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Ectomycorrhizal Symbionts of Scots Pine and Silver Birch Forest Ecosystems in the Natural Reserve Ertis Ormany in Kazakhstan

Ektomykorrhiza-Symbionten in Waldökosystemen der Waldkiefer und Hängebirke im Naturschutzgebiet Ertis Ormany in Kasachstan

Dani Sarsekova¹, Olga Vaishlya², Ainur Nurlabi¹, Sezgin Ayan^{3*}

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symbiotic relationships, species saturation coefficient,
Agaricales, Russulales, Boletales
- Schlüsselbegriffe: Betula pendula, Pinus sylvestris, Pilzdiversität, Symbiose, symbiotische Beziehungen, Artensättigungskoeffizient, Agaricales, Russulales, Boletales

Abstract

Symbiotic relationships maintain the balance of forest ecosystems, with ectomycorrhizal (EcM) symbiosis being one of the most significant. EcM symbiosis in forests dominated by Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) has been often observed, but remain understudied in parts of world. This study was conducted in the State Forest Natural Reserve "Ertis Ormany" in Kazakhstan. The aim of this study was to identify EcM symbionts on Scots pine and silver birch by analyzing ribosomal DNA sequences isolated from hyphal endings. Our results show that among all EcM symbionts the order *Agaricales* (13 species/28.8% of total species numer) had highest species diversity in Scots pine, followed by *Boletales* (9/20%) and *Russulales* (8/17.7%). For silver birch, the order *Russulales* (7/15.5%) had highest species diversity, followed by *Agaricales* (5/11.1%), and *Boletales* (3/6.7%). A total of 15

¹ S. Seifullin Kazakh AgroTech. Univ., Faculty of Forestry, Wildlife and Environment, Department of Forest Resources and Forestry, Nur-Sultan, Kazakhstan

² Tomsk State University, Biological Institute, Tomsk, Russia

³ Kastamonu University, Faculty of Forestry, Silviculture Department, Kastamonu, Turkiye

^{*}Corresponding author: Sezgin Ayan, sezginayan@gmail.com

symbiont families were identified: *Agaricaceae* (2 species/4,4% of the total number of species identified in the study area), *Amanitaceae* (4/8.9%), *Boletacea* (5/11.1%), *Cortinariaceae* (3/6.7%), *Gloeophyllaceae* (1/2.2%), *Inocybaceae* (1/2.2%), *Lycoperdaceae* (1/2.2%), *Lycophyllaceae* (2/4.4%), *Paxillaceae* (1/2.2%), *Polyporaceae* (3/6.7%), *Psathyrellaceae* (2/4.4%), *Pseudoclitocybaceae* (2/4.4%), *Russulaceae* (8/17.8%), *Suillaceae* (6/13.3%), and *Tricholomataceae* (4/8.9). A higher symbiotic association with EcM was found in Scots pine (66.5%) compared to silver birch (33.3%).

Zusammenfassung

Symbiotische Beziehungen sind wichtig für die Stabilität von Waldökosystemen, wobei Ektomykorrhiza (EcM)-Symbiose einen besonderen Stellenwert hat. Die EcM-Symbiose an Waldkiefer (Pinus sylvestris L.) und Hängebirke (Betula pendula Roth.) wurde recht häufig beobachtet, ist aber in vielen Teilen der Welt wenig erforscht. Das Forschungsgebiet war das Naturschutzgebiet "Ertis Ormany" in Kasachstan. Unsere Ergebnisse zeigen, dass unter allen Symbionten der Waldkiefer die Ordnung Agaricales (13 Arten/28,8 % der gesamten Artenzahl) und Boletales (9 Arten/20 %) die höchste Artenvielfalt aufwiesen, gefolgt von Russulales (8/17,7 %). Bei der Hängebirke waren die Ordnungen Agaricales (5/11,1%), Boletales (3/6,7%) und Russulales (7/15,5 %) führend. Insgesamt wurden hier bei den Symbionten der Waldkiefer und Hängebirke 16 Familien identifiziert: Agaricaceae (2/4,4%), Amanitaceae (4/8,9%), Boletacea (5/11,1%), Cortinariaceae (3/6,7%), Gloeophyllaceae (1/2,2%), Inocybaceae (1/2,2 %), Lycoperdaceae (1/2,2 %), Lyophyllaceae (2/4,4 %), Paxillaceae (1/2,2 %), Polyporaceae (3/6,7%), Psathyrellaceae (2/4,4%), Pseudoclitocybaceae (2/4,4%), Russulaceae (8/17,8%), Suillaceae (6/13,3%) und Tricholomataceae (4/8,9%). Es gibt einen Trend zu einem höheren Koeffizienten der Artensättigung mit EcM-Symbionten bei der Waldkiefer (66,5 %) im Vergleich zu der Hängebirke (33,3 %).

1 Introduction

Symbiotic relationships are one of the most important components for maintaining the balance and stability of forest ecosystems (Courty *et al.*, 2010). A common form of symbiotic relationship in forest ecosystems is the ectomycorrhizal (EcM) symbiosis. It is well known that the diversity and structure of EcM symbiosis are influenced by a number of biotic and abiotic factors such as host tree genotype, mycosymbiont interaction strategy, soil characteristics, availability of nutrients, the activity of pathogens, and quality and quantity of soil organic matter (Vaishlya *et al.*, 2019). The impacts of climate change may alter belowground fungal communities (Pickles *et al.*, 2012), so that they may become a limiting factor in tree migration. Furthermore, knowledge of the linkages among soil fungal diversity, community structure, and environmental

factors is critical to understand the organization and stability of forest ecosystems (Simard and Austin, 2010; Karst *et al.*, 2014).

The EcM symbiosis of Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) is quite often observed in forest ecosystems. Ectomycorrhiza is formed by about 5-6 thousand plant species (Voronina, 2006; 2008), almost exclusively woody or shrub species from Gymnosperms (family *Pinaceae*, *Cupressaceae*) and Angiosperms (18 families, most important are *Fagaceae*, *Betulaceae*, *Salixaceae*, *Myrtaceae*, *Aceraceae*, *Tiliaceae*, *Ulmaceae*) (Molina *et al.*, 1992).

