

VILNIUS UNIVERSITY

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**HYPOGEOUS FUNGI OF LITHUANIA: DIVERSITY,
DISTRIBUTION AND LINKS WITH SMALL MAMMALS**

Summary of doctoral dissertation
Biomedical sciences, biology (01 B)

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The research was carried out in the period of 2004 – 2008 at Vilnius University.

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VILNIAUS UNIVERSITETAS

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**LIETUVOS POŽEMINIŲ GRYBŲ ĮVAIROVĖ,
PAPLITIMAS IR SAITAI SU SMULKIAISIAIS
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INTRODUCTION

Hypogeous and other mycorrhizal fungi are important and active components of forest ecosystems. They provide various functions – water and nutrient supply to the plants, protection of plants from negative environmental conditions and pathogens, maintenance of the soil homeostasis, and are the food source for various animals (MASER et al., 1978; ALLEN, 1991). The research of hypogeous fungi is complicated and requires special efforts, however, the interest in these fungi has recently significantly increased, because 1) their diversity is much higher than was known before, 2) there is a lack of knowledge about their structure and distribution, and 3) the links with other organisms still not well understood.

The thorough research on the diversity and biology of hypogeous fungi in Lithuania was not carried out before. The data concerning these fungi, mostly accidentally recorded in the places disturbed by forest animals, were published in a few mycological publications (BUCHOLTZ, 1904, 1907; MAZELAITIS, 1982; KUTORGA, 2000; etc.). Only further studies based on special research methods could significantly increase the knowledge on the diversity and distribution of hypogeous fungi in the country.

Mycologists of various countries have studied the structure and dynamics of the macromycete communities in different natural habitats, and tried to evaluate the influence of various biotic and abiotic factors on their functioning (ARNOLDS, 1992; CASTELLANO et al., 2004). Mycocoenological studies increases the knowledge on the ecology of different fungal species, and on the whole biodiversity of various ecosystems. The qualitative and quantitative studies on mycorrhizal macromycete in Lithuanian natural habitats have started recently (STANKEVIČIENĖ, URBONAS, 2006; STANKEVIČIENĖ, KASPARAVIČIUS, 2007; STANKEVIČIENĖ et al., 2008), however, only little or no attention was paid to hypogeous fungi in these studies.

Large forest animals, such as wild boar, could substantially disturb the forest floor and affect the fructification of mycorrhizal fungi (SCHLEY, ROPER, 2003; ŁAWRYNOWICZ et al., 2006). The impact of such disturbance on development and fruiting of macromycetes in Lithuanian forests is still not studied.

It is well known that large and small mammals consume hypogeous fungi and disseminate their spores (MASER et al., 1978, 2008; CLARIDGE, MAY, 1994). The mycophagy of small mammals was studied in North America, Australia and in some European countries (MASER et al., 1978, 2008; CLARIDGE, MAY, 1994; VIRO, SULKAVA, 1985; BLASCHKE, BÄUMLER, 1989; BERTOLINO et al., 2004). Small mammals mycophagy has not been properly investigated in Lithuania before.

Aims and tasks of the dissertation. The aims of the present research were to investigate the species diversity, distribution and communities of hypogeous fungi in Lithuania, and to analyse the composition of fungi in small mammals diet. To achieve these aims, the following tasks have been formulated:

1. To collect the samples of hypogeous fungi in different geographical places and forest habitats of Lithuania; to examine the morphological and anatomical structures of fruit-bodies; to identify collected specimens and to examine critically the specimens of hypogeous fungi preserved in Lithuanian herbariums.
2. To compile the checklist of hypogeous fungi of Lithuania; to analyse the taxonomic structure, distribution and phenology of these fungi.

3. To determine the structure of communities of hypogeous and epigeous fungi, the quantitative and seasonal characteristics of fructification in spruce, oak and mixed tree stands.
4. To evaluate the influence of abiotic (precipitation, air temperature, chemical characteristics of the soil) and biotic (type and flora of tree stands, forest floor disturbances made by wild boars) factors on the fructification and species diversity of the mycorrhizal fungi.
5. To analyse the quantitative and seasonal characteristics of mycophagy of different small mammals in spruce, oak and mixed tree stands by the mycological examination of fresh fecal pellets.

Defensive statements:

1. The species diversity of hypogeous fungi in Lithuania is greater than was known before, and their taxonomic spectrum is broader as well.
2. Hypogeous fungi occur in all explored tree stands of various type and age, however, the frequency, distribution and fructification of particular species are different.
3. The composition and seasonal dynamics of communities of hypogeous and epigeous mycorrhizal fungi varies and depends on various abiotic and biotic factors.
4. Various small mammals in Lithuania consume hypogeous and epigeous fungi, however, the level and seasonality of mycophagy are specific.

Novelty of the study. In this study, the species diversity, distribution and phenology of hypogeous fungi were ascertained in detail for the first time in Lithuania. Two research methods of hypogeous fungi were effectively applied in Lithuania: 1) the raking with garden cultivator of the uppermost soil layer, 2) the examination of fecal pellets of small mammals captured in live traps (this method is not harmful to animals and does not alter the natural ecosystem). An annotated checklist of hypogeous fungi of Lithuania was compiled and illustrated with digital images of fungal macro- and microscopic structures. 8 species and 5 genera of hypogeous fungi have been identified for the first time in Lithuania. The communities of both hypogeous and epigeous mycorrhizal fungi in different tree stands were investigated for the first time in the country. New approaches were undertaken in studies of small mammal mycophagy.

Significance of the study. Obtained data provide new knowledge on Lithuanian mycobiota and mycophagy, and subsequently could be used for the preparation of forthcoming volumes of the editions "Mycota Lithuaniae" and "Fauna of Lithuania". The results of the study improve the understanding of functional links among fungi, small mammals and plants in forest ecosystems. The results can be also used in the protection of the components of the environment, e.g. in defining valuable areas for fungal diversity. Collected specimens of hypogeous and epigeous fungi are deposited in the herbarium of Vilnius University (WI).

Presentation of the results. The results of the research were presented at the following conferences and seminars: 1) "Development of mycology in Lithuania – history and present trends" (Vilnius, 2007); 2) "Science – the future of Lithuania" (Vilnius, 2007); 3) "Hypogeous fungi in Lithuania: diversity, taxonomy and ecology" (Vilnius, 2007); 4) "Theoretical and practical aspects of plant diversity protection" (Šiauliai, 2007); 5) "Understanding species composition, diversity and dynamics in forest ecosystems" (Lammi, Finland, 2008); 6) "XVII Symposium of the Baltic

Mycologists and Lichenologists” (Saaremaa, Estonia, 2008); 7) “Science in the Faculty of Natural Sciences of Vilnius University” (Vilnius, 2008).

Volume and structure of the dissertation. The volume of dissertation is 168 pages (excluding appendix). The thesis is written in Lithuanian and consists of Introduction, Literature review, Materials and methods, Results and discussion, Conclusions, List of references (215 reference sources), Short glossary of terms, Appendix (21 table). The dissertation is illustrated with 83 figures and 33 tables.

MATERIALS AND METHODS

The research material was collected mainly in four different geographical parts of Lithuania: in north-western part – Žemaitija National Park (Žemaitija NP), western – Curonian Spit National Park (Curonian Spit NP), eastern – Kamasta Landscape reserve (Kamasta LR), and southern – Dzūkija National Park (Dzūkija NP).

During 2005–2007 the diversity and communities of hypogeous and epigeous mycorrhizal fungi, and the mycophagy of small mammals were investigated in Žemaitija NP in five permanent rectangular study plots (Ž1–Ž5), each 1000 m² in size. The study was conducted in different tree stands: plot Ž1 – *Picea abies* dominated stand (85 years old, forest floor disturbed by *Sus scrofa* animals), plot Ž2 – *Picea abies* dominated stand (95 years old, forest floor disturbed by *Sus scrofa*), plot Ž3 – *Picea abies* dominated stand (70 years old, forest floor not disturbed by *Sus scrofa*), plot Ž4 – *Quercus robur* dominated stand (108 years old), and plot Ž5 – mixed tree stand (117 years old, dominated by *Quercus robur*, *Picea abies* and *Betula pendula*). The impact of forest floor disturbance done by *Sus scrofa* animals on fructification of epigeous mycorrhizal fungi was explored in six study subplots (Ž1p1–3 and Ž2p1–3), each ~ 20 m² in size, which were established in study plots Ž1 and Ž2. The vegetation was examined in each study plot. Five soil samples were taken from each study plot, and the soil chemical composition (N, P₂O₅, K₂O, humus and pH_{KCL}) was measured.

Epigeous mycorrhizal fungi in these plots were studied during August–October (2005–2007) in every three weeks. Counted fruit-bodies were removed from the study plots. Some fungi were identified in the field, other fungi were sampled and identified in the laboratory. Each plot was visited 14 times. The search of hypogeous fungi was performed in March (2006–2007) and August–November (2005–2007) by raking with garden cultivator of the uppermost soil layer. Fruit-bodies of hypogeous fungi were counted in raked 4 m² size temporal plots established nearby permanent plots Ž3–Ž5, and in both 2 m² size plots with disturbed forest floor by *Sus scrofa* and in 2 m² size undisturbed plots established nearby permanent plots Ž1 and Ž2. Each visit a new temporal plots were explored. In total, 280 m² area was searched for hypogeous fungi. Collected specimens were examined microscopically and identified in the laboratory according various literature sources.

The species diversity and distribution of hypogeous fungi was also studied during 2007 in different type and age tree stands in Žemaitija NP (plots Ž6–Ž10), Dzūkija NP (D1–D5), Kamasta LR (K1–K5) (permanent rectangular study plots 1000 m² in size), and in Curonian Spit NP (N1–N15) (plots 500 m² in size). In May and September–October the plots Ž6–Ž10, D1–D5, K1–K5 were visited 2 times (search time

was 100–120 person minutes per each visit), and the plots N1–N15 – 3 times (30–45 person minutes).

Additional material of hypogeous fungi, which was occasionally collected during 2005–2007 in other places of Lithuania, was also included in this study. 72 specimens of hypogeous fungi in fungal reference collections of the Institute of Botany (BILAS) and Vilnius University (WI) have been located and re-examined. Available literature data on hypogeous fungi recorded in Lithuania was analysed.

We used fecal pellet analysis, which allows examination of an animal's recent meals, to examine diets of mycophagous animals. During 2005 (September–November) and 2006–2007 (in spring (March–May), summer (June–July) and autumn (September–October)) the small mammals were captured in live traps in study plots Ž1–Ž5. Total number of trap nights was 100. Fresh fecal pellets were collected from traps and placed in a vials of 1 ml 10 % formalin. For laboratory analysis of each individual collection, the pellets were macerated, 2 droplets of the resulting solution and a drop of Melzer's reagent were placed on each of 3 glass slides and covered by cover slips. For each cover slips 25 systematically selected fields of view were examined at 400× magnification, resulting in total of 75 fields per fecal sample. Fungal spores were counted and identified. The spores of hypogeous fungi were identified according CASTELLANO et al. (1989).

In total, 144 specimens of hypogeous fungi and 131 samples of small mammal excrements were collected. This material is deposited in the Herbarium of Vilnius University (WI).

