lower than that in natural pine forests. By the studied taxonomic structure of litter mycocenosis under lodgepole pine plantation, its species composition includes 34 species from 8 genera (including sterile mycelium) belonging to two divisions. The species diversity of fungi increases at the end of the growing season: 12 species from 3 genera of fungi were identified in May and 24 species from 7 genera – in September.

Most species belong to the *Penicillium* genus. Common for any sampling dates are *Penicillium thomii*, *P. jensenii*, *P. lividum*, *Trichoderma viride* and Mycelia sterilia. *Penicillium thomii* dominates by the frequency of occurrence and the relative abundance. Its abundance increases from May to September.

Viewing the seasonal dynamics, the fungal community changes its characteristics. In August–September, the fungal community changes its dominant groups with the increasing number of rare and occasional species, which may have been isolated from the litter in form of sterile mycelium at the beginning of the growing season. The end of the growing season is characterised by the development of saccharolytic fungi, which first inhabit fresh plant fall and decompose simple organic compounds. At the same time, biopolymer degraders and oligotrophic fungi undergo active development. They complete mineralisation of the last year's fall. Plant fungi serve an additional source of fungal diversity at the end of the growing season. They enter the soil litter within plant fall. The number of fungi increases from $17.1 \pm 7.5 \times 10^3$ CFU/g in May to $60.9 \pm 19.2 \times 10^3$ CFU/g in September.

Fungi participating in the process of litter formation are characterised by comparatively high biomass indices. The maximum biomass development is observed at the beginning of the vegetation period (May) dominated by the fungal mycelium (by 99%). The high biomass of fungi at the beginning of the vegetation period against relatively low indices of species diversity and abundance is possibly associated with a decrease in intraspecific competition and abundant development of sterile mycelium.

According to the analysis of the obtained quantitative and qualitative indices and by the comparison with the data of other researchers (Evdokimova and Mozgova, 2001; Khabibullina and Tvorozhnikova, 2007; Khabibullina et al., 2018; Korneikova et al., 2018), the litter fungal community of lodgepole pine plantation is represented by the species typical of taiga natural forest ecosystems and cosmopolitan species occurring everywhere. This allows us to conclude that 20 years gone since forest plantation replaced once logged pine forest are enough for the forest litter to host the fungal community similar to natural forest ecosystems.

References

Aleksandrova, A.V., Zayats, A.L., Velikanov, L.L., Sidorova, I.I., 2006a. Raznoobrazie pochvennykh mikromitsetov v lesnykh ekosistemakh Tverskoi oblasti [Diversity of soil micromycetes in forest ecosystems of the Tver region]. *Mikologiia i fitopatologiia [Micology and phytopathology]* **40** (1), 3–12. (In Russian).

Aleksandrova, A.V., Velikanov, L.L., Sidorova, I.I., 2006b. Kliuch dlia opredeleniia vidov roda *Trichoderma* [Key for identifying species of the genus *Trichoderma*] *Mikologiia i fitopatologiia [Micology and phytopathology]* **40** (6), 457–468. (In Russian).

Bakhmet, O.N., Medvedeva, M.V., 2022. Razlozhenie opada khvoi v pochvakh lesnykh kul'tur sosny vostochnoi Fennoskandii [Decomposition of needle litter in soils of pine forest crops in eastern Fennoscandia]. *Lesovedenie [Forest Sciences]* **3**, 239–249. (In Russian). http://www.doi.org/10.31857/S0024114822030032

Berestetskiy, A.O., 2008. Fitotoksiny gribov: ot fundamental'nykh issledovanii k prakticheskomu ispol'zovaniiu (Obzor) [Fungal phytotoxins: from basic research to practical use (Review)]. *Prikladnaia biokhimiia i mikrobiologiia [Applied Biochemistry and Microbiology]* **44** (5), 501–514. (In Russian).

Dobrovol'skii, G.V., Nikitin, E.D., 2006. Ekologiia pochv. Uchenie ob ekologicheskikh funktsiiakh pochv [Soil ecology. The doctrine of the ecological functions of soils]. Moscow State University, Moscow, Russia, 412 p. (In Russian).

Dobrovol'skaya, T.G., Zvyagintsev, D.G., Chernov, I.Yu., Golovchenko, A.V., Zenova, G.M. et al., 2015. Rol' mikroorganizmov v ekologicheskikh funktsiiakh pochv [The role of microorganisms in the ecological functions of soils]. *Pochvovedenie [Soil Science]* **9**, 1087–1087. (In Russian). http://www.doi.org/10.7868/S0032180X15090038

Domsch, K.H., Gams, W., Anderson, T.H., 2007. Compendium of soil fungi. IHW-Verlag, Eching, Germany, 672 p.