EcM fungi are obligate mutualistic symbionts and hence rely entirely on carbon supply from host plants (Smith and Read, 2008). While they are abundant in root systems of herbaceous plants (Hiiesalu et al., 2014), they are also associated with various tree species (Liu et al., 2015). EcM fungi play a major role in forest community dynamics (Smith and Read, 2008) as they promote the dominance of specific plant families e.g., Pinaceae, Fagaceae, Betulaceae, and Dipterocarpaceae (Tedersoo and Smith, 2013). Ectomycorrhizae are found in the upper layer of the soil, which mostly contains humus, rather than the lower layers which contain mineral-rich substances (Dogmus Lehtijarvi, 2007). These fungi improve plant nutrition in exchange for carbohydrates (Smith and Read, 1997; Sebastiana et al., 2018). They have an important role in the intake of Zn, Cu, Mn, Fe, Ca, K, N, and particularly P, due to slow uptake from the soil. Moreover, mycorrhiza increase water use efficiency, as well as improve soil structure and protect against soil erosion (Dogmus Lehtijarvi, 2007). Previous studies stated that the use of mycorrhizal seedlings in afforestation, rehabilitation and restoration works in marginal sites can significantly increase the success of plantations (Arocena and Glowa, 2006; Qiang-Sheng and Ren-Xue, 2006; Bennett et al., 2017; Kharuk et al., 2019). This subject is important in marginal sites with extreme ecological conditions and higher climate change influence (Barbati et al., 2018). The environmental conditions on poor sites favour numerous harmful biotic factors including pathogens (Haavik et al., 2015).

Studies of the ecology and physiology of EcM have been concentrated mainly in Europe, North America, and Australia (Smith and Read, 1997; 2008; Read, 1999; Finlay, 2005; Polenov, 2013). In the Republic of Kazakhstan, first studies of mycobiota and EcM macromycetes were carried out by Nam (1998), Abiev *et al.* (2000), and Abiev (2015). Applied aspects of the mycorrhization were investigated by Meshkov (2010). He obtained four types of macromycetes from the investigated culture and developed a technology for their scaling and application in inocculated compost for reforestation in Zailiysky Alatau (Meshkov *et al.*, 2009; Meshkov 2010). However, some researchers emphasize that for optimal development of trees, specialized strains of macromycetes fungi forming EcM are needed (Alvarez and Trappe, 1983; Valdes, 1986). Especially, coniferous seedlings are not able to achieve adequate growth, if they are excluded from mycorrhizal occurrence (Kais *et al.*, 1981; Alvarez and Trappe, 1983; Valdes, 1986).

Preservation of environmentally favorable living conditions in various regions of the world directly depends on the rational and careful use of forest resources. Forest ecosystems of Central and Northeast Kazakhstan are one of the most important components of the Earth's biosphere, contributing to the ecological balance on the entire planet (Sarsekova *et al.*, 2021). In this context, Godbold *et al.* (2006) draw attention that an increase in mycorrhizal hyphal biomass and turnover would increase carbon sequestration in terrestrial ecosystems. The assessment of EcM symbionts of forest trees in Kazakhstan's forest ecosystems could help to improve regeneration, afforestation, rehabilitation, and restoration efforts in this region which is affected by climate change and extreme ecological conditions. The main objectives of this study were:

- to establish basic information about EcM associated with Silver birch and Scots pine forests in the protected area "Ertis Ormany" in Kazakhstan, using molecular methods isolating DNA from hyphal endings of the EcM and subsequent sequencing of ribosomal DNA,
- (2) to determine whether there are differences in the quantity of mycorrhizal symbiosis and in the preference of forest tree species, and
- (3) to investigate if there are new undescribed ectomycoriza species in these silver birch and Scots pine forests.

2 Materials and Methods

2.1 Study area

The Republican State Institution State Forest Natural Reserve "Ertis Ormany" is located on the eastern part of the Pavlodar region on the right bank of the Irtysh river in Kazakhstan (Figure 1) (Northern latitude 51°23″ – 52° 15″, Eastern longitude 78° 01″ – 79° 21″). It is within the borders of Shcherbaktinsky district and Akkulinsky district (Anonymous, 2009) and covers an area of 277,961 hectares.

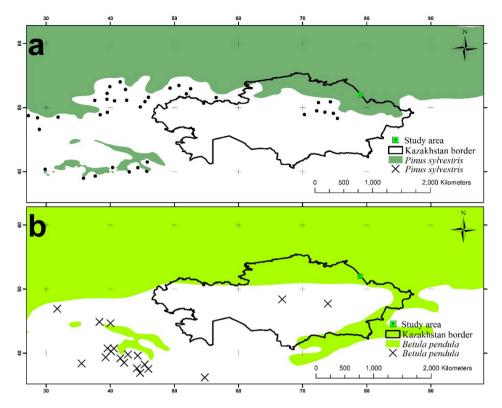


Figure 1: The natural distribution area of Pinus sylvestris L. and Betula pendula Roth. (Caudullo et al., 2018) and the location of the study area in Kazakhstan.

Abbildung 1: Das natürliche Verbreitungsgebiet von *Pinus sylvestris* L. und *Betula pendula* Roth. (Caudullo *et al.*, 2018) und die Lage des Untersuchungsgebiets in Kasachstan.



Figure 2: Satellite image map showing sampling areas of the study area.

Abbildung 2: Satellitenbild mit Position der Probenahmen im Untersuchungsgebiet.

Territories of the state nature reserves are divided into zones according to different types of protection and use:

- i) a protected area is a core zone intended for the long term conservation of genetic resources, biological diversity, ecological systems, and landscapes, having sufficient features to achieve such goals;
- ii) buffer zone a section of territory that is used for conducting environmentally oriented economic activities and sustainable reproduction of biological resources (Figure 2, 3) (Forest Code of the Kazakhstan Republic, 2003).



Figure 3: Sample areas of Scots pine and silver birch; a) \mathbb{N}^{0} 1 sample area of Scots pine in Shaldai forest; b) \mathbb{N}^{0} 6 Scots pine in Taybagarskoe forest; c) example of selected seedlings of Scots pine; d) \mathbb{N}^{0} 3 sample area of Silver birch in Taybagarskoe forest; e) \mathbb{N}^{0} 8 silver birch in Zavodskoe forest; f) example of soil blocks under crown of silver birch.

Abbildung 3: Untersuchungsflächen der Waldkiefer und der Hängebirke; a) Nr. 1 Untersuchungsgebiet der Waldkiefer im Shaldai-Wald; b) Nr. 6 Waldkiefer im Taybagarskoe-Wald; c) Beispiel eines ausgewählten Sämlings der Waldkiefer; d) Nr. 3 Untersuchungsgebiet mit Hängebirke im Pervomayskoe-Wald; e) Nr. 8 Versuchsfläche der Hängebirke im Zavodskoe-Wald; f) Beispiel eines Bodenblocks unter der Krone von Hängebirke.

2.2 Natural and climatic conditions of the study area

The climate in the study area is continental characterized by dry conditions due to dry and hot winds blowing from the Central Asian deserts during summer and winter. The area is open to cold air flows coming from the north. Winters are cold and last long (5.5 months) and summers are short and hot with low precipitation, with extreme temperature fluctuations between winter and summer (range 88 °C) and

between day and night (range 22 °C). The average annual air temperature is between +2.5 and +3 °C, average temperature of the coldest month (January) ranges between -17 and -19 °C and about +21 °C in the warmest month (July). The absolute minimum and maximum temperatures ever recorded at the Shaldai weather station were -49 °C and +41°C, respectively. The growing season lasts 137 days on average. In summer, relative air humidity (at 13:00) is about 40%, sometimes decreasing to 10% causing intensive transpiration of plants and a large loss of moisture from the soil. Mean annual precipitation sum ranges between 240 to 310 mm (Anonymous, 2015).