An annotated checklist of hypogeous fungi of Lithuania was compiled. For each fungus the information is given in the following order: scientific name, it's synonym, data on distribution, ecology, examined fungal specimens, literature, and notes. New taxa for Lithuania were described in detail.

Statistical data analysis was completed with SPSS version 12.0 (Statistical Package for Social Sciences) (SPSS INC., 2003), PAST (Palaeontological Statistics) (HAMMER, HARPER, 2008) and Biodiversity Pro version 2.0 (MC ALEECE, 1997) software packages. Jack-knife 1 estimate and the Shannon diversity index (H') was used for evaluation of fungal diversity (COLWELL, CODDINGTON, 1994). The Kruskal-Wallis (H) and the Pearson Chi-squared (χ^2) non-parametrical tests were performed for comparison of different variables (ČEKANA VIČIUS, MURAU SKAS, 2004). The Spearman correlation coefficient (r_s) was calculated to find the correlation between different variables. The Sørensen index was used to compare similarity of fungi and plant species compositions. Comparison of the fungi composition and abundance in plots and in small mammal fecal pellets were carried out using Bray-Curtis cluster analysis (ZAK, WILLIG, 2004). The canonical correspondence analysis (CCA) was used in analysis of impact of environmental factors on fungal species distribution.

RESULTS AND DISCUSSION

Diversity and distribution of hypogeous fungi in Lithuania

Species diversity. In total, 29 species from 16 genera, 12 families, 7 orders and 3 phyla (*Ascomycota*, *Basidiomycota* and *Glomeromycota*) have been recorded in Lithuania (Table 1; Fig. 1–2). 8 species were recorded for the first time in Lithuania. *Chamonixia caespitosa* was identified only from the spore material in the fecal pellets of small mammals, the fruit-bodies of this species are not found yet in Lithuania. Hypogeous taxa from the genus *Genea* were identified also only from the spores observed in fecal pellets. The specimens of 8 species are no longer extant, and these taxa are currently known only from the literature.

The analysis of species diversity in adjacent countries indicates that the species diversity of hypogeous fungi in Lithuania could be greater, presumably up to 70–90 species.

Geographical distribution, frequency. The knowledge about the distribution of species of hypogeous fungi in Lithuania is different and strongly depends on the research intensity and the number of collected samples. Majority of species were recorded in north-western (15 species) and western (16) parts of Lithuania. There is little data about these fungi from northern part of the country (known only 2 species). Few species, e.g. *Elaphomyces asperulus*, *E. granulatus*, *E. muricatus* and *Geopora arenicola*, are widespread in the country. *Choiromyces meandriformis* was recorded in different regions of Lithuania, however, the current distribution of this species is unknown – the last time it was observed 20 years ago. Two recently discovered species in Lithuania, *Cenococcum geophilum* and *Tuber puberulum*, were often recorded during our studies in different regions – that suggest a wide distribution of these species. The distribution pattern of *Peziza ammophila* is limited to sand dunes of the Baltic seashore.

The number of known localities of hypogeous species is different. Most frequent species are *Elaphomyces asperulus* (41 locality), *E. granulatus* (31), *E. muricatus* (18), *Rhizopogon luteolus* (20), *Cenococcum geophilum* (18) and *Geopora arenicola* (16) (Table 1). 11 species (37.9 %) are known only from the single locality.

Three rare and endangered species of hypogeous fungi (*Choiromyces meandriformis*, *Hydnotrya tulasnei* and *Peziza ammophila*) are included in the list of species of Lithuanian Red Data Book (KUTORGA, 2007)

Table 1. Taxa of hypogeous fungi found in Lithuania. ° – known only from the literature; * – recorded for the first time in Lithuania; number of localities presented in brackets

Hypogeous fungi known in Lithuania from fruit-bodies	Hypogeous fungi known in Lithuania from fecal pellets of small mammals
1	2
GLOMEROMYCOTA	
ENDOGENALES	
Endogonaceae	
* <i>Endogone lactiflua</i> Berk. & Broome (5)	<i>Endogone</i> sp. 1 (6) <i>Endogone</i> sp. 2 (4)
GLOMERALES	
Glomeraceae	
* <i>Glomus macrocarpum</i> Tul. & C. Tul. (1)	<i>Glomus</i> spp.1 (4)
* <i>Glomus</i> aff. <i>macrocarpum</i> Tul. & C. Tul. (1)	* <i>Glomus</i> spp.2 (3)

Table 1 (continued)

1	2
	* <i>Glomus</i> spp.3 (5)
	ASCOMYCOTA
	EUROTIALES
	<i>Elaphomycetaceae</i>
* <i>Elaphomyces anthracinus</i> Vittad. (1)	<i>Elaphomyces</i> spp. (7)
<i>Elaphomyces asperulus</i> Vittad. (41)	
<i>Elaphomyces granulatus</i> Fr. (34)	
<i>Elaphomyces muricatus</i> Fr. (18)	
	PEZIZALES
	<i>Discinaceae</i>
<i>Hydnotrya tulasnei</i> (Berk.) Berk. & Broome (1)	<i>Hydnotrya</i> sp. (3)
	<i>Pezizaceae</i>
* <i>Pachyphloeus conglomeratus</i> Berk. & Broome (1)	<i>Pachyphloeus</i> spp. (7)
<i>Peziza ammophila</i> Durieu & Mont. (5)	
	<i>Pyrenomataceae</i>
<i>Geopora arenicola</i> (Lév.) Kers (16)	
	* <i>Genea</i> sp. 1 (4)
	* <i>Genea</i> spp. (7)
	<i>Tuberaceae</i>
<i>Choiromyces meandriformis</i> Vittad. (8)	
<i>Tuber borchii</i> Vittad. (2)	<i>Tuber</i> sp. 1 (2)
° <i>Tuber exiguum</i> R. Hesse (1)	<i>Tuber</i> spp. (5)
* <i>Tuber puberulum</i> Berk. & Broome (11)	
° <i>Tuber rufum</i> Pico: Fr. f. <i>nitidum</i> (Vittad.) Montecchi & Lazzari (1)	
DOTHIDIOMYCETES	
	<i>Incertae sedis</i>
<i>Cenococcum geophilum</i> Fr. (22)	
BASIDIOMYCOTA	
	AGARICALES
	<i>Cortinariaceae</i>
° <i>Hymenogaster arenarius</i> Tul. & C. Tul. (2)	<i>Hymenogaster</i> spp. 1 (3)
° <i>Hymenogaster citrinus</i> Vittad. (1)	<i>Hymenogaster</i> spp. 2 (4)
* <i>Hymenogaster olivaceus</i> Vittad. (2)	
* <i>Hymenogaster rehsteineri</i> Bucholtz (1)	
° <i>Hymenogaster niveus</i> Vittad. (1)	
	BOLETALES
	<i>Boletaceae</i>
	* <i>Chamonixia caespitosa</i> Rolland (4)
	<i>Paxillaceae</i>
<i>Melanogaster ambiguus</i> (Vittad.) Tul. & C. Tul. (2)	
° <i>Melanogaster variegatus</i> (Vittad.) Tul. & C. Tul. (2)	
	<i>Rhizopogonaceae</i>
° <i>Rhizopogon angustisepta</i> Zeller & C. W. Dodge (1)	
<i>Rhizopogon luteolus</i> Fr. & Nordholm (21)	
<i>Rhizopogon roseolus</i> (Corda) Th. Fr. (9)	
<i>Rhizopogon vulgaris</i> (Vittad.) M. Lange (6)	
	RUSSULALES
	<i>Albatrellaceae</i>
° <i>Leucogaster nudus</i> (Hazsl.) Hollós (1)	

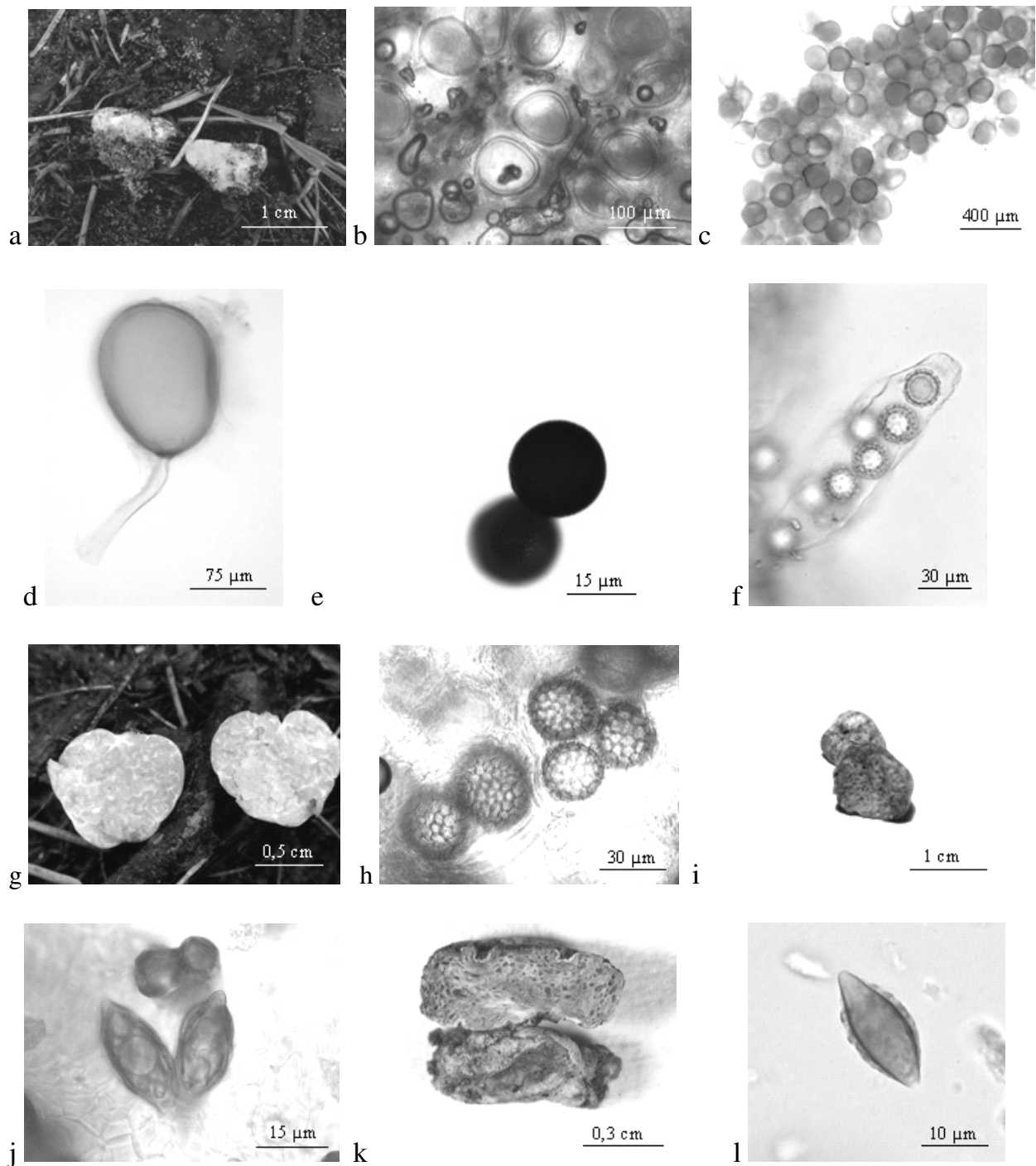


Fig. 1. Hypogeous fungi new for Lithuania: a, b – *Endogone lactiflua*: fruit-body (a), zygospores in gleba (b); c, d – *Glomus macrocarpum*: chlamydospores (c), chlamydospore (d); e – *Elaphomyces anthracinus*: ascospores; f – *Pachyphloeus conglomeratus*: ascus with ascospores (f); g, h – *Tuber puberulum*: cross-section of fruit-body (g), asci with ascospores (h); i, j – *Hymenogaster olivaceus*: cross-section of fruit-body (i), basidiospores (j); k, l – *Hymenogaster rehsteineri*: cross-section of fruit-body (k), basidiospores (l)