Elais, T.S., 2014. Severoamerikanskie derev'ia: opredelitel' [North American trees: A guide]. Geo, Novosibirsk, Russia, 959 p. (In Russian).

Elfving, B., Ericsson, T., Rosvall, O., 2001. The introduction of lodgepole pine for wood production in Sweden – a review. *Forest Ecology and Management* **141** (1–2), 15–29.

Ellis, M.B., 1971. Dematiaceous Hyphomycetes. Kew, UK, 608 p.

Evdokimova, G.A., Mozgova, N.P., 2001. Mikroorganizmy tundrovykh i lesnykh podzolov Kol'skogo Severa [Microorganisms of tundra and forest podzols of the Kola North]. Publishing House of the Karelian Research Centre of the RAS, Apatity, Russia, 184 p. (In Russian).

Egorova, L.N., 1986. Pochvennye griby Dal'nego Vostoka: Gifomitsety [Soil fungi of the Far East: Hyphomycetes]. Nauka, Saint Petersburg, Russia, 207 p. (In Russian).

Fedorkov, A., Gutiy, L., 2017. Performance of lodgepole pine and Scots pine in field trials located in north-west Russia. *Silva Fennica* **51** (1)б 1–10. Gaspar, M.L., Cabello, M.N., Pollero, R., Aon, M.A., 2001. Fluorescein diacetete hydrolysis as a measure of fungal biomass in soil. *Current Microbio*logy **42**, 339–344. https://www.doi.org/10.1007/s002840010226

Feklistov, P.A., Biriukov, S.Yu., Fediaev, A.L., 2008. Sravnitel'nye ekologo-biologicheskie osobennosti sosny skruchennoi i obyknovennoi v severnoi podzone evropeiskoi taigi [Comparative ecological and biological features of lodgepole and Scots pine in the northern subzone of the European taiga]. Arkhangelsk State Technical University, Arkhangel'sk, Russia, 118 p. (In Russian).

Karlovsky, P., 2008. Secondary metabolites in soil ecology. *Springer Berlin Heidelberg* **7**, 1–19.

Kazeev, K.Sh., Kolesnikov, S.I., Val'kov, V.F., 2003. Biologicheskaia diagnostika i indikatsiia pochv: metodologiia i metody issledovanii [Biological diagnostics and indication of soils: methodology and research methods]. Rostov State University, Rostov-on-Don, Russia, 216 p. (In Russian).

Khabibullina, F.M., Tvorozhnikova, T.A., 2007. Rol' mikromitsetov v transformatsii rastitel'nykh ostatkov v el'nike chernichno-zelenomoshnom srednei podzony taiga [The role of micromycetes in the transformation of plant residues in the blueberry-green moss spruce forest of the middle taiga subzone]. *Izvestiia vysshikh uchebnykh zavedenii. Lesnoi zhurnal [News of Higher Educational Institutions. Forest Journal]* **4**, 40–47. (In Russian).

Khabibullina, F.M., Kuznetsova, E.G., Paniukov, A.N., Kurakov, A.V., 2018. Pochvennaia mikobiota na nachal'nykh etapakh posttekhnogennoi suktsessii v podzone srednei taigi [Soil mycobiota at the initial stages of post-technogenic succession in the middle taiga subzone]. *Mikologiia i fitopatologiia [Micology and Phytopathology]* **52** (5), 356–364. (In Russian). http://www.doi.org/10.1134/S0026364818050045

Kitikidou, K., 2012. Forest floor nutrient dynamics in chestnut plantation ecosystems. *Journal Agricultural Science* **4** (4), 51–54. http://www.doi.org/10.5539/jas.v4n4p51

Kovaleva, V.A., Vinogradova, Yu.A., Pristova, T.A., Fedorkov, A.L., 2023. Kharakteristika mikromitsetnogo kompleksa v podstilke eksperimental'nykh kul'tur sosny skruchennoi (*Pinus contorta* Dougl.) [Characteristics of the micromycete complex in the litter of experimental lodgepole pine (*Pinus contorta* Dougl.)]. *Printsipy ekologii [Principles of the Ecology]* **2** (48). 67–77. (In Russian). http://www.doi.org/10.15393/j1.art.2023.13642