2.3 Methods

The "Ertis Ormany" reserve is covered by various forest ecosystems – pure and mixed forests with silver birch and Scots pine (Figure 1). Within this forests, seven permanent transects were established. In each transect, macromycetes were collected and inventoried every 10-15 days during the spring season from May to September in 2020-2022. A total of 110 samples were collected, 60 of these were soil samples and the other 50 samples were collected from the root systems of tree seedlings. Transects were established according to the methodology of Villarreal-Ruiz and Neri-Luna (2018). In total, 60 soil cores were taken about every 2 meters along each 125 m transect.

Collection and identification of the EcM fruit bodies was performed following standard methods, using available determinants and different web sources (http://www. indexfungorum.org and http://www.mycobank.org). Micromorphological studies were carried out using a light microscope ("Altami SM745-T", Russia) at a magnification of 400-1000. To identify the natural color of microstructures, samples were viewed in distilled water and in 3-5% KOH solution. Hyaline structures were stained with a 5% aqueous solution of safranin, and the presence or absence of amyloid and dextrinosis structures were determined using Meltzer reagent (Vaishlya *et al.*, 2012).

To determine the type of fungal symbiont of the EcM, the Agerer morphotyping method was used (Agerer, 1987; 1991; Agarer *et al.*, 2002). For this purpose, soil samples were selected within the projection of the crown of mature trees according to the method of concentric sampling (Vaishlya *et al.*, 2019). Before sampling, the upper layer of litter was removed. The seedlings were extracted from the soil without disturbing their root systems. In total, 210 root ends were examined, 113 for Scots pine and 97 for silver birch.

The samples were wrapped in aluminum foil and stored at a temperature of +4 °C. The roots were washed with running water and cut into segments of 3-5 cm. EcM endings were separated under a magnifying glass with tweezers and scissors. Morphotyping of ectomycorrhizae was performed using a binocular microscope "Alta-

mi SM745-T" with a camera Altami UCMOSO3100KPA and according to the DEEMY (http://deemy.de) system, based on the nature of branching, the color of the EcM termination, features of the mantle surface, the presence or absence of external mycelium and rhizomorphs. The selected EcM samples (113 for *Pinus sylvestris* and 97 for *Betula pendula*) were photographed and fixed in 70% ethanol for DNA isolation. DNA isolation from the sampled EcM hyphal endings was performed using a standard Quiagen kit based on the attached protocol (Vaishlya, 2017). ITS-1F and ITS-4B primers were used for amplification and sequencing of the ITS nuclear DNA site. Sequencing was performed on the ABI 3130 Genetic Analyzer (Applied Biosystems) with subsequent processing of the data obtained in the BioEdit Sequence Alignment Editor application. Identification of EcM fungi to generic and species taxa was performed using the M algorithm by comparison with reference sequences from the open GenBank database (http://www.ncbi.nlm.nih.gov/genbank/), taking into account the lower threshold of 97-98% established for ITS regions of ribosomal genes of fungal DNA (Köljalg *et al.*, 2013).

The nucleotide sequences were checked and manually edited using SeqScape V3.0 or Vector NTI Advance 11.5.1 software. Subsequently, they were compared with sequences deposited in GenBank using the BlastN search (Altschul *et al.*, 1990). The newly obtained ITS sequences were deposited in GenBank under unique accession numbers.

Of all the known DNA marker sequences, the International Fungal Barcoding Consortium has recognized the ITS region of ribosomal genes of nuclear DNA as the main marker in the molecular genetic method for fungi species identification (Schoch *et al.*, 2014). When determining the boundaries of the studied operational taxonomic units, we proceeded from the previously established lower cutoff value (treshold) = 97-98% for fungi' ITS (Köljal *et al.*, 2013).

3 Results and Discussion

The distribution of ectomycorrhizas (EcM species) according to tree species is given in table 1. Our results reveal, that among all the symbionts of Scots pine forests (Figure 4), the orders *Agaricales* (13 species/28.8%) and *Boletales* (9/20%) had the highest species diversity, followed by the order *Russulales* (8/17.7%) with a smaller number of species (Table 1).

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Figure 4: Photos of various ectomycorrhizae morphotypes of the root system of Scots pine and silver birch. *a*-Lyophyllum decastes (Fr.) Singer, b-Lactarius sp., c-Lactarius rimosellus Peck, d-Russula sp.1, e-Amanita sp., f-Suillus sp., g-Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer, h-Psathyrella sp., i-Pseudosperma sp., j-Lycoperdon norvegicum Demoulin, k-Russula medullata Romagn, l-Tricholoma sp.

Abbildung 4: Fotos verschiedener Ektomykorrhizae-Morphotypen des Wurzelsystems von Waldkiefer und Hängebirke. a- Lyophyllum decastes (Fr.) Singer, b- Lactarius sp., c- Lactarius rimosellus Peck, d-Russula sp.1, e- Amanita sp., f- Suillus sp., g- Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer, h- Psathyrella sp., i- Pseudosperma sp., j- Lycoperdon norvegicum Demoulin, k- Russula medullata Romagn, I- Tricholoma sp.

Table 1: Ectomycorrhizal symbionts identified from root endings and macromycetes of Pinus sylvestris and Betula pendula.

Tabelle 1: Ektomykorrhiza-Symbionten identifiziert aus Wurzelenden und Makromyceten von *Pinus sylvestris* und *Betula pendula*.