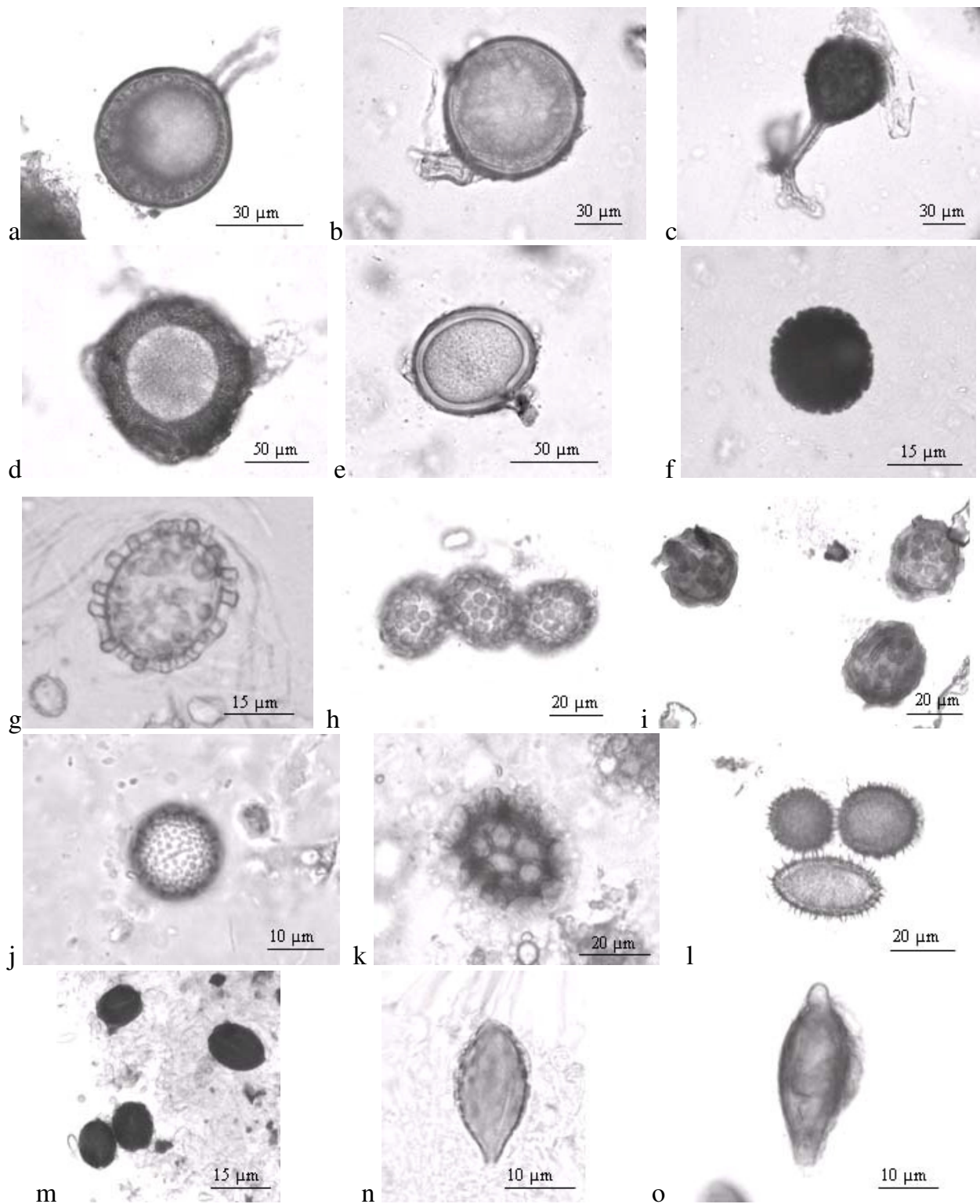


Fig 2. The spores of hypogeous fungi in small mammal fecal pellets: a – *Glomus* spp. 1 chlamydospore; b – *Glomus* spp. 2 chlamydospore; c – *Glomus* spp. 3 chlamydospore; d – *Endogone* sp. 1 zygospore; e – *Endogone* sp. 2 zygospore; f – *Elaphomyces* spp. ascospore; g – *Genea* sp. 1 ascospore; h – *Genea* spp. ascospores; i – *Hydnotrya* sp. ascospores; j – *Pachyphloeus* spp. ascospore; k – *Tuber* spp. ascospore; l – *Tuber* sp. 1 ascospores; m – *Chamonixia caespitosa* basidiospores; n – *Hymenogaster* spp. 1 basidiospore; o – *Hymenogaster* spp. 2 basidiospore

Symbiotic partners. The distribution patterns of most hypogeous fungi depend on the presence of their symbiotic partners. Exact determination of symbiotic partners is complicated in some cases, because fruit-bodies could grow in-between the roots of several neighbouring trees and shrubs of different species. The results of the research conducted during 2007 in study plots (Ž6–Ž10, K1–K5, D1–D5, N1–N15) showed that the hypogeous fungi are associated with different tree species (Fig. 3). 12 fungal species were associated with 7 plant species, which belong to *Pinus*, *Picea*, *Corylus*, *Tilia* and *Quercus* genera. *Tuber puberulum* was recorded under both deciduous and coniferous trees and shrubs (in total 6 species), but in most cases (38 %) this species was in symbiotic association with *Pinus sylvestris* trees. *Cenococcum geophilum* sclerotia and *Elaphomyces asperulus* fruit-bodies were gathered under the trees of 3 plant species, the largest part of the samples (respectively 58 % and 55 %) was also collected near *Pinus sylvestris* trees. The rest of recorded fungi grew under trees belonging to one or two plant species. The fungi from the genus *Rhizopogon* were recorded only under *Pinus* trees. The largest number of hypogeous species belongs to *Pinus sylvestris* (8 species) and *Betula pendula* (7).

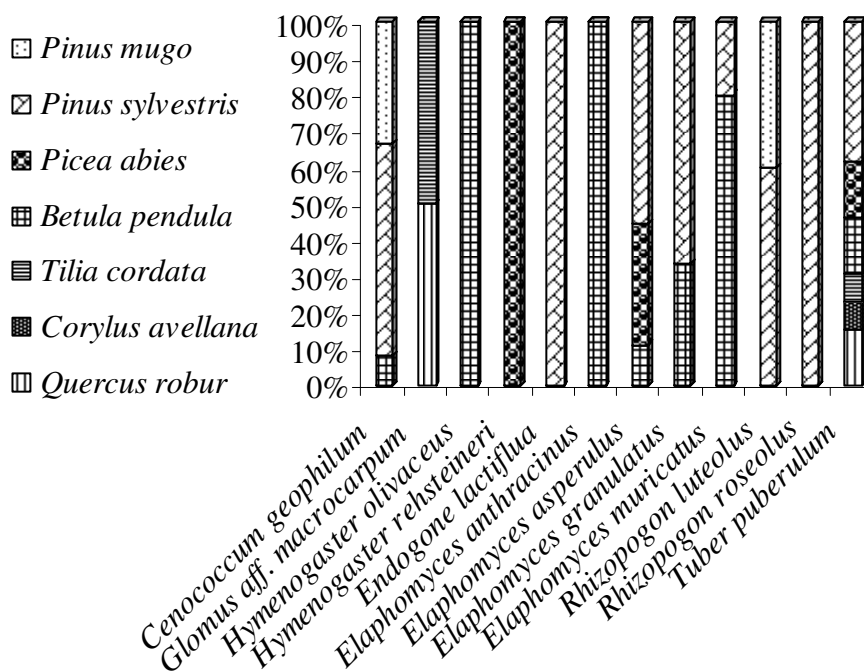


Fig. 3. Proportions of symbiotic plant species according hypogeous fungal species

The analysis of the available whole material on Lithuanian hypogeous fungi has demonstrated that most species are ectomycorrhizal. *Endogone lactiflua* and fungi from the genus *Glomus* could be either endomycorrhizal or ectomycorrhizal (GERDEMANN, TRAPPE, 1974; BŁASZKOWSKI, 2003). Only two semi-hypogeous fungal species, namely *Geopora arenicola* and *Peziza ammophila*, are the soil saprotrophs.

In total, recorded hypogeous fungi in Lithuania have associations with 9 tree species (Table 2). The majority of fungi were found under *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Quercus robur* trees. The greatest numbers of specimens were gathered under *Picea abies* (77 specimens) and *Pinus sylvestris* (69) trees. *Tuber puberulum* fruit-bodies and *Cenococcum geophilum* sclerotia were found in the adjacency of 6 species of coniferous and deciduous trees. *Rhizopogon luteolus* and *R.*

roseolus species recorded exceptionally under *Pinus* trees. Although the fruit-bodies of *Chamonixia caespitosa* were not found in Lithuania, the spores of this fungus were observed in small mammal fecal pellets collected in *Picea abies* and mixed (*Quercus robur*, *Picea abies*, *Betula pendula*) tree stands. As suggested by LANGE, HAWKER (1951) and MONTECCHI, SARASINI (2000), this species is associated with coniferous trees, e.g. *Picea* and *Abies*.

Table 2. The numbers of fungal specimens collected under the different tree species. The data presented for two or more times recorded fungal species

Taxa	<i>Cenococcum geophilum</i>	<i>Choitomyces meandriformis</i>	<i>Elaphomyces asperulus</i>	<i>Elaphomyces granulatus</i>	<i>Elaphomyces muricatus</i>	<i>Endogone lactiflua</i>	<i>Glomus macrocarpum</i> <i>Glomus</i> aff. <i>macrocarpum</i>	<i>Hymenogaster olivaceus</i>	<i>Pachyphloeus conglomeratus</i>	<i>Rhizopogon luteolus</i>	<i>Rhizopogon roseolus</i>	<i>Rhizopogon vulgaris</i>	<i>Tuber puberulum</i>	Total of fungal species
<i>Alnus</i> spp.		1												1
<i>Betula pendula</i>	2	1	1	2	4			1					2	7
<i>Corylus avellana</i>	1												1	2
<i>Picea abies</i>	13		21	40	4	4		1	1				4	8
<i>Pinus mugo</i>	4									1				2
<i>Pinus sylvestris</i>	7		16	3	1	2		1		20	6	3	10	10
<i>Quercus robur</i>	1	1		3			2		1				6	6
<i>Salix</i> spp.		1												1
<i>Tilia cordata</i>					1								1	2
Total of tree species	6	4	3	4	4	2	1	3	2	2	1	1	6	

Species distribution in different type and age tree stands. In total, 57 specimens of 12 species have been collected during the research conducted in 2007 in study plots (Ž6–Ž10, K1–K5, D1–D5, N1–N15), which were established in different type and age tree stands. *Cenococcum geophilum* and *Tuber puberulum* were the most frequently observed fungi. On the contrary, *Glomus macrocarpum*, *Hymenogaster olivaceus*, *H. rehsteineri* and *Elaphomyces anthracinus* were collected only once. In average 2 specimens per plot (s.d. = ± 1,97) and 1 fungal species per plot (s.d. = ± 1,17) was determined.