Korneikova, M.V., Red'kina, V.V., Shalygina, R.R., 2018. Al'go-mikologicheskaia kharakteristika pochv v sosnovom i berezovom lesakh na territorii zapovednika “Pasvik” [Algo-mycological characteristics of soils in pine and birch forests on the territory of the Pasvik Nature Reserve]. *Pochvovedenie [Soil Science]* **2**, 211–220. (In Russian). https://www.doi.org/10.7868/S0032180X18020090

Kurakov, A.V., 2001. Metody vydeleniia i kharakteristika kompleksov mikroskopicheskikh gribov nazemnykh ekosistem: Uchebnoe posobie [Methods for isolating and characterizing complexes of microscopic fungi of terrestrial ecosystems: Textbook]. Maks Press, Moscow, Russia, 92 p. (In Russian).

Kurakov, A.V., Semenova, T.A., 2016. Vidovoe raznoobrazie mikroskopicheskikh gribov v lesnykh ekosistemakh iuzhnoi taigi evropeiskoi chasti Rossii [Species diversity of microscopic fungi in forest ecosystems of the southern taiga of the European part of Russia]. *Mikologiia i fitopatologiia [Micology and Phytopathology]* **50** (6), 367–378. (In Russian).

Looby, C.I., Treseder, K.K., 2018. Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest. *Soil Biology and Biochemistry* **117**, 87–96. https://doi.org/10.1016/j.soilbio.2017.11.014

McIntosh, A.C.S., Macdonald, S.E., Gundale, M.J., 2012.Tree species versus regional controls on ecosystem properties and processes: an example using introduced *Pinus contorta* in Swedesh boreal forests, *Canadian Journal of Forest Research* **42**, 1228–1238. https://doi.org/10.1139/X2012-049

Melekhov, I.S., 1984. Introduktsiia khvoinykh v lesnom khoziaistve [Introduction of conifers in forestry]. *Lesovedenie [Forest Sciences]* **6**, 72–78. (In Russian).

Metody pochvennoi mikrobiologii i biokhimii [Methods of soil microbiology and biochemistry], 1991. Moscow State University, Moscow, Russia, 304 p. (In Russian).

Osono, T., 2007. Ecology of ligninolytic fungi associated with leaf litter ecomposition. *Ecological Research* **22** (6), 955–974. https://doi.org/10.1007/s11284-007-0390-z

Osono, T., Takeda, H., 2001. Organic chemical and nutrient dynamics in decomposing beech leaf litter in relation to fungal ingrowth and succession during 3-year decomposition processes in a cool temperate deciduous forest in Japan. *Ecological Research* **16**, 649–670.

Osono, T., Fukasawa, Y., Takeda, H., 2003. Roles of diverse fungi in larch needle-litter decomposition. *Mycologia* **95** (5), 820–826.

Pitt, J., 1991. A laboratory guide to common *Penicillium* species. Commonwealth scientific and industrial research organization, North Ryde, New South Wales, Australia, 47 p.

Polianskaia, L.M., 1996. Mikrobiologicheskaia suktsessiia v pochve [Microbiological succession in soil]. *Doctor of Sciences in Biology thesis abstract*. Moscow, Russia, 96 p. (In Russian).

Pristova, T.A., Khabibullina, F.M., Vinogradova, Yu.A., 2012. Rol' mikromitsetov v formirovanii lesnoi podstilki listvennykh nasazhdenii srednei taiga [The role of micromycetes in the formation of forest litter of deciduous plantations in the middle taiga]. *Lesovedenie [Forest Sciences]* **4**, 47–55. (In Russian).

Ramirez, C., 1982. Manual and atlas of the *Penicillia*. Elsevier Biomedical Press, Oxford – Amsterdam - New York, 874 p.

Raevskii, B. V., 2015. Selektsiia i semenovodstvo sosny obyknovennoi (*Pinus sylvestris* L.) i sosny skruchennoi (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) na Severo-Zapade taezhnoi zony Rossii [Selection and seed production of Scots pine (*Pinus sylvestris* L.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm) in the North-West taiga zone of Russia]. *Doctor of Sciences in Agriculture thesis.* Saint Petersburg, Russia, 322 p. (In Russian).

Rakhleeva, A.A., Semenova, T.A., Striganova, B.R., Terekhova, V.A., 2011. Dinamika zoomikrobnykh kompleksov pri razlozhenii rastitel'nogo opada v el'nikakh iuzhnoi taigi [Dynamics of zoomicrobial complexes during the decomposition of plant litter in the spruce forests of the southern taiga]. *Pochvovedenie [Soil Science]* **1**, 44–55. (In Russian).