Genus/Species name of the EcM	Order/Family	Genbank number	The result of Blast (Genbank Unite)	Similarity, %	Tree species of the symbiotic relationship
1. Agaricus sp.	Agaricales, Agaricaceae	ON704909	<i>Agaricus litoralis</i> (Wakef. & A. Pearson) Pilát	98.98	Pinus sylvestris L.
2. Amanita pantherina (DC.) Krombh	Agaricales, Amanitaceae	ON704911	Amanita sp.	97.46	Pinus sylvestris L., Betula pendula Roth.
3. Amanita sp.	Agaricales, Amanitaceae	ON704908	Amanita pseudopantherina Zhu L. Yang ex Y.Y. Cui	98.84	Pinus sylvestris L., Betula pendula Roth.
4. Bonomyces sp.	Agaricales, Pseudoclitocybaceae	ON704912	Bonomyces sp.	99.85	Pinus sylvestris L.
5. Candolleomyces sp.	Agaricales, Psathyrellaceae	OP215188	Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer	99.16	Pinus sylvestris L., Betula pendula Roth.
6. Cortinarius sp.	Agaricales, Cortinariaceae	ON704900	Cortinarius croceus (Schaeff.) Gray	99.67	Pinus sylvestris L.
7. Chlorophyllum sp.	Agaricales, Agaricaceae	ON704902	Chlorophyllum sp.	96.70	<i>Betula pendula</i> Roth.
8. Lactarius sp.	Russulales, Russulaceae	OP215189	<i>Lactarius</i> rimosellus Peck	100	<i>Betula pendula</i> Roth.
9. Lactarius sp.	Russulales, Russulaceae	ON704904	Lactarius sp.	99.82	<i>Betula pendula</i> Roth.
10. Lycoperdon sp.	Agaricales, Lycoperdaceae	ON704897	<i>Lycoperdon norvegicum</i> Demoulin	100.00	Pinus sylvestris L.
11. Lyophyllum sp.	Agaricales, Lyophyllaceae	ON704896	Lyophyllum decastes (Fr.) Singer	99.38	<i>Betula pendula</i> Roth.

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13. Pseudosperma sp.	Agaricales, Inocybaceae	ON704906	Pseudosperma sp.	97.14	Pinus sylvestris L.
14. Russula sp. 1	Russulales, Russulaceae	ON704914	<i>Russula medullata</i> Romagn.	100.00	Betula pendula Roth
15. Russula sp. 2	Russulales, Russulaceae	OP215195	Russula sp.1	99.82	Betula pendula Roth
16. Russula sp. 3	Russulales, Russulaceae	OP215193	Russula sp.2	99.70	Betula pendula Roth
17. Russula sp. 4	Russulales, Russulaceae	ON704905	Russula sp.3	99.77	Betula pendula Roth
18. Russula sp. 5	Russulales, Russulaceae	ON704898	Russula sp.4	94.94	Betula pendula Roth
19. Suillus sp. 1	Boletales, Suillaceae	ON704899	Suillus brunnescens A.H. Sm. & Thiers	98.47	Pinus sylvestris L.
20. Suillus sp. 2	Boletales, Suillaceae	OP215196	Suillus sp.	97.28	Pinus sylvestris L.
21.Tricholoma sp. 1	Agaricales, Tricholomataceae	ON704910	Tricholoma robustum (Alb. & Schwein.) Ricken	99.87	Pinus sylvestris L.

A similar ratio of the number of species in the orders was found in Russia, for example, for the Stolby Nature Reserve of the Krasnoyarsk Territory (Kosheleva, 2007), the Urals (Fefelov, 2005) and the Lower Volga Region (Zemlyanskaya, 2003). Regional differences are manifested only at the level of species saturation of genera and families. According to recent studies, EcM has a close functional connection with the formation of the structure, diversity, and stability of plant communities (Püschel et al., 2007; Lambers et al., 2008; Veselkin, 2012a; 2012b). Different forest types and favorable environmental conditions in forests promote high EcM species richness in top soil presumably with both high functional diversity and phylogenetic redundancy while stressful environmental conditions lead to lower species richness and functional redundancy (Pena et al., 2017). The ratio of symbionts in EcM may depend on factors such as the functional age state and the phenological state of the tree (Veselkin, 2013). Bahram et al. (2012) emphasized that EcM fungal diversity became lower at the elevated sites and was correlated with the soil temperature. In addition, Sizonenko and Dubrovskiy (2018) stated that a decline in the ectomycorrhiza linear dimensions accompanied by a compensatory growth of the ectomycorrhiza density with the raised elevation and the deterioration of environmental conditions. The composition of EcM communities is affected by large-scale patterns such as stand age, climatic conditions, soil-fauna and spore dispersal. The relationship between mycorrhizal fungi and soil acidity has long been discussed in the literature (Kalliokoski *et al.*, 2010; Pena *et al.*, 2017). EcM fungi are an important source of organic acids in soil (Griffiths *et al.*, 2009) and affect the pH of the rhizosphere (Smith and Read, 2008). On the other hand, soil conditions affect species diversity of EcM fungi as demonstrated by the dramatic decrease in species richness along a gradient of increasing nitrogen deposition (Lilleskov *et al.*, 2002). Altering nitrogen conditions in soil affects the outcome of species interactions possibly disadvantaging species adapted to the pre-change conditions while favoring generalists (Koide *et al.*, 2005). Mycorrhiza has been noted to decrease the pH in the rhizosphere, because of the selective absorption of ammonium NH+ ions and the release of H+ ions (Eremin and Popova, 2016). Smith *et al.* (2003) stated that the low effectiveness of root and mycorrhizal functions in the cold soils is due to insufficient mineral elements supply.

Otgonsuren et al. (2020) detected 24 different ectomycorrhizal morphotypes associated with Pinus sylvestris and Pinus sibirica, and 18 morphotypes were identified to taxa in forests in Mongolia. The two Pinus species had dissimilar ectomycorrhizal communities, and only 2 ectomycorrhizal fungal taxa were common to both species. In another survey conducted by Sarsekova et al. (2020), 30 ectomycorrhizas belonging to Agaricomycetes were identified on the right bank of the Irtysh River in a mixed forest of Pinus sylvestris, Picea obovata and Betula pendula trees of northern and central Kazakhstan. In their study, the distribution of 30 species into families was as follows; Suillaceae (8 species), Russulaceae (7), Cortinariaceae (4), Boletaceae (3), Tricholomataceae (2), Amanitaceae (1), Cantharellaceae (1), Gomphaceae (1), Gomphidiaceae (1), Paxillaceae (1), and Bankeraceae (1). The genus with the highest number of recorded species was Suillus (8). At the same time Sarsekova et al. (2020)'s study, 17 ectomycorrhizas were recorded under Pinus sylvestris, 8 under Betula pendula, 6 under Populus tremula, 1 under Picea obovata, 1 under Quercus robur, 1 under Salix sp., and 1 under Pinus densiflora. It should be noted that some species such as Paxillus involutus. Russula undulata, Cortinarius sp. and Cantharellus cibarius formed a symbiotic relationship with both coniferous and broadleaved tree species (Sarsekova et al., 2020). According to Garcia et al. (2016) the basidiomycete Rhizopogon spp. is typical in the root systems of the genus Pinus which is represented by the most species in the dominant regions of the Pinaceae family in the Pacific northwest of the USA. However, the symbiotic relationship of Scots pine and Rhizopogon sp. has not been found within the scope of our study. Massicotte et al. (1992) stated that the ascomycete Cenococcum graniforme (Sow.) Fred and Winge is the most common ectomycorrhizal fungus in the World, surprisingly this species has not been found in our study.