Hypogeous fungi were recorded in stands of different maturity (age) – in young, middle-aged, premature and mature stands (Table 3). 6 species observed in young stands, most frequently *Cenococcum geophilum* and *Tuber puberulum*. 4 species recorded in middle-aged stands, most frequently *Elaphomyces muricatus*. In premature stand 5 species were found. The greatest number of species (8) determined in mature stands, *Cenococcum geophilum* and *Tuber puberulum* were the most frequent in them. *Elaphomyces asperulus* inhabited the stands of all maturity groups. According the Jack-knife 1 estimate, the greatest number of species presumable could be in young and mature stands (respectively 9 and 14 species), less – in premature and middle-aged stands (respectively 7 and 8 species). The quantity of hypogeous fungal species not

depended on the stand maturity group (Kruskal-Wallis $H = 4.04$; d.f. = 3; $p = 0.257$; Spearman's $r_s = -0.069$, $p = 0.759$).

From 1 to 4 hypogeous species were found in different type tree stands. The biggest species diversity and average of species numbers (about 2 species) were determined in *Pinus sylvestris*, mixed and coniferous tree stands (Table 3). According the Jack-knife 1 estimate, the greatest number of species presumable could be in mixed and *Pinus sylvestris* tree stands (9 species in both), 7 – in *Quercus robur* and coniferous tree stands, 3 – in *Pinus mugo*, and 1 – in *Picea abies* and *Betula pendula* tree stands. The stand type did not affected significantly the number of recorded hypogeous species (Kruskal-Wallis $H = 8.304$; d.f. = 7; $p = 0.307$). We noticed that singly growing trees could enrich the species diversity of hypogeous fungi in stands dominated by other tree species. For example, two fungal species, namely *Hymenogaster olivaceus* and *Elaphomyces anthracinus*, were recorded in *Populus tremula* dominated stand, however, both of them were found under *Betula pendula* trees.

Table 3. The numbers of fungal specimens collected in different tree stands

	Study plots	<i>Cenococcum geophilum</i>	<i>Elaphomyces anthracinus</i>	<i>Elaphomyces asperulus</i>	<i>Elaphomyces granulatus</i>	<i>Elaphomyces muricatus</i>	<i>Endogone lactiflua</i>	<i>Glomus</i> aff. <i>macrocarpum</i>	<i>Hymenogaster olivaceus</i>	<i>Hymenogaster rehsteineri</i>	<i>Rhizopogon luteolus</i>	<i>Rhizopogon roseolus</i>	<i>Tuber puberulum</i>	Total of fungal species
Numbers of plots with fungal records		14	1	4	2	5	2	1	1	1	3	2	7	
Stand types														
<i>Quercus robur</i> stands	Ž6, K3							1					3	2
<i>Populus tremula</i> stand	Ž7		1						1					2
Coniferous stands	Ž9, Ž10	1		2	2						1		1	5
Mixed stands	Ž8, K1, K5	1		2	1	1				1			2	6
<i>Picea abies</i> stands	K2, D1					3								1
<i>Betula pendula</i> stands	D2, K4			1										1
<i>Pinus sylvestris</i> stands	D3–D5, N5, N7, N9, N11, N12	5		3		2	2				2	1	5	7
<i>Pinus mugo</i> stands	N1–N4, N6, N8, N10, N13 –N15	8									2			2
Stand maturity groups														
Young stands	Ž8, Ž9, K5	2		2		1				1		1	3	6
Middle-aged stands	Ž6, K2, K4, D1, D2, D4			1		4		1					3	4
Premature stands	Ž10, D3	1		1	1	1					1			5
Mature stands	Ž7, K1, K3, N6, N7, N9, N11–N13, N15	8	1	3	1		2				3	1	4	8

The analysis of the available whole material on the habitats of Lithuanian hypogeous fungi showed that most species (13) were recorded in mixed (deciduous-coniferous) forests (Fig. 4). In such type of habitat the variety of symbiotic partners of hypogeous fungi is usually high. In addition, the mixed forests maintain abundant populations of small mammals (BALČIAUSKAS, JUŠKAITIS, 1997; ULEVIČIUS et al., 2002), which are important for distribution of fungal spores. Although the greatest number of collected specimens was in *Pinus sylvestris* (52 specimens) and *Picea abies* (43) stands, the total number of species (10 in both) was smaller than in mixed forests. Some hypogeous species prefer another type of habitats. *Geopora arenicola* inhabits usually sandy and disturbed grounds, occasionally the bonfire places. *Peziza ammophila* grows in open sand dunes in-between *Ammophila arenaria* and *Festuca arenaria*.

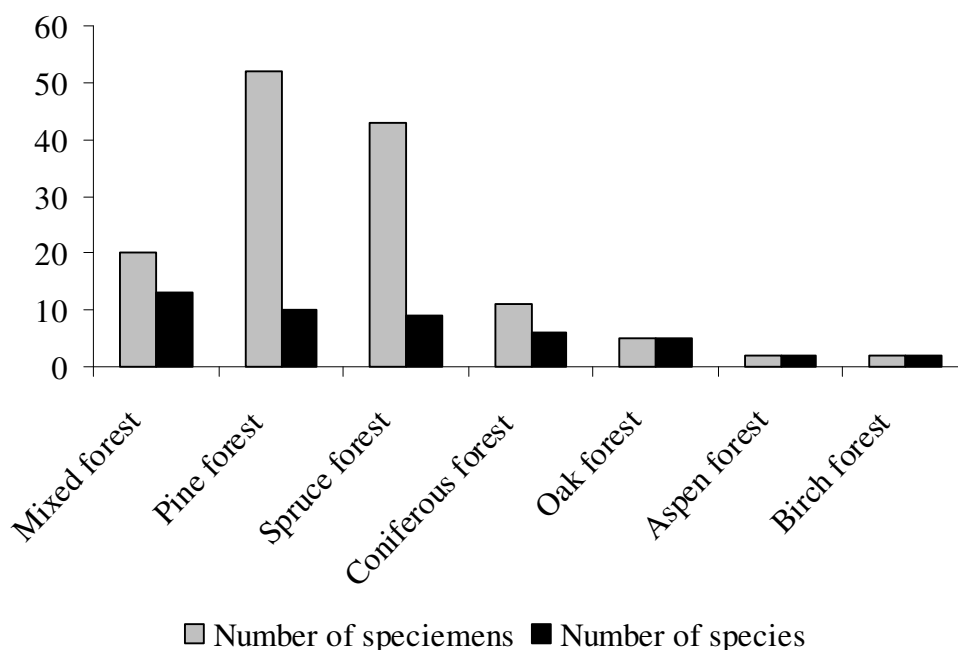


Fig. 4. The numbers of specimens and species of hypogeous fungi in different tree stands

Fructification phenology. The research conducted in 2007 in study plots (Ž6–Ž10, K1–K5, D1–D5, N1–N15) has revealed a seasonal difference in formation of fruit-bodies of hypogeous fungi. 13 specimens of 6 species collected in spring (May), 44 specimens of 11 species – in autumn (September–October).

The summation of all data concerning the fructification phenology of Lithuanian hypogeous fungi showed that fungi produce fruit-bodies from April to December. Most fungal specimens were collected in September (68 specimens, 12 species) and October (82, 17). Individual fungal species demonstrated different patterns of fructification phenology. Species of the genus *Elaphomyces* and *Geopora arenicola* formed the fruit-bodies from the spring till late autumn. Most fungi, e.g. *Choiromyces meandriformis*, *Tuber puberulum*, *Hymenogaster olivaceus*, *Rhizopogon luteolus* and *R. roseolus*, fruited during summer and autumn. *Peziza ammophila* formed an apothecia only in the autumn.

Structure and dynamics of communities of mycorrhizal hypogeous and epigeous fungi in different tree stands

Species composition. Overall, 7 species of hypogeous fungi and 79 species of epigeous macromycetes were collected in five study plots (Ž1–Ž5). On average 4 species of hypogeous fungi and 30 species of epigeous fungi were recorded in one study plot. Hypogeous fungi were observed in 26 (37 %) temporal plots.

On average 5 species of epigeous fungi were recorded in August, 15 – in September, and 10 – in October. Variation of number of species in different months was statistically significant (Kruskal-Wallis $H = 24$; d.f. = 2; $p = 0$). On average about one species of hypogeous was recorded in September, and one – in October (Kruskal-Wallis $H = 7.6$; d.f. = 4; $p = 0.105$).

The greatest number of species of hypogeous fungi (6 species) recorded in mixed stand (Ž5), in other tree stands the number ranged from 2 to 3 species (Fig. 6a). The greatest number of epigeous mycorrhizal species was in *Picea abies* (Ž1) and mixed (Ž5) stands (respectively 35 and 34 species). The least number of species (22) was in oak stand (Ž4). In general, the species diversity of mycorrhizal fungi was higher in *Picea abies* stands and in mixed stand than in *Quercus robur* stand. Similar results obtained other researchers: more species of fungi were found in coniferous than in deciduous tree stands (BIERI et al., 1992). Only two fungal species, *Elaphomyces granulatus* and *Russula ochroleuca*, were present in all study plots.

A comparison of the compositions of fungal species in the different plots using Sørensen's index showed that most similar species compositions were in the two *Picea abies* tree stands (Ž1, Ž2), in which the forest floor was partially disturbed by wild boars (Fig. 5a). The compositions of plant species in these plots were most similar as well (Fig. 5b). The compositions of fungi and plant species in *Quercus robur* stand (Ž4) were most similar to species compositions in mixed tree stand (Ž5), and were rather different in comparison with the species compositions defined in all *Picea abies* stands (Ž1, Ž2, Ž3). Other mycologists also noted that the similarity of fungal species compositions depends on the similarity of plant species compositions, as well as on similar climatic conditions and other factors (BIERI ET AL., 1992; LAGANÁ ET AL., 2002b).

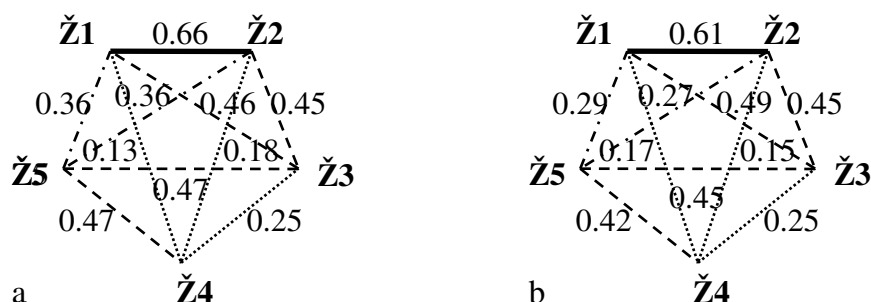


Fig. 5. The similarity of fungal (a) and plant (b) species compositions in different study plots (according Sørensen's index)

Abundance of fruit-bodies. In total, 123 hypogeous and 3784 epigeous fruit-bodies were counted in the study plots (Ž1–Ž5). Calculations showed that on a per hectare basis there were 4393 fruit-bodies of hypogeous fungi and 7568 fruit-bodies of epigeous fungi. *Cenococcum geophilum* was recorded 15 times (sclerotia were not

counted). The fruit-bodies of 20 species (24 %) were found only once in one study plot. *Elaphomyces granulatus* produced the majority of fruit-bodies of hypogeous species (77 fruit-bodies), and *Paxillus involutus* produced the majority of fruit-bodies of epigeous fungi (510). The largest amount of hypogeous fruit-bodies (47) was collected in *Picea abies* stand (Ž3), the least amount (5) – in *Quercus robur* stand (Ž4). The largest amount of epigeous fruit-bodies was calculated in *Picea abies* (Ž2) and mixed tree (Ž5) stands, the least amount – in *Quercus robur* stand (Ž4).