Semenova, T.A., 2002. Suktsessiia mikromitsetov na razlichnykh estestvennykh substratakh v khode mnogoletnego model'nogo eksperimenta [Succession of micromycetes on various natural substrates during a long-term model experiment]. In: Kovaleva, N.O. (ed.), *Rol' pochv v biosfere* (*Trudy Instituta pochvovedeniia MGU – RAN. Vyp. 1) [The role of soils in the biosphere (Proceedings of the Institute of Soil Science MSU – RAS. Issue 1)].* Moscow State University, Moscow, Russia, 185–201. (In Russian).

Shebalova, N.M., 2008. Pochvennaia mikroflora sosnovykh nasazhdenii, raspolozhennykh v tekhnogennykh zonakh [Soil microflora of pine plantations located in technogenic zones]. *Agrarnyi vestnik Urala [Agrarian Bulletin of the Urals]* **7**, 69–72. (In Russian).

Shebalova, N.M., Zalesov, S.V., 2006. Mikromitsety lesnykh pochv sosnovykh nasazhednii, proizrastaiushchikh v zonakh tekhnogennogo zagriazneniia [Micromycetes of forest soils of pine plantations growing in zones of technogenic pollution]. *Izvestiia vysshikh uchebnykh zavedenii. Lesnoi zhurnal [News of Higher Educational Institutions. Forest Journal]* **1**, 28–32. (In Russian).

Sizonenko, T.A., Zagirova, S.V., Khabibullina, F.M., 2010. Mikrobnye soobshchestva v podstilke el'nika chernichnogo srednei taiga [Microbial communities in the litter of blueberry spruce forests in the middle taiga]. *Pochvovedenie [Soil Science]* **10**, 1221–1228. (In Russian).

Terekhova, V.A., Semenova, T.A., Trofimov, S.Ya., 1998. Struktura kompleksov mikromitsetov v podstilke zapovednykh el'nikov Tverskoi oblasti [The structure of micromycete complexes in the litter of protected spruce forests in the Tver region]. *Mikologiia i fitopatologiia [Micology and Phytopathology]* **32** (3), 18–24. (In Russian).

Vinogradova, Yu.A., Lapteva, E.M., Kovaleva, V.A., Perminova, E.M., 2019. Raspredelenie mikroskopicheskikh gribov v mnogoletnemerzlykh torfianikakh lesotundry [Distribution of microscopic fungi in permafrost peatlands of forest-tundra]. *Mikologiia i fitopatologiia [Micology and phytopathology]* **53** (6), 342–353. (In Russian). http://www.doi.org/10.31857/S0026364822030126

Vinogradova, Y.A., Kovaleva, V.A., Perminova, E.M, Shakhtarova, O.V., Lapteva, E.M., 2023. Zonal patterns of changes in the taxonomic composition of culturable microfungi isolated from permafrost peatlands of the European Northeast. *Diversity* **15** (5), 639–650. http://www.doi.org/10.3390/d15050639

Voříšková, J., Baldrian, P., 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. *The ISME journal* **7** (3), 477–486. https://www.doi.org/10.1038/ismej.2012.116

Zagurskaya, Yu.V., 2022. Main aspects of studying invasive species of the genus *Solidago. Ecosystem transformation* **5** (2), 102–115. http://www.doi.org/10.23859/estr-211029

Список литературы

Александрова, А.В., Заяц, А.Л., Великанов, Л.Л., Сидорова, И.И., 2006a. Разнообразие почвенных микромицетов в лесных экосистемах Тверской области. *Микология и фитопатология* **40** (1), 3–12.

Александрова, А.В., Великанов, Л.Л., Сидорова, И.И., 2006b. Ключ для определения видов рода *Trichoderma*. *Микология и фитопатология* **40 (**6), 457–468.

Бахмет, О.Н., Медведева, М.В., 2022. Разложение опада хвои в почвах лесных культур сосны восточной Фенноскандии. *Лесоведение* **3**, 239–249.

Берестецкий, А.О., 2008. Фитотоксины грибов: от фундаментальных исследований к практическому использованию (Обзор). *Прикладная биохимия и микробиология* **44** (5), 501–514.

Виноградова, Ю.А., Лаптева, Е.М., Ковалева, В.А., Перминова, Е.М., 2019. Распределение микроскопических грибов в многолетнемерзлых торфяниках лесотундры. *Микология и фитопатология* **53** (6), 342–353.