In the present study, five ectomycorrhiza families were identified in the silver birch stands: (5 species/25% of the total number of species identified in the studied area), *Amanitaceae* (3/6.7%), *Boletaceae* (3/6.7%), *Lycoperdaceae* (1/2.2%), *Paxillaceae* (1/2.2%), and *Russulaceae* (3/6.7%) (Tab. 1).

The list of families (with number and proportion) for all recorded species in the investigated area is as follows: *Agaricaceae* (2 species 2/4.4%), *Amanitaceae* (4/8.9%), *Boletacea* (5/11.1%), *Cortinariaceae* (3/6.7%), *Gloeophyllaceae* (1/2.2%), *Inocybaceae* (1/2.2%), *Lycoperdaceae* (1/2.2%), *Lyophyllaceae* (2/4.4%), *Paxillaceae* (1/2.2%), *Polyporaceae* (3/6.7%), *Psathyrellaceae* (2/4.4%), *Pseudoclitocybaceae* (2/4.4%), *Russulaceae* (8/17.8%), *Suillaceae* (6/13.3%), and *Tricholomataceae* (4/8.9). The coefficient of species saturation orders is: *Agaricales* 28.8, *Boletales* 20, *Russulales* 17.7. They included 45 of all species defined and identified with DNA 28 species in the study area (Figure 4). The remaining 16 genera included 6.2% of all identified species.

The average species saturation of pine forests is 10.0, which is lower than the average species saturation of 18.6 in the Republic of Kazakhstan (Novozhilov, 2005). This trend is explained by the locality of the territory and the absence of many types of substrates that have been studied in other regions of the Republic of Kazakhstan. For example, those that are often found in the steppe and desert (excrement of herbivorous animals, remnants of succulents, wormwood Artemísia absínthium L.). The leading families are those families where the number of species exceeds the average species saturation of families in the study area. As a result of this study, fundamental differences were found between the species saturation of EcM symbionts of Scots pine and Silver birch forests. In addition, Shi et al. (2016) stated that there are still critical gaps remaining in our understanding of biogeographic patterns of mycorrhizal associations. Further, our limited knowledge of the anthropogenic factors responsible for shifting plant-mycorrhizal distributions has hindered the efforts to predict ecosystem feedbacks to climate change. Mäkelä et al. (2022) suggest that EcM can use a significant proportion of the carbon assimilated by vegetation and hence be an important driver of the decline in carbon use efficiency at higher latitudes. Within this context, Godbold et al. (2006) emphasized that the turnover of the mycorrhizal external mycelium may be a fundamental mechanism for the transfer of root-derived C to soil organic material.

In total, 110 samples were collected during field work. Seventeen species were identified using classical methods via macromycete determinants, including EcM list of De Roman *et al.* (2005), and 28 were identified using DNA sequencing analysis (Figure 5). In the 60 soil samples 22 morphotypes of ectomycorrhizal fungal taxa associated with Scots pine and silver birch were determined. For the identify, a list from the study by De Roman *et al.* (2005), Tedersoo (2007), electronic resources (Ilyina, 2019; Polenov, 2013), as well as the Index Fungorum database and MycoBank (Robert *et al.*, 2020) were used.

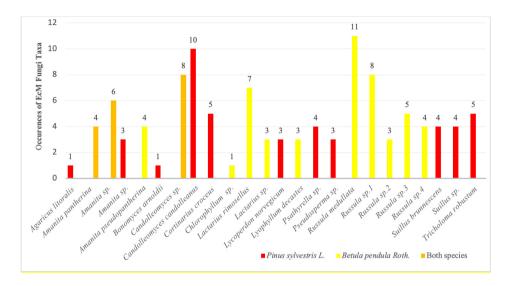


Figure 5: The number of occurrences of taxa of EcM fungi in soil samples of Scots pine and silver birch.

Abbildung 5: Die Anzahl der Vorkommen von Taxa von EcM-Pilzen in Bodenproben von Waldkiefer und Hängebirke.

4 Conclusion

Five EcM families (*Psathyrellaceae, Russulaceae, Amanitaceae, Tricholomataceae,* and *Boletaceae*) were predominant in the Scots pine and silver birch forests studied here, with in total 11 species. These species are *Candolleomyces pseudocandolleanus* (A.H. Sm.) D. Wächt. & A. Melzer, *Amanita muscaria* (L.) Lam., *A. pantherina* (DC.) Krom., *Russula medullata* Romagn, *Suillus bovinus* (L.) Roussel, *Tricholoma robustum* (Alb. & Schwein.) Ricken, *Russula* sp.1, *Leccinum scabrum* (Bull.) Gray, L. *versipelle* (Fr. & Hök) Snell, *Psathyrella* sp., *Cortinarius croceus* (Schaeff.) Gray. In total, we managed to isolate the DNA of only 28 fungi species and the remaining species were determined by classical method using macromycetes.

In this study, a higher symbiotic association with EcM was found in Scots pine forests compared to Silver birch forests. A similar trend is observed not only in this study area but also in other parts of Kazakhstan. Our study allow us to conclude that the species and quantitative composition of Scots pine and silver birch forests vary considerably. The findings of this study are important for restoring unforested areas. In this context, EcM may be used as a major performance-enhancing tool in afforestation practices in the Irtysh River basin, where extreme ecological conditions and climate change effects prevail.

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Conflict of Interest

The authors declare that they have no conflict of interest.

References

- Abiev S., Abdildina D.I., Feoktistov A. 2000. Collection of cultures of basidiomycetes of the Institute of Botany and Phytointroduction//Proceedings of the International Conference "Mycology and Cryptogamous Botany in Russia". SPb., p. 47, (In Russian).
- Abiev S.A. 2015. Edible fungi of the order Agaricales of specially protected natural territories of central and north-eastern Kazakhstan: the creation of a collection of strains and their molecular identification. Abiev S.A., Shnyreva A.V., Nam G.A., Asilkhanova R.Z., Abisheva G.//News of Nat. Academy of Sciences of the Republic of Kazakhstan, p.154-161, 2015. (In Russian).
- Agerer R. 1987. Colour atlas of ectomycorrhizae. Einhorn-Verlag Eduard Dietenberger, Schwabisch Gmund, Germany.
- Agerer R. 1991. Characterization of ectomycorrhiza. In Methods in microbiology. Vol. 23. Edited by J.R. Norris, D.J. Read, and A.K. Varma. Academic Press, New York. pp. 25–73.
- Agerer R., Grote R., & Raidl S. 2002. The new method 'micromapping', a means to study species-specific associations and exclusions of ectomycorrhizae. Mycological Progress, 1(2), 155-166.
- Alvarez I.F., Trappe J.M. 1983. Dusting roots of *Abies concolor* and other conifers with *Pisolithus tinctorius* spores at out planting time proves ineffective. Canadian Journal of Forest Research, 13: 1021-1023.