According to Shannon's diversity index values, the species diversity of fruit-bodies in different study plots was similar (Fig. 6b). The highest diversity of hypogeous fungi was in mixed stand ($H' = 1.2$), the lowest ($H' = 0.5$) – in *Quercus robur* stand (Ž4) (Fig. 6b).

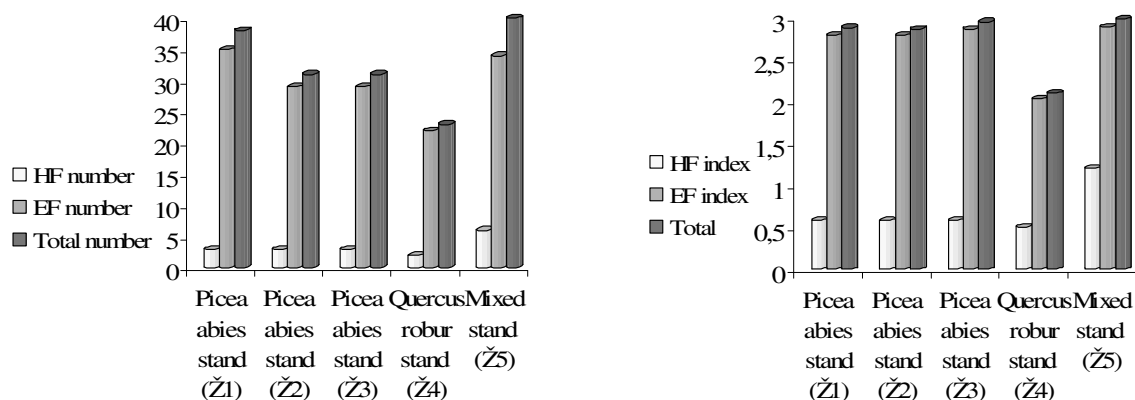


Fig. 6. The numbers of hypogeous (HF) and epigeous (EF) fungal species (a) and the Shannon's diversity index values (b) in different tree stands (plots Ž1–Ž5)

The mycobiotas (species and the amount of their fruit-bodies) of two *Picea abies* tree stands (Ž1 and Ž2) were most similar (BI = 60.8 %), and the mycobiota of *Quercus robur* stand (Ž4) was most distant (Fig. 7)

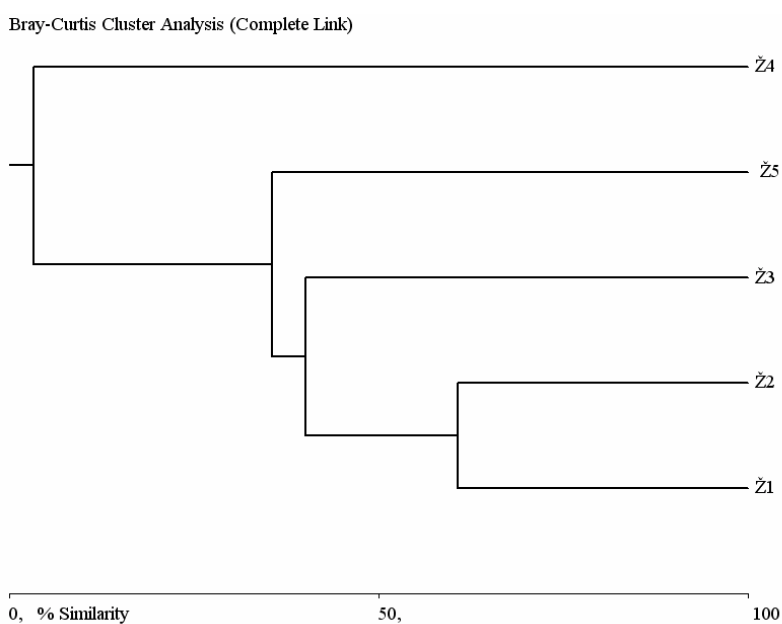


Fig. 7. Dendrogram of tree stand similarity according the mycobiotas

Dominant genera and species. Those genera or species, which produced more than 10 % of the total amount of the fruit-bodies in the plot, were treated in this study as dominant. *Boletus*, *Cortinarius* and *Lactarius* were the dominant genera in all three plots established in *Picea abies* stands, *Russula* was the predominant genus in *Quercus robur* stand, and *Lactarius*, *Paxillus* and *Russula* dominated in mixed stand (Table 4). From 3 to 4 epigeous fungal species and from 0 to 3 hypogeous fungal species were dominant in different tree stands. Epigeous *Paxillus involutus* and hypogeous *Elaphomyces granulatus* were predominant species in study plots (Ž1–Ž3) established in *Picea abies* forests and mixed stand (Ž5). Hypogeous species *Endogone lactiflua* formed abundant fruit-bodies in *Picea abies* stands (Ž2–Ž3), and *Tuber puberulum* – in *Picea abies* (Ž1) and mixed (Ž5) stands.

Table 4. Dominant genera and species of the fungi in study plots Ž1–Ž5

Study plots		Ž1	Ž2	Ž3	Ž4	Ž5
Genera	<i>Amanita</i>			+		
	<i>Boletus</i>	+	+	+		
	<i>Cortinarius</i>	+	+	+		
	<i>Lactarius</i>	+	+	+		+
	<i>Paxillus</i>	+	+			+
	<i>Russula</i>	+	+		+	+
Epigeous fungi species	<i>Boletus badius</i>	+	+	+		
	<i>Lactarius mitissimus</i>			+		
	<i>Lactarius necator</i>					+
	<i>Lactarius theiogalus</i>	+				
	<i>Paxillus involutus</i>	+	+	+		+
	<i>Russula delica</i>				+	
	<i>Russula illota</i>				+	
	<i>Russula nigricans</i>				+	+
	<i>Russula ochroleuca</i>		+			+
Hypogeous fungi species	<i>Elaphomyces granulatus</i>	+	+	+		+
	<i>Elaphomyces muricatus</i>					+
	<i>Endogone lactiflua</i>		+	+		
	<i>Tuber puberulum</i>	+				+

Influence of environmental factors. The number of calculated fruit-bodies of epigeous fungi in different months significantly varied (Kruskal-Wallis $H = 22.6$; d.f. = 2, $p = 0$). After on average big precipitation (167.1 mm) and high average temperature (17.3 °C) in August the fungi formed abundant fruit-bodies (on average 154 fruit-bodies) in September. Greater number of fruit-bodies was counted in the beginning of September than in the middle or the end of this month. After less rainfall (73 mm) and a decrease of average air temperature (13.0 °C) in September the fungi formed on average less fruit-bodies (73) in October. An average number of hypogeous fruit-bodies did not varied significantly during different months (Kruskal-Wallis $H = 12$; d.f. = 4; $p = 0.17$), more fruit-bodies were formed in September and October (on average 3 fruit-bodies).

The variables of soil chemical composition did not correlated significantly with the numbers of hypogeous and epigeous fruit-bodies. The greatest number of fruit-bodies (869) was recorded in the least acidic soil (pH = 3.73) of mixed stand (Ž5).

Results of the canonical correspondence analysis showed in the ordination (Fig. 8). Ordination axes 1 and 2 explained to 74.5 % of the variation of fungal species

distribution. Longer lines indicate a stronger relationship with the ordinate axes than the shorter lines. The numbers of plant and tree species positively correlated with the ordinate axis 1, the soil characteristics, such as P_2O_5 and humus, – with the ordination axis 2. The ordinate axis 1 explained to 43.8 % of the variation of fungal species distribution.

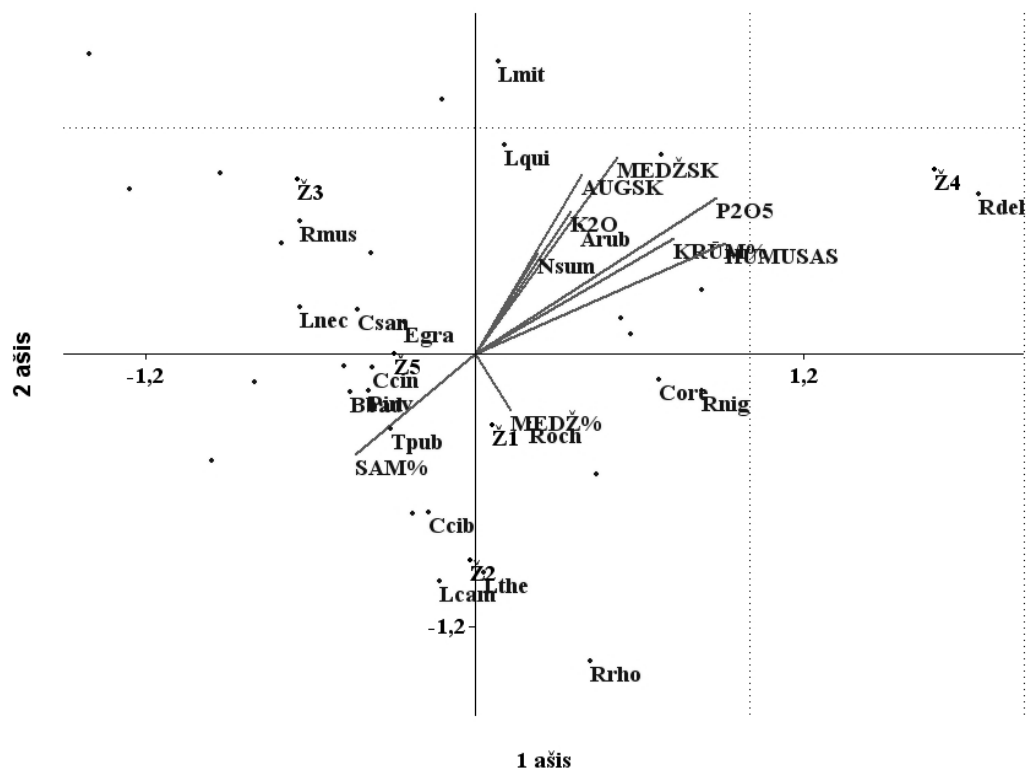


Fig. 8. CCA ordination of environmental factors (lines), study plots and fungal species (dots). Eigenvalues: 1 axis – 0.6157, 2 axis – 0.4311. Environmental factors: AUGSK – plant species number; HUMUSAS – soil humus, %; K_2O – soil mobile K_2O , mg/kg; KRŪM% – shrub coverage, %; MEDŽ% – tree canopy coverage, %; MEDŽSK – tree species number; N_{sum} , % – cumulative soil N amount, %; P_2O_5 – soil mobile P_2O_5 , mg/kg; SAM% – moss coverage, %. Abbreviations are given for species, which fruit-bodies made ≥ 1 % of total fruit-body number (Arub – *Amanita rubescens*; Bbad – *Boletus badius*; Ccib – *Cantharellus cibarius*; Ccin – *Cortinarius cinnamomeus*; Core – *Cortinarius orellanus*; Csan – *Cortinarius sanguineus*; Egra – *Elaphomyces granulatus*; Lame – *Laccaria amethystina*; Lnec – *Lactarius necator*; Lmit – *Lactarius mitissimus*; Lqui – *Lactarius quietus*; Lruf – *Lactarius rufus*; Lthe – *Lactarius theiogalus*; Lcam – *Lactarius camphoratus*; Pinv – *Paxillus involutus*; Rdel – *Russula delica*; Rnig – *Russula nigricans*; Roch – *Russula ochroleuca*; Rgra – *Russula grata*; Rmus – *Russula mustelina*; Rrho – *Russula rhodopoda*; Tpub – *Tuber puberulum*)