Добровольский, Г.В., Никитин, Е.Д., 2006. Экология почв. Учение об экологических функциях почв. МГУ, Москва, Россия, 412 с.

Добровольская, Т.Г., Звягинцев, Д.Г., Чернов, И.Ю., Головченко, А.В., Зенова, Г.М. и др., 2015. Роль микроорганизмов в экологических функциях почв. *Почвоведение* **9**, 1087–1087. https://doi.org/10.7868/S0032180X15090038

Евдокимова, Г.А., Мозгова, Н.П., 2001. Микроорганизмы тундровых и лесных подзолов Кольского Севера. Издательство КНЦ РАН, Апатиты, Россия, 184 с.

Егорова, Л.Н., 1986. Почвенные грибы Дальнего Востока: Гифомицеты. Наука, Санкт-Петербург, СССР, 207 с.

Загурская, Ю.В., 2022. Основные аспекты изучения инвазийных видов рода *Solidago Трансформация экосистем* **5** (2), 102–115. http://www.doi.org/10.23859/estr-211029

Казеев, К.Ш., Колесников, С.И., Вальков, В.Ф., 2003. Биологическая диагностика и индикация почв: методология и методы исследований. РГУ, Ростов-на-Дону, Россия, 216 с.

Ковалева, В.А., Виноградова, Ю.А., Пристова, Т.А., Федорков, А.Л., 2023. Характеристика микромицетного комплекса в подстилке экспериментальных культур сосны скрученной (*Pinus contorta* Dougl.). *Принципы экологии* **2** (48), 67–77. http://www.doi.org/10.15393/j1.art.2023.13642

Корнейкова, М.В., Редькина, В.В., Шалыгина, Р.Р., 2018. Альго-микологическая характеристика почв в сосновом и березовом лесах на территории заповедника «Пасвик». *Почвоведение* **2**, 211–220. https://www.doi.org/10.7868/S0032180X18020090

Кураков, А.В., 2001. Методы выделения и характеристика комплексов микроскопических грибов наземных экосистем. Макс Пресс, Москва, Россия, 92 с.

Кураков, А.В., Семенова, Т.А., 2016. Видовое разнообразие микроскопических грибов в лесных экосистемах южной тайги европейской части России. *Микология и фитопатология* **50** (6), 367–378.

Мелехов, И.С., 1984. Интродукция хвойных в лесном хозяйстве. *Лесоведение* **6**, 72–78.

Методы почвенной микробиологии и биохимии, 1991. МГУ, Москва, Россия, 304 с.

Полянская, Л.М., 1996. Микробиологическая сукцессия в почве. *Автореферат диссертации на соискание ученой степени доктора биологических наук.* Москва, Россия, 96 с.

Пристова, Т.А., Хабибуллина, Ф.М., Виноградова, Ю.А. 2012. Роль микромицетов в формировании лесной подстилки лиственных насаждений средней тайги. *Лесоведение* **4**, 47–55.

Раевский, Б.В., 2015. Селекция и семеноводство сосны обыкновенной (*Pinus sylvestris* L.) и сосны скрученной (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) на Северо-Западе таежной зоны России. *Диссертация на соискание ученой степени доктора сельскохозяйственных наук*. Санкт-Петербург, Россия, 322 с.

Рахлеева, А.А., Семенова, Т.А., Стриганова, Б.Р., Терехова, В.А., 2011. Динамика зоомикробных комплексов при разложении растительного опада в ельниках южной тайги. *Почвоведение* **1**, 44–55.

Семенова, Т.А., 2002. Сукцессия микромицетов на различных естественных субстратах в ходе многолетнего модельного эксперимента. В: Ковалева, Н.О. (ред.), *Роль почв в биосфере* (*Труды Института почвоведения МГУ – РАН. Вып. 1).* МГУ, Москва, Россия, 185–201.

Сизоненко, Т.А., Загирова, С.В., Хабибуллина, Ф.М., 2010. Микробные сообщества в подстилке ельника черничного средней тайги. *Почвоведение* **10**, 1221–1228.

Терехова, В.А., Семенова, Т.А., Трофимов, С.Я., 1998. Структура комплексов микромицетов в подстилке заповедных ельников Тверской области. *Микология и фитопатология* **32** (3), 18–24.

Феклистов, П.А., Бирюков, С.Ю., Федяев, А.Л., 2008. Сравнительные эколого-биологические особенности сосны скрученной и обыкновенной в северной подзоне европейской тайги. Архангельский государственный технический университет, Архангельск, Россия, 118 с.