- Altschul, S.F., Gish, W., Miller, W., Myers, E. W., David J. Lipman (1990). Basic local alignment search tool. Journal of Molecular Biology, 215(3), 403-410. https://doi. org/10.1016/S0022-2836(05)80360-2.
- Anonymous 2009. Management Plan of the State Forest Natural Reserve "Ertis Ormany", Shalday. (in Russian).
- Anonymous 2015. Information on the scientific and research work of the Department of Information Science and Monitoring of the GLPR "Ertis Ormany". (in Russian).
- Arocena J.M., Glowa K.R. 2006. Mineral weathering in ectomycorrhizosphere of Subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) as revealed by soil solution composition. Forest Ecology and Management, 133:61-70 https://doi.org/10.1016/S0378-1127(99)00298-4
- Bahram M., Polme, S., Koljalg, U., Zarre, S., Tedersoo, L. 2012i Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. New Phytologist 193 (2): 465-473. https://doi.org/10.1111/j.1469-8137.2011.03927.x
- Barbati A., Scarascia G., Ayan S., Blasi E., Calama R., Canaveira P., Cicatiello C., Collalti A., Corona P., Del Rio M., Ducci F., Perugini L. 2018. State of Mediterranean Forests 2018. Chapter 8: Adaptation and mitigation, p. 128-146, Published by the FAO of the United Nations and Plan Bleu, Regional Activity Center of UN Environment / Mediterranean Action Plan, ISBN FAO: 978-92-5-131047-2 ISBN Plan Bleu: 978-2-912081-52-0, Rome, 2018. http://www.fao.org/3/CA2081EN/ca2081en.PDF
- Bennett J.A., Maherali H., Reinhart K.O., Lekberg Y., Hart M.M., Klironomos J. 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science, 355: 181–184.
- Christensen M., Heilmann-Clausen J. 2013. Fungi of Northern Europe. Vol. 4. The genus *Tricholoma*- The Danish Mycological Society, — 228 p. - P. 104.
- Clayton R.A., Sutton G., Hinkle P.S., Bult Jr. C., Fields C. 1995. Intraspecific variation in small-subunit rRNA sequences in GenBank: why single sequences may not adequately represent prokaryotic taxa. International Journal of Systematic Bacteriology 45: 595–599.
- Courty P. E., Buée M., Diedhiou A. G., Frey-Klett P., Le Tacon F., Rineau F., & Garbaye J. 2010. The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. Soil Biology and Biochemistry, 42(5), 679-698.
- De Roman M., Claveria V., Miguel M. 1961. A revision of the descriptions of ectomycorrhizas published since 1961. Mycology research. The British Mycological Society. UK, 2005. - T.109 (10). - P. 1063 – 1104.
- De Román M., & de Miguel A. M. 2005. Post-fire, seasonal and annual dynamics of the ectomycorrhizal community in a *Quercus ilex* L. forest over a 3-year period. Mycorrhiza, 15(6), 471-482.
- Dogmus Lehtijarvi T. 2007. Mycorrhiza inoculation and its effects, 6th Section (Editors: Yahyaoğlu, Z. and M. Genç, Seedling Standardization: Quality Seedling Propagation and Principals of Seedling Qualification Norms) Publication of Suleyman Demirel University, Pub. Nu: 75, p. 301-352, ISBN 978-9944-452-07-6, Isparta (In Turkish).
- Eremin D.I., Popova, O.N. 2016. Agroecological characteristics of micromycetes that live in soil. Bulletin of GAU of Northern Trans-Urals, 1 (32) 12-18.

- Fefelov K. A. 2005. Myxomycetes (class Myxomycetes) Ural: taxonomic composition, ecology, geography. Autoref. for the degree of Candidate of Sciences. biol. nauk. SPb.
- Finlay R. D. 2005. Mycorrhizal symbiosis: myths, misconceptions, new perspectives and future research priorities. Mycologist, v. 19, n. 3, 90–95, 2005.
- Forest Code of the Kazakhstan Republic 2003. Forest Code (No.477-II of 2003). Country. Kazakhstan. Type of law. Legislation. Source. https://leap.unep.org/countries/kz/ national-legislation/forest-code-no477-ii-2003 15.09.2022, 22:58:48
- Fungorum I. 2021. Index Fungorum Home Page. URL: http://www.index fungorum.org
- Garcia M.O., Smith J.E., Luoma D.L., Jones M.D. 2016. Ectomycorrhizal communities of ponderosa pine and lodgepole pine in the south-central Oregon pumice zone. My-corrhiza 26:275-286. https://doi.10.1007/s00572-015-0668-x
- Godbold D.L., Hoosbeek M.R., Lukac M., Cotrufo M.F., Janssens I.A., Ceulemans R., Polle A., Velthorst E.J., Scarascia-Mugnozza G., De Angelis P., Miglietta F., Peressotti, A. 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. Plant Soil 281(1–2):15–24. https://doi.org/10.1007/s11104-005-3701-6
- Griffiths B.R., Madritch M.D., Swanson A.K. 2009. The effects of topography on forest soil characteristics in the Oregon Cascade Mountains (USA): Implications for the effects of climate change on soil properties. Forest Ecology and Management 257: 1-7 https://doi.org/10.1016/j.foreco.2008.08.010
- Qiang-Sheng W., Ren-Xue X. 2006. Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. Journal of Plant Physiology, 163 (4) 417-425.
- Haavik L.J., Billings S.A., Guldin J.M., Stephen F.M. 2015. Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. Forest Ecology and Management 354: 190–205. https://doi.org/10.1016/j.foreco.2015.06.019.
- Harley J.L., & Loughman B. C. 1963. The uptake of phosphate by excised mycorrhizal roots of the beech: ix. The nature of the phosphate compounds passing into the host. New Phytologist, 62(3), 350-359.
- Hiiesalu I., Pärtel M., Davison J., Gerhold P., Metsis M., Moora M., *et al.* 2014. Species richness of arbuscular mycorrhizal fungi: associations with grassland plant richness and biomass. New Phytol. 203, 233–244. https://doi.org/10.1111/nph.12765
- Ilyina T.A. (2019). Illustrated guide-determinant of mushrooms sur // https://mycology. su /. 29.09.2019.
- Kais A.G., Snow G.A., Marx D.H. 1981. The effects of benomyl and *Pisolithus tinctorius* ectomycorrhizae on survival and growth of longleaf pine seedlings. Southern Journal of Applied Forestry, 5: 189-194.
- Kalliokoski T., Pennanen T., Nygren P., Sievänen R., Helmisaari H.S. 2010. Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant and Soil 330: 73-89. https://doi.org/10.1007/s11104-009-0177-9
- Karst J., Randall M.J., Gehring C.A. 2014. Consequences for ectomycorrhizal fungi of the selective loss or gain of pine across landscapes. Botany 92:855–865. https:// doi:10.1139/cjb-2014-0063