Fructification in wild boar rooted sites. In total, 13 epigeous and 2 hypogeous species formed fruit-bodies during 2005–2007 in six subplots Ž1p1–3 and Ž2p1–3, in which the forest floor was rooted by *Sus scrofa* animals (Table 5). All these species were also recorded in not disturbed places of the study plots Ž1 and Ž2. Most abundant in disturbed places were two epigeous species – *Paxillus involutus* and *Boletus badius*. The number of fruit-bodies of both these species was greater in disturbed subplots than in undisturbed areas of plots. *Tylopilus felleus* formed major part of the fruit-bodies in

disturbed places in study plot Ž1. Nearly half (46.9 %) of all fruit-bodies produced of hypogeous fungus *Elaphomyces granulatus* in study plots Ž1 and Ž2 were counted in subplots Ž1p1–3 and Ž2p1–3. Another hypogeous fungus *Endogone lactiflua* formed more fruit-bodies in disturbed places (75 %) than in undisturbed places of study plot Ž2.

Table 5. The numbers of fruit-bodies in subplots (Ž1p1–3, Ž2p1–3) and the percentage from all collected fruit-bodies in the study plots (Ž1, Ž2)

Epigeous species	Numbers of fruit-bodies			Percentage, %		
	Ž1p1-3	Ž2p1-3	Total	Ž1	Ž2	Total
<i>Paxillus involutus</i>	179	64	243	88.6	56.6	77.1
<i>Boletus badius</i>	67	37	104	57.8	45.1	52.2
<i>Russula ochroleuca</i>	10	26	36	18.5	24.1	22.2
<i>Cantharellus cibarius</i>		18	18	0	32.7	27.7
<i>Cortinarius cinnamomeus</i>	6	10	16	25	12.7	15.5
<i>Cortinarius flexipes</i>	7	4	11	41.2	28.6	35.5
<i>Lactarius rufus</i>		7	7	-	14	14
<i>Cortinarius camphoratus</i>		6	6	0	24	24
<i>Lactarius theiogalus</i>		8	8	0	17	6.5
<i>Tylopilus felleus</i>		5	5	0	83.3	38.5
<i>Cortinarius sanguineus</i>	3		3	10.3	0	4
<i>Cortinarius multififormis</i>		2	2	-	22.2	22.2
<i>Boletus edulis</i>	1		1	25	0	0.17
Hypogeous species						
<i>Elaphomyces granulatus</i>	8	7	15	72.7	33.3	46.9
<i>Endogone lactiflua</i>		3	3	-	75	75

These observations suggest the possible positive influence of wild boar rooting for formation of fruit-bodies of some fungal species, such as *Boletus badius*, *Paxillus involutus*, *Tylopilus felleus*, *Elaphomyces granulatus* and *Endogone lactiflua*. Rooting activity of wild boars favours the development of *Elaphomyces*, because stripping off the layers of mosses and humus improves the mineral soil moisture conditions for the mycelium (ŁAWRYNOWICZ et al., 2006).

Fungal composition in small mammal diet

Overall, 58 individuals of *Apodemus* spp., 67 – *Myodes glareolus*, 4 – *Sorex araneus* and 2 – *S. minutus* were captured in the study plots Ž1–Ž5. Mycological investigation of small mammal fresh fecal pellets showed that rodents (*Apodemus*, *Myodes*) and some insectivorous animals (*Sorex*) consume hypogeous and epigeous fungi.

Fungal diversity in fecal pellets. In total, 22 taxa of fungi belonging to *Ascomycota*, *Basidiomycota* and *Glomeromycota* were identified in 131 small mammal fecal samples (Table 6). 15 taxa from 9 genera represent hypogeous fungi.

Mycorrhizal fungi (hypogeous taxa, *Russulales*, *Boletales*) were recorded in 98 (74.8 %) fecal samples. The spores of presumably not mycorrhizal fungi were observed in 42 (32.1 %) fecal samples. This suggests that mycorrhizal fungi, especially ectomycorrhizal, are important part of small mammal diet. The spores of hypogeous and epigeous fungi were observed in examined fecal samples, respectively in 109 (83.2 %) and 78 (59.5 %) samples. This indicates that hypogeous fungi could be preferred food of

small mammals. The spores of hypogeous fungi predominate in the excrements or stomach contents of various animals (BLASCHKE, BÄUMLER, 1989; BERTOLINO et al., 2004; WHEATLEY, 2007; MASER et al., 1978).

The spores of hypogeous *Elaphomyces* spp. and *Endogone* sp. 1 fungi prevailed in fecal samples (Table 6). Fruit-bodies of *Elaphomyces* are important food for small mammals, although their indigestible spores and relatively indigestible cell wall of the peridium have low nutritional value (CORK, KENAGY, 1989).

Table 6. Fungal taxa in small mammal fecal pellets collected in study plots (Ž1–Ž5), frequency and relative frequency (frequency/ Σ frequency); ^h – hypogeous fungi

Taxa	Ž1	Ž2	Ž3	Ž4	Ž5	Frequency (%)	Relative frequency (%)
Non-specific fungal mycelia	+	+	+	+	+	71	23,5
<i>Elaphomyces</i> spp. ^h	+	+	+	+	+	37,4	12,4
<i>Endogone</i> sp. 1 ^h	+	+	+	+	+	22,9	7,6
<i>Ascomycota</i> spp. (anamorphs)	+	+	+	+	+	18,3	6,1
<i>Boletales</i> spp.	+	+	+	+	+	17,6	5,8
<i>Pachyphloeus</i> spp. ^h	+	+	+	+	+	17,6	5,8
<i>Genea</i> spp. ^h	+	+		+	+	15,3	5,1
<i>Chamonixia caespitosa</i> ^h	+	+	+		+	14,5	4,8
<i>Russulales</i> spp.	+	+	+	+	+	13	4,3
<i>Glomus</i> spp. 3 ^h	+	+	+	+	+	11,5	3,8
<i>Tuber</i> spp. ^h	+	+	+		+	10,7	3,5
<i>Pezizales</i> spp.	+	+	+	+	+	9,2	3
<i>Endogone</i> sp. 2 ^h	+	+	+	+		6,1	2,0
<i>Hydnotrya</i> sp. ^h	+	+				6,1	2,0
<i>Hymenogaster</i> spp. 2 ^h		+		+	+	6,1	2,0
<i>Genea</i> sp. 1 ^h		+	+		+	5,3	1,8
<i>Glomus</i> spp. 1 ^h		+	+	+	+	5,3	1,8
<i>Fungi</i> sp.		+			+	3,8	1,3
<i>Glomus</i> spp. 2 ^h		+		+	+	3,1	1,0
<i>Hymenogaster</i> spp. 1 ^h			+	+	+	2,3	0,8
<i>Tuber</i> sp. 1 ^h			+		+	2,3	0,8
<i>Sordariomycetes</i> spp.				+		1,5	0,5
<i>Basidiomycota</i> sp.		+				0,8	0,3
Total	13	19	15	15	18	22	

It is important to note that the examination of small mammal fecal pellets revealed nearly two times more hypogeous fungal genera (9 genera) in all study plots than the search of the fruit-bodies (5 genera). For example, the fungi from the genera *Chamonixia*, *Genea*, *Hydnotrya* and *Hymenogaster* were recorded only from the fecal pellets. Mycophagous small mammals can detect very accurately hypogeous fruit-bodies due to their smells and needs very small energy to dig them out (MASER et al., 2008).

Small mammal diet. Most small mammals individuals (more than 66 %) caught in study plots consumed fungi. Fungal spores were not observed in 38 % of *Apodemus* spp. and in 6 % of *Myodes glareolus* fecal samples. Various fungal structures were detected more frequently in *M. glareolus* than in *Apodemus* spp. excrements. For example, spores of epigeous and hypogeous fungi were observed more frequently, respectively 2.4 and 1.6 times, in *M. glareolus* than in *Apodemus* spp. excrements. It is known that the nutritional value of mushrooms is not high (CORK, KENAGY, 1989), and *M. glareolus*

may eat less calorific food, for example, nibble tree bark in winter (ULEVIČIUS, JUŠKAITIS, 2005), while *Apodemus flavicollis* consume more calorific food, is granivorous, store the seeds for wintertime (BELOVA, 2000; JĘDRZEJEWSKA et al., 2004).

The greatest number of fungal taxa (22) was detected in fecal pellets of *M. glareolus*, the lowest (4 taxa) – of *Sorex araneus*. It should be noted that during our study only few *Sorex* individuals were caught, therefore the data on the diet of this mammal species are unrepresentative. Spores of *Elaphomyces* and *Ascomycota* spp. (anamorphs) were frequent in *Apodemus* spp. excrements, and spores of *Elaphomyces*, *Endogone*, *Genea*, *Glomus* and *Boletales* were frequent in *M. glareolus* fecal pellets (Table 7).

Table 7. Frequency (%) of fungal spores in small mammal fecal pellets

Fungal taxa	Taxa of small mammals			
	<i>Apodemus</i> spp. (n=58)	<i>Myodes glareolus</i> (n=67)	<i>Sorex araneus</i> (n=4)	<i>Sorex minutus</i> (n=2)
<i>Ascomycota</i> (anamorphs)	20,7	17,9	-	-
<i>Boletales</i>	8,6	23,9	25	-
<i>Chamonixia</i>	8,6	15	50	50
<i>Elaphomyces</i>	24,1	49,3	75	100
<i>Endogone</i>	13,8	32,8	-	50
<i>Genea</i>	5,2	32,8	-	100
<i>Glomus</i>	7	28,4	-	50
<i>Hydnotrya</i>	-	12	-	-
<i>Hymenogaster</i>	1,7	15	-	-
<i>Pachyphloeus</i>	19	13,4	50	50
<i>Pezizales</i>	8,6	7,5	-	-
<i>Russulales</i>	5,2	20,9	-	-
<i>Tuber</i>	5,2	16,4	-	50

Spore abundance of each fungal taxon was estimated in fecal samples of each small mammal, and it was used for counting the diversity indices. Diversity of all fungal taxa (Kruskal-Wallis $H = 34.6$; d.f. = 3; $p < 0.001$) and of hypogeous taxa separately ($H = 30.5$; d.f. = 3; $p < 0.001$) significantly differed in fecal pellets of various small mammal taxa. The greatest value of the Shannon's diversity index of all fungal taxa was in fecal pellets of *Sorex minutus* (mean $H' \pm s.n. = 1.42 \pm 0.75$) and *Myodes glareolus* (0.932 ± 0.537), the smallest – in fecal pellets of *S. araneus* (0.42 ± 0.467) and *Apodemus* spp. (0.341 ± 0.467). Averages of hypogeous fungi diversity indices were smaller in fecal pellets of both *M. glareolus* (0.615 ± 0.527) and *Apodemus* sp. (0.170 ± 0.333).