Хабибуллина, Ф.М., Творожникова, Т.А., 2007. Роль микромицетов в трансформации растительных остатков в ельнике чернично-зеленомошном средней подзоны тайги *Известия высших учебных заведений. Лесной журнал* **4**, 40–47.

Хабибуллина, Ф.М., Кузнецова, Е.Г., Панюков, А.Н., Кураков, А.В., 2018. Почвенная микобиота на начальных этапах посттехногенной сукцессии в подзоне средней тайги. *Микология и фитопатология* **52** (5), 356–364. http://www.doi.org/10.1134/S0026364818050045

Шебалова, Н.М., 2008. Почвенная микрофлора сосновых насаждений, расположенных в техногенных зонах. *Аграрный вестник Урала* **7**, 69–72.

Шебалова, Н.М., Залесов, С.В., 2006. Микромицеты лесных почв сосновых насажедний, произрастающих в зонах техногенного загрязнения. *Известия высших учебных заведений. Лесной журнал* **1**, 28–32.

Элайс, Т.С., 2014. Североамериканские деревья: определитель. Гео, Новосибирск, Россия, 959 с.

Domsch, K.H., Gams, W., Anderson, T.H., 2007. Compendium of soil fungi. IHW-Verlag, Eching, Germany, 672 p.

Elfving, B., Ericsson, T., Rosvall, O., 2001. The introduction of lodgepole pine for wood production in Sweden – a review. *Forest Ecology and Management* **141** (1–2), 15–29.

Ellis, M.B., 1971. Dematiaceous Hyphomycetes. Kew, UK, 608 p.

Fedorkov, A., Gutiy, L., 2017. Performance of lodgepole pine and Scots pine in field trials located in north-west Russia. *Silva Fennica* **51** (1)б 1–10. Gaspar, M.L., Cabello, M.N., Pollero, R., Aon, M.A., 2001. Fluorescein diacetete hydrolysis as a measure of fungal biomass in soil. *Current Microbio*logy **42**, 339–344. https://www.doi.org/10.1007/s002840010226

Karlovsky, P., 2008. Secondary metabolites in soil ecology. *Springer Berlin Heidelberg* **7**, 1–19.

Kitikidou, K., 2012. Forest floor nutrient dynamics in chestnut plantation ecosystems. *Journal Agricultural Science* **4** (4), 51–54. http://www.doi.org/10.5539/jas.v4n4p51

Looby, C.I., Treseder, K.K., 2018. Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest. *Soil Biology and Biochemistry* **117**, 87–96. https://doi.org/10.1016/j.soilbio.2017.11.014

McIntosh, A.C.S., Macdonald, S.E., Gundale, M.J., 2012.Tree species versus regional controls on ecosystem properties and processes: an example using introduced *Pinus contorta* in Swedesh boreal forests, *Canadian Journal of Forest Research* **42**, 1228–1238. https://doi.org/10.1139/X2012-049

Osono, T., 2007. Ecology of ligninolytic fungi associated with leaf litter ecomposition. *Ecological Research* **22** (6), 955–974. https://doi.org/10.1007/s11284-007-0390-z

Osono, T., Takeda, H., 2001. Organic chemical and nutrient dynamics in decomposing beech leaf litter in relation to fungal ingrowth and succession during 3-year decomposition processes in a cool temperate deciduous forest in Japan. *Ecological Research* **16**, 649–670.

Osono, T., Fukasawa, Y., Takeda, H., 2003. Roles of diverse fungi in larch needle-litter decomposition. *Mycologia* **95** (5), 820–826.

Pitt, J., 1991. A laboratory guide to common *Penicillium* species. Commonwealth scientific and industrial research organization, North Ryde, New South Wales, Australia, 47 p.

Ramirez, C., 1982. Manual and atlas of the *Penicillia*. Elsevier Biomedical Press, Oxford – Amsterdam - New York, 874 p.

Vinogradova, Y.A., Kovaleva, V.A., Perminova, E.M, Shakhtarova, O.V., Lapteva, E.M., 2023. Zonal patterns of changes in the taxonomic composition of culturable microfungi isolated from permafrost peatlands of the European Northeast. *Diversity* **15** (5), 639–650. http://www.doi.org/10.3390/d15050639

Voříšková, J., Baldrian, P., 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. *The ISME journal* **7** (3), 477–486. https://www.doi.org/10.1038/ismej.2012.116