- Kharuk V.I., Ranson K.J., Petrov I.A., Dvinskaya M.L., Im S.T., Golyukov A.S. 2019. Larch (*Larix dahurica* Turcz) growth response to climate change in the Siberian permafrost zone. Regional Environmental Change 19:233–243. https://doi.org/10.1007/ s10113-018-1401-z
- Koide R.T., Xu B., Sharda J., Lekberg Y., & Ostiguy N. 2005. Evidence of species interactions within an ectomycorrhizal fungal community. New Phytologist 165, 305-316.
- Köljalg U., Nilsson R. H., Abarenkov K., Tedersoo L., Taylor A. F., Bahram M., Bates S.T., Bruns T.D., Bengtsson-Palme J., Callaghan T.M., Douglas B., Drenkhan T., Eberhardt U., Dueñas M., Grebenc T., Griffith G.W., Hartmann M., Kirk, P.M. Kohout P., Larsson E., Lindahl B.D., Lücking R., Martín M.P., Matheny P.B., Nguyen N.H., Niskanen T., Oja J., Peay K.G., Peintner U., Peterson M., Põldmaa K., Saag L., Saar İ., Schüßler A., Scott J.A., Senés C., Smith M.E., Suija A., Taylor D.L., Telleria M.T., Weiss M., & Larsson K.H. 2013. Towards a unified paradigm for sequence-based identification of fungi. Mol Ecol 22(21):5271-7. https://doi:10.1111/mec.12481.
- Kosheleva A. P. 2007. Myxomycetes of the Stolby Nature Reserve (Eastern Sayan): taxonomic composition and ecology. Kosheleva AP–SPb.
- Lambers H., Raven J.A., Shaver G.R., Smith S.E. 2008. Plant nutrient acquisition strategies change with soil age. Trends Ecol Evol 23 (2): 95-103. https://doi.org/10.1016/j. tree.2007.10.008.
- Lilleskov E.A., Fahey T.J., Horton T.R., & Lovett G.M. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology, 83, 104-115.
- Liu B., Li H., Zhu B., Koide R.T., Eissenstat D.M., Guo D. 2015. Complementarity in nutrient foraging strategies of absorptive fine roots and arbuscular mycorrhizal fungi across 14 coexisting subtropical tree species. New Phytol. 208, 125–136. https:// doi.org/10.1111/nph.13434
- Mäkelä A., Tian X., Repo A., Ilvesniemi H., Marshall J., Minunno F., Näsholm T., Schiestl-Aalto P., Lehtonen A. 2022. Do mycorrhizal symbionts drive latitudinal trends in photosynthetic carbon use efficiency and carbon sequestration in boreal forests? Forest Ecology and Management 520 (January):120355. https://doi.org/10.1016/j.foreco.2022.120355
- Massicotte H., Trappe J., Peterson R.L., Melville L.H. 1992. Studies on *Cenococcum geophilum*. II. Sclerotium morphology, germination, and formation in pure culture and growth pouches. Can J Bot 70(1):125–132. https://doi:10.1139/b92-017
- Caudullo G., Welk E., San-Miguel-Ayanz J. 2018. Mendeley Data: Chorological data for the main European woody species. URL: https://data.mendeley.com/datasets/ hr5h2hcgg4/6; Access date: 18 May, 2023.
- Meshkov V.V. 2010. Justification and technology for the production of mycorrhized compost for forest growing and mushrooms for commercial purposes (for example, the ribbon burs of Irtysh). Abstract. diss ... cand. s. sciences. Almaty, p.24 (In Russian).
- Meshkov V.V., Nam G.A., Rakhimova E.V. 2009. Use of mycorrhizal fungi for reforestation and afforestation in Zailiysky Alatau. Proceedings of the International Conference "Problems of Forest Phytopathology and Mycology". Perm, (In Russian).
- Molina R., Massicotte H., Trappe J.M. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. Allen M.F. (Ed.) Mycorrhizal functioning: an integrative plant-fungal process. N.Y. 357-423.

- Moser M. 1978. Die Rohrlinge und Blätterpilze. Polyporales, Boletales, Agaricales, Russulales in: M. Moser (Ed.) KleineKryptogamenflora (Jena: VEB Gustav. Fischer Verlag) p. 532.
- Moukha S., Férandon C., Beroard E., Guinberteau J., Castandet B., Callac P., Creppy E., Barroso G. 2013. A molecular contribution to the assessment of the *Tricholoma equestre* species complex. Fungal Biology 117 (2) 145–155. https://doi:10.1016/j. funbio.2013.01.003
- Nam G.A. 1998. To the mycobiota of hat mushrooms of the Dzungarian Alatau//Search. Ser. natures sciences. 1: 35-41. (In Russian).
- Nordic Macromycetes 1992. Polypoles, Boletales, Agaricales, Russulales. Vol. 2 Nordsvamp – Copenhagen- p.62
- Novozhilov Yu. K. 2005. Myxomycetes (class Myxomycetes) of Russia: taxonomic composition, ecology and geography. Dis.... doct. biol. sciences. St. Petersburg, 377p.
- Otgonsuren B., Rosinger C., Wang L., Godbold D.L. 2020. Winter soils of Mongolian forests have viable ectomycorrhizas and soil enzymatic activity. Soil. Biol. Biochem 148. 107-914 https://doi.org/10.1016/j.soilbio.2020.107914
- Pena R., Lang C., Lohaus G., Boch S., Schall P., Schöning I., Ammer C., Fischer M., Polle A. 2017. Phylogenetic and functional traits of ectomycorrhizal assemblages in topsoil from different biogeographic regions and forest types. Mycorrhiza 27: 233-245 https://doi.org/10.1007/s00572-016-0742-z
- Pickles B.J., Egger K.N., Massicotte H.B., Green D.S. 2012. Ectomycorrhizas and climate change. Fungal Ecol 5(1):73–84. https://doi:10.1016/j.funeco.2011.08.009
- Polenov A.B. 2013. Mushrooms. Edible and inedible: The most complete and modern atlas-determinant. SP. b.: LLC Polygon Publishing House, 160 pp. https://books.google.kz (In Russian).
- Püschel D., Rydlova J., Vosatka M. 2007. Mycorrhiza influences plant community structure in succession on spoil banks. Basic Appl Ecol 8(6): 510-520. https://doi. org/10.1016/j.baae.2006.09.002.
- Read D.J. 1999. Plant-microbe mutualisms and community structure. Biodiversity and ecosystem function. In: Schulze E. D., Mooney H. A. Springer-Verlag. pp. 181–209.
- Robert V., Vu, D., & Cock Ad, S.C. 2020. The MycoBank. Website: http://www.mycobank. org [accessed 19 Dec. 2013].
- Sarycheva L. A. et al. 2009. Mycobiota of the Lipetsk region VSU, Reserve "Galichya Gora"; ed. V. A. Melnik; rec.: A. E. Kovalenko, O. V. Morozova. Voronezh: CPI VSU, 2009. 287 p.
- Sarsekova D., Ayan S., Abzhanov T. 2020. Ectomycorrhizal Flora Formed by Main Forest Trees in the Irtysh River Region of Central and Northeastern Kazakhstan. Southeast Eur for 11(1): 61-69. https://doi.org/10.15177/seefor.20-06.
- Sarsekova D., Ayan S., Abzhanov T., Nurlabi A. 2021. Preliminary results of the effect of artificial mycorrization on the growth of Siberian spruce (*Picea obovata* Ledeb.) seedlings and soil properties. Agriculture and Forestry 67 (3): 43-59.
- Sarsekova D.N. 2020. The project (The state registration No: 13005/844) titled "Mycorrhiza macromycetes of the main forest-forming species of Central and North-East Kazakhstan and their use for artificial mycorrhization of seedlings of forest tree species" has been financed by the Ministry of Agriculture of the Republic of Kazakhstan.