The most similar mycobiotas in fecal pellets were in *Myodes glareolus* and *Apodemus* spp. pair (BCI = 54.2 %), and *Sorex araneus* and *S. minutus* pair (BCI = 53.8 %), the least similar – in fecal pellets of *Apodemus* spp. and *S. minutus* (BCI = 28.4 %).

All captured small mammals are casual mycophagists – animals that consume truffles during the search of other food items, or alternatively consume truffles when preferred food source is temporarily unavailable. For *Apodemus flavicollis* the main food is seeds, seldom – plants and invertebrates, for *Myodes glareolus* – plants, additionally seeds, fruits and invertebrates (JĘDRZEJEWSKA et al., 2004). Individuals of *Sorex* consume various invertebrates (PRŪSAITĖ, 1988).

Seasonal peculiarities of mycophagy. In spring 3 from 5 (60 %) fecal pellets had spores, in summer – 24 from 30 (80 %) and in autumn – 79 from 96 (82 %). Fungal taxa and spore frequency varied during different seasons. Spring fecal samples contained only *Elaphomyces* spores. In summer the frequency of fungal spores in fecal pellet samples of *Myodes glareolus* and *Apodemus* sp. was rather similar, respectively fungal spores were observed in 12 (100 %) and 12 (66 %) samples. The mycophagy was significantly different in autumn – fungal spores were detected in 93 % of *M. glareolus* and only in 62 % of *Apodemus* spp. excrement pellets (Pearson's Chi-square $\chi^2 = 12.8$; d.f. = 1; $p = 0$). This means that in summer and especially in autumn *M. glareolus* disperse fungal spores more frequently than *Apodemus* spp.

Shannon's diversity index values significantly varied in respect of different seasons ($H' = 9.42$; d.f. = 2; $p = 0.01$). The greatest diversity of all fungal taxa was in fecal pellets collected in autumn (mean $H' \pm$ s.n. = 0.74 ± 0.63), the less – in summer (0.52 ± 0.63). Other studies also confirm that excrements contain the spores of hypogeous fungi more frequently in autumn (HAYES et al., 1986; BLASCHKE, BÄUMLER, 1989; BERTOLINO et al., 2004).

Peculiarities of mycophagy in different tree stands. In *Picea abies* stand (plot Ž1) the smallest number of small mammals was captured, and their fecal pellets contained the least number of fungal taxa (Table 6). Shannon's diversity index value of fungal taxa was lowest in this plot (mean $H' \pm$ s.n. = 0.43 ± 0.62). Spores of *Elaphomyces* and *Endogone* were observed most frequently (Table 8). In other *Picea abies* stand (Ž2) the greatest number of all fungal taxa and hypogeous taxa was detected in fecal pellets. Spores of *Elaphomyces* and *Endogone* were observed most frequently. In fecal pellets collected in *Quercus robur* stand (Ž4) 15 fungal taxa were recorded, and in comparison with other tree stands the smallest number of hypogeous genera (6) was determined. The largest amount of small mammals was caught in mixed tree stand (Ž5) and the fungal composition was comparatively rich (18 fungal taxa). The greatest diversity index value of all fungal taxa was in this tree stand (mean $H' \pm$ s.n. = 0.94 ± 0.65). The diversity index of hypogeous fungi was greatest as well (mean $H' \pm$ s.n. = 0.75 ± 0.56). Spores of *Elaphomyces* and *Genea* were observed most frequently (Table 8).

Table 8. Frequency (%) of fungal taxa in small mammal fecal pellets collected in different study plots

Fungal taxa	Study plots				
	Ž1 (n=21)	Ž2 (n=27)	Ž3 (n=24)	Ž4 (n=22)	Ž5 (n=37)
<i>Elaphomyces</i>	28.6	40.7	37.5	45.4	35.1
<i>Endogone</i>	28.6	48.2	20.8	27.3	5.4
<i>Pachyphloeus</i>	9.5	29.6	4.2	31.8	13.5
<i>Genea</i>	14.3	29.6	4.2	13.6	32.4
<i>Chamonixia</i>	19	33.3	4.2	–	10.8
<i>Glomus</i>	5	22.2	12.5	22.7	24.3
<i>Tuber</i>	25	11.1	16.7	–	8.1
<i>Hydnotrya</i>	5	25.9	–	–	–
<i>Hymenogaster</i>	–	3.7	4.2	13.6	16.2
Ascomycota (anamorphs)	9.5	3.7	16.7	45.5	18.9
<i>Boletales</i>	9.5	18.5	12.5	22.7	18.9
<i>Russulales</i>	5	18.5	12.5	18.2	10.8
<i>Pezizales</i>	5	7.4	4.2	13.6	8.1

The numbers of all fungal taxa and hypogeous taxa significantly varied in different tree stands (for all fungal taxa Kruskal-Wallis $H = 11.256$; d.f. = 4; $p = 0.024$; for hypogeous taxa $H = 11.505$; d.f. = 4; $p = 0.014$).

Most similar mycobiotas in small mammal fecal pellets were in the pair of *Picea abies* stands (Ž1 and Ž3) (BCI = 71.4 %) (Fig. 9). Least similar mycobiotas in fecal pellets were in the pair of *Picea abies* (Ž1) and *Quercus robur* (Ž4) stands (BCI = 52.9 %). The similarities of plant species compositions and fruit-body mycobiotas in these two stands were also low.

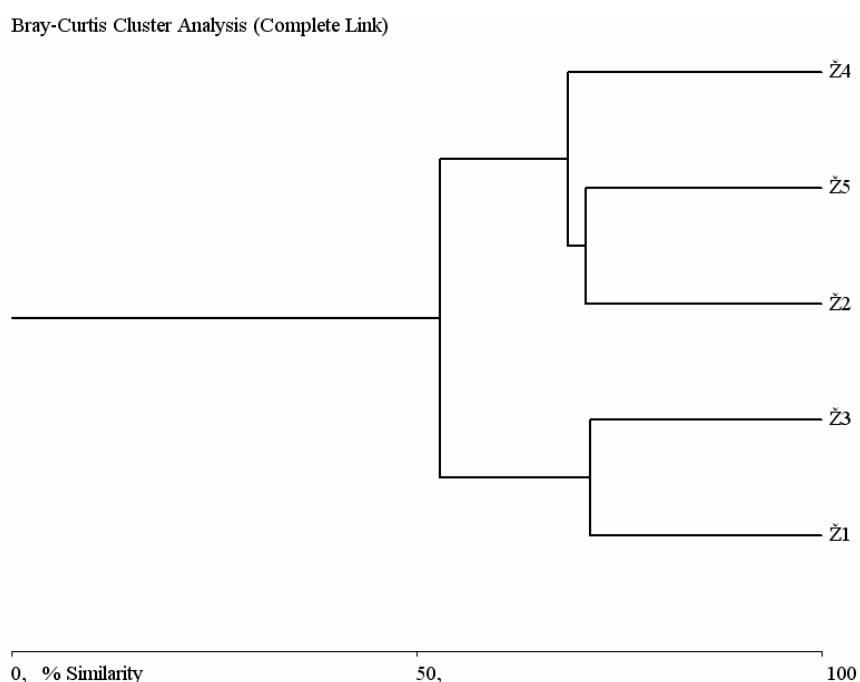


Fig. 9. Dendrogram of similarity of mycobiotas in small mammal fecal pellets collected in different study plots

We assume that the diversity of hypogeous fungi determined in small mammal fecal pellets reflects the composition of hypogeous fungi of studied tree stands, because the home range of small mammals is not large. For example, the home range area of *Apodemus flavicollis* is up to 0.22 ha, and of *Myodes glareolus* – up to 0.14 ha (CRAWLEY, 1969). Sometimes the home range of active individuals can be greater. M. P. NORTH (2002) argues that the forest types with the highest densities of truffle consumers also contain the greatest truffle abundance. This statement is in accordance with the results obtained during independent investigations provided in Žemaitija NP. We found that the greatest diversity of hypogeous fungi (according both the survey of fruit-bodies and the examination of spores in fecal pellets) is in mixed stand. Zoologists found that populations of *M. glareolus* and *A. flavicollis* in Žemaitija NP are more abundant in mixed coniferous and deciduous forests than in pure spruce forests (ULEVIČIUS et al., 2002). Some studies suggest that mycophagy differs significantly between different tree stands (REDDELL et al., 1997), other – do not (NORTH et al., 1997).

CONCLUSIONS

1. 29 species of hypogeous fungi belonging to 16 genera, 12 families, 7 orders and 3 phyla have been recorded in Lithuania. 5 genera (*Chamonixia*, *Endogone*, *Genea*, *Glomus* and *Pachyphloeus*) and 8 species (*Chamonixia caespitosa*, *Elaphomyces anthracinus*, *Endogone lactiflua*, *Glomus macrocarpum*, *Hymenogaster olivaceus*, *H. rehsteineri*, *Pachyphloeus conglomeratus* and *Tuber puberulum*) are new for Lithuania. The most frequent species are *Elaphomyces asperulus*, *E. granulatus*, *E. muricatus*, *Rhizopogon luteolus*, *Cenococcum geophilum* and *Geopora arenicola*.
2. In Lithuania hypogeous fungi produce fruit-bodies from April to December. Majority of species are mycorrhizal, two species (*Geopora arenicola*, *Peziza ammophila*) are saprobic. Recorded fungi in Lithuania have associations with 9 tree species. The majority of fungal species recorded under *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Quercus robur* trees.
3. Hypogeous fungi were found in all investigated tree stands of different type and age. The analysis of the habitats of Lithuanian hypogeous fungi showed that the majority of species were recorded in mixed (13 species), *Pinus sylvestris* (10) and *Picea abies* (10) forests.
4. During investigation in Žemaitija NP in different tree stands (plots Ž1–Ž5) on average 4 species of hypogeous fungi and 30 species of epigeous fungi were recorded in one study plot. The highest diversity of hypogeous and epigeous fungi was in mixed stand, the lowest – in *Quercus robur* stand. The mycobiotas (species and the amount of their fruit-bodies) of two *Picea abies* tree stands (Ž1 and Ž2) were most similar, and the mycobiota of *Quercus robur* stand (Ž4) was most distant.
5. The species composition and fructification of hypogeous and epigeous fungi depended on biotic factors (stand type and vegetation, forest floor disturbance caused by *Sus scrofa* animals). Statistically significant influence of abiotic factors (chemical composition of soil, precipitation and air temperature) to hypogeous fungal species composition and fructification were not detected.
6. In different tree stands rodents (*Apodemus* spp., *Myodes glareolus*) and insectivores (*Sorex araneus* and *S. minutus*) consumed hypogeous and epigeous fungi during spring, summer and autumn. In total, 22 taxa of fungi were identified in small mammal fresh fecal pellets. The spores of hypogeous *Elaphomyces* and *Endogone* fungi prevailed in fecal samples. The greatest diversity of hypogeous and other fungi was detected in fecal pellets collected in mixed tree stand.
7. The greatest number of hypogeous taxa and the most frequent presence of hypogeous fungal spores were detected in fecal pellets of *Myodes glareolus*. This suggests that *M. glareolus* play more important role in dispersal of spores of hypogeous fungi than *Apodemus* spp. in studied stands.
8. Research method of small mammal mycophagy provided additional information about the diversity of hypogeous fungi. The examination of small mammal fecal pellets revealed nearly two times more hypogeous fungal genera (9 genera) in study plots than the search of the fruit-bodies (5 genera).