- Schoch C.L., Robbertse B., Robert V., Vu D., Cardinali G., Irinyi L., Meyer W., Nilsson R.H., Hughes K., Miller A.N., Kirk P.M., Abarenkov K., Aime M.C., Ariyawansa H.A., Bidartondo M., Boekhout T., Buyck B., Cai Q., Chen J., Crespo A., Crous P.W., Damm U., et al. 2014. Finding needles in haystacks: linking scientific names, reference specimens and molecular data for fungi. Database: J. Biol. Databases Cur. https://doi. org/10.1093/database/bau06
- Sebastiana, S., Bernardes da Silva, A., Matos, A.R, Alcântara, A., Silvestre, S., Malhó, R., 2018. Ectomycorrhizal inoculation with *Pisolithus tinctorius* reduces stress induced by drought in cork oak. Mycorrhiza 28(3):247-258.
- Shubin V.I. 1973. Mycotrophy of tree species and its significance in forest cultivation in the taiga zone / V.I. Shubin. L.: Nauka, pp. 1-262.
- Shi M., Fisher J.B., Brzostek E.R., Phillips R.P. 2016. Carbon cost of plant nitrogen acquisition: Global carbon cycle impact from an improved plant nitrogen cycle in the Community Land Model. Glob Chang Biol 22(3): 1299-1314. https://doi.org/10.1111/ gcb.13131.
- Simard S.W., Austin M.E. 2010. The role of mycorrhizas in forest soil stability with climate change. In: Simard SW (ed) Climate change and variability. InTech p 275–302. doi:10.5772/9813
- Smith S.E., Read D.J. 2008. Mycorrhizal symbiosis. London, Academic Press Limited, 678 p.
- Smith S.E., Read D.J. 1997. Mycorrhizal Symbiosis. London, Academic Press Limited, 514 p.
- Smith W.K., Germino M.J., Hancock T.E., Johnson D.M. 2003. Another perspective on altitudinal limits of alpine timberlines. Tree Physiology, v. 23, p. 1101-1112. https:// doi.org/10.1093/treephys/23.16.1101
- Sizonenko T.A., Dubrovskiy Y.A. 2018. Ectomycorrhiza of *Larix sibirica* Ledeb. along the gradients of main ecological factors and elevation at the Northern and Subpolar Urals. Journal of Mountain Science 15(12). https://doi.org/10.1007/s11629-018-5074-3
- Tedersoo L. 2007. Ectomycorrhizal fungi: diversity and community structure in Estonia, Seychelles and Australia. Tartu University Press.
- Tedersoo L., Smith M.E. 2013. Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. Fungal Biol. Rev. 27, 83–99. https://doi.org/10.1016/j.fbr.2013.09.001
- Taylor M.K., Lankau R.A., Wurzburger N. 2016. Mycorrhizal associations of trees have different indirect effects on organic matter decomposition. Journal of Ecology 104: 1576–1584.
- Vaishlya O. (2017). First list of macromycetes forming ectomycorrhizas in cedar and pine forests of Tomsk region of West Siberia. International Journal of Environmental Studies 74:5, 752-770.
- Vaishlya O., Karbysheva K., Sarsekova D., & Aidarkhanova G. 2019. Ecological Aspects of *Pinus sibirica* Du Tour Mycotrophy in Forest Ecosystems of West Siberia. In IOP Conference Series: Earth and Environmental Science (Vol. 224, No. 1, p. 012-049). IOP Publishing
- Vaishlya O.B., Danchenko A. M., & Dement'eva A.G. 2012. Mikotrofnost' podrosta *Pinus sibirica* Du Tour v podzone yuzhnoj tajgi Tomskoj oblasti. Izvestiya Samarskogo nauchnogo centra Rossijskoj akademii nauk, 14 (1-8), 1963-1967.

- Valdes M. 1986. Survival and growth of pines with specific ectomycorrhizae after 3 years on a highly eroded site. Canadian Journal of Botany, 64: 885-888.
- Veselkin D.V., 2012a. Stabilization of the ratio between the numbers of species of different mycorrhizal status: An attractor of progressive succession. Izv Samarsk Nauch Tsentra Ross AkadNauk 14(1)5: 1206-1209.
- Veselkin D.V., 2012b. Participation of plants of different mycotrophic status in the succession leading to "agrosteppe" formation. Russ J Ecol 43(4): 289-293. https://doi. org/10.1134/S1067413612030174.
- Veselkin D.V. 2013. Sizes of ectomycorrhizal endings of *Picea obovata* Ledeb., Abies sibirica Ledeb., Pinus sylvestris L. and ratio of symbionts in them. Species features. Coniferous boreal zone. XXI, No. 1. C. 66-72.
- Villarreal-Ruiz, L., & Neri-Luna, C. (2018). Testing sampling effort and relative abundance descriptors of belowground ectomycorrhizal fungi in a UK planted scots pine woodland. Mycology 9(2), 106-115.
- Voronina E. Y. 2008. The influence of ectomycorrhizae of spruce and birch on the structure of complexes of soil-dwelling microorganisms (Doctoral dissertation, Lomonosov Moscow State University (MSU)).
- Voronina E.Y. 2006. Mycorrhizae and their role in community formation. Bulletin of the Moscow University. Ser. 16, Biology, (4), 17-26.
- Zemlyanskaya I. V. 2003. Myxomycetes of steppes and deserts of the Lower Volga region: Dis.... cand. biol. sciences. Volgograd; St. Petersburg, 2003. 213 p.
- Zhang Q., Kennon R., Koza M. A., Hulten K., Clarridge III J. E. 2002. Pseudoepidemic due to a unique strain of Mycobacterium szulqai: genotypic, phenotypic, and epide-miological analysis. Journal of Clinical Microbiology. 40: 1134–1139.