LIST OF PUBLICATIONS

Publications in editions included in the list of the Institute of Scientific Information (ISI):

KATARŽYTĖ M., KUTORGA E., 2007: Diversity of hypogeous fungi in the diet of small mammals in Lithuanian forests. – *Botanica Lithuanica*, **13(4)**: 229–235. – ISSN 1392-1665.

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SANTRAUKA

Požeminiai (hipogėjiniai) grybai kartu su kitais mikoriziniais grybais yra vieni iš svarbiausių ir aktyviausių miško ekosistemos komponentų, jie atlieka įvairias gyvybiškai svarbias funkcijas – aprūpina augalus vandeniu ir kitomis maisto medžiagomis, saugo juos nuo nepalankių aplinkos sąlygų ir patogenų, palaiko dirvožemio homeostazę ir yra kai kurių gyvūnų maisto šaltinis (MASER et al., 1978; ALLEN, 1991). Nors požeminių grybų paieška yra gana sudėtinga ir reikalauja specialių pastangų, susidomėjimas šiais grybais pasaulyje labai išaugo, kadangi 1) jų įvairovė yra žymiai didesnė nei manyta, 2) nepakankamai sukaupta žinių apie jų sandarą ir paplitimą, 3) menkai pažintas jų funkcionavimas ir ryšiai su kitais organizmais.

Lietuvoje išsamesnių požeminių grybų įvairovės ir biologijos tyrimų iki šiol nebuvo. Kai kurie duomenys apie Lietuvoje augančius grybus, dažniausiai rastus atsitiktinai miško gyvūnų išknistose vietose, pateikti keliose mikologinėse publikacijose (BUCHOLTZ, 1904, 1907; MAZELAITIS, 1982; KUTORGA, 2000 ir kt.). Tyrimų tąsa, panaudojant specialius įrankius ir metodikas, leistų geriau pažinti šių grybų rūšių įvairovę ir paplitimą.

Makromicetų bendrijų struktūros ir dinamikos varijavimas natūraliomis sąlygomis bei įvairių biotinių ir abiotinių veiksnių įtaka grybų bendrijų funkcionavimui domina įvairių šalių mikologus (ARNOLDS, 1992; CASTELLANO et al., 2004). Mikocenologiniai grybų tyrimai papildė žinias apie rūšių ekologiją, miškų ir kitų ekosistemų bioįvairovę. Lietuvos gamtinėmis sąlygomis makroskopinių grybų bendrijų kokybiniai ir kiekybiniai tyrimai pradėti gana neseniai (GRICIUS et al., 1999; IRŠĖNAITĖ, 2003; KATARŽYTĖ, KUTORGA, 2005a; STANKEVIČIENĖ, URBNAS, 2006; STANKEVIČIENĖ, KASPARAVIČIUS, 2007; STANKEVIČIENĖ et al., 2008), tačiau požeminių grybų bendrijos šiuose tyrimuose nenagrinėtos arba joms skirta labai mažai dėmesio.

Gerai žinoma, kad stambieji ir smulkieji žinduoliai minta požeminių ir antžeminių grybų vaisiakūniais ir padeda išplatinti jų sporas (MASER et al., 1978, 2008; CLARIDGE, MAY, 1994). Smulkiųjų žinduolių mikofagija tirta Šiaurės Amerikoje, Australijoje ir tik kai kuriose Europos šalyse (MASER et al., 1978, 2008; CLARIDGE, MAY, 1994; VIRO, SULKAVA, 1985; BLASCHKE, BÄUMLER, 1989; BERTOLINO et al., 2004). Lietuvoje smulkiųjų žinduolių mikofagija specialiai netirta, todėl beveik nežinoma, kokie gyvūnai, kur ir kada, kiek ir kokiais grybais minta. Atsakymai į šiuos klausimus domina mikologus, zoologus ir ekologus.

Stambiųjų miško gyvūnų, pavyzdžiui, šernų, kurie taip pat minta požeminiais grybais, padarytos dirvožemio pažaidos gali turėti įtakos mikorizinių grybų fruktifikacijai (SCHLEY, ROPER, 2003; ŁAWRYNOWICZ et al., 2006). Ši problematika Lietuvoje taip pat netyrinėta.

Darbo tikslai:

1. Išaiškinti Lietuvos požeminių grybų rūšių įvairovę ir paplitimą.
2. Palyginti mikorizinių požeminių ir antžeminių makromicetų bendrijų struktūrą ir dinamiką skirtingose sudėties medynuose.
3. Išaiškinti grybų sudėtį smulkiųjų žinduolių maisto racione.

Darbo uždaviniai:

- 1) Skirtingose Lietuvos geografinėse vietose ir augavietėse surinkti požeminių grybų pavyzdžius, ištirti jų morfologines ir anatomines savybes ir identifikuoti. Kitiškai ištirti Lietuvos herbariumuose saugomų požeminių grybų pavyzdžius.

- 2) Sudaryti Lietuvos požeminių grybų konspektą, atlikti požeminių grybų taksonominės, struktūros, paplitimo ir fruktifikacijos sezoniškumo analizę.
- 3) Nustatyti mikorizinių požeminių ir antžeminių grybų bendrijų struktūrą, fruktifikacijos kiekybinius ir sezoninius ypatumus eglynuose, ažuolyne ir mišriame medyne.
- 4) Įvertinti abiotinių (kritulių, oro temperatūros, dirvožemio cheminių rodiklių) ir biotinių (medynų tipo ir augmenijos, miško paklotės ir dirvožemio pažaidų, atsiradusių dėl šernų knisimo) veiksnių daromą įtaką mikorizinių grybų fruktifikacijai.
- 5) Šviežių ekskrementų mikologinio tyrimo metodu išanalizuoti skirtingų smulkiųjų žinduolių mikofagijos kiekybinius ir sezoninius ypatumus eglynuose, ažuolyne ir mišriame medyne.

Ginami teiginiai. 1. Lietuvos požeminių grybų rūšių įvairovė yra kur kas didesnė nei buvo žinoma iki šiol, taip pat platesnis yra ir jų taksonominis spektras. 2. Požeminiai grybai paplitę visuose tirtuose skirtingo tipo ir amžiaus medynuose, tačiau atskirų rūšių dažnumas, paplitimas ir fruktifikacija yra skirtingi. 3. Požeminių ir antžeminių mikorizinių makromicetų bendrijų sudėtis ir sezoninė dinamika varijuoja ir priklauso nuo įvairių abiotinių ir biotinių veiksnių. 4. Įvairūs smulkieji žinduoliai Lietuvoje minta požeminiais ir antžeminiais grybais, tačiau jų mikofagijos lygis ir sezoniškumas yra specifiniai.

Darbo naujumas. Darbe pirmą kartą detaliai ištirta Lietuvos požeminių grybų rūšių įvairovė, paplitimas ir fenologija. Lietuvoje efektyviai išbandyti du požeminių grybų paieškos metodai: 1) dirvožemio paviršius ardytas grėbliukais; 2) smulkiųjų žinduolių gaudymui ir jų ekskrementų surinkimui naudoti gyvagaudžiai spąsteliai (pastarasis metodas nekenkia patiems gyvūnams ir nekeičia ekosistemos natūralumo). Sudarytas išplėstinis požeminių grybų konspektas, kuriame apibendrinti duomenys apie šių grybų paplitimą, biologiją ir ekologiją, ir skaitmeniniais vaizdais iliustruota jų makro- ir mikroskopinė sandara. Išaiškinti nauji Lietuvai požeminių grybų taksonai (8 rūšys ir 5 gentys), pateikti jų originalūs aprašymai.

Lietuvoje pirmą kartą tirtos požeminių ir antžeminių mikorizinių grybų bendrijos skirtingos sudėties medynuose ir analizuota šernų sukeltų miško paklotės ir dirvožemio pažaidų įtaka grybų įvairovei ir fruktifikacijai.

Pradėti smulkiųjų žinduolių mikofagijos tyrimai skirtingos sudėties medynuose, aprašytos ir iliustruotos grybų sporos, kurios rastos smulkiųjų žinduolių ekskrementuose.

Mokslinė ir taikomoji darbo reikšmė. Tyrimų duomenys papildė žinias apie Lietuvos mikrobiotą ir gali būti panaudoti daugiatomio leidinio „Lietuvos grybai“ ir knygos „Lietuvos fauna. Žinduoliai“ rengimui. Gautos žinios apie mikorizinių makromicetų bendrijas ir smulkiųjų žinduolių ypatumų išaiškinimas leidžia geriau suprasti grybų, augalų ir gyvūnų funkcinius saitus miško ekosistemose. Tyrimų rezultatai gali būti naudingi aplinkosaugos ir aplinkotvarkos klausimų sprendimui, pavyzdžiui, mikologinių požiūriu vertingų teritorijų išskyrimui ar miško produktyvumo ir ekologinės būklės įvertinimui. Sukaupta nemaža požeminių ir antžeminių grybų kolekcija, kuri saugoma Vilniaus universiteto herbariume (WI).

Išvados:

1. Lietuvoje nustatytos 29 požeminių grybų rūšys, kurios priklauso 16 genčių, 12 šeimų, 7 eilėms ir 3 skyriams. Išaiškintos naujos Lietuvai požeminių grybų 5 gentys (*Chamonixia*, *Endogone*, *Genea*, *Glomus* ir *Pachyphloeus*) ir 8 rūšys (*Chamonixia caespitosa*, *Elaphomyces anthracinus*, *Endogone lactiflua*, *Glomus macrocarpum*, *Hymenogaster olivaceus*, *H. rehsteineri*, *Pachyphloeus conglomeratus* ir *Tuber puberulum*). Dažniausios rūšys Lietuvoje yra *Elaphomyces asperulus*, *E. granulatus*, *E. muricatus*, *Rhizopogon luteolus*, *Cenococcum geophilum* ir *Geopora arenicola*.
2. Lietuvoje požeminiai grybai vaisiakūnius formuoja nuo balandžio iki gruodžio mėn. Didžioji dalis požeminių grybų rūšių yra mikoriziniai grybai, dvi rūšys (*Geopora arenicola*, *Peziza ammophila*) yra saprotrofės. Lietuvoje nustatyti požeminių grybų ryšiai su 9 medžių rūšimis. Daugiausia rūšių nustatyta šalia *Pinus sylvestris*, *Picea abies*, *Betula pendula* ir *Quercus robur* medžių.
3. Požeminiai grybai rasti visuose tirtuose skirtingo tipo ir amžiaus medynuose. Išanalizavus visą turimą medžiagą apie Lietuvos požeminių grybų augavietes, daugiausia požeminių grybų rūšių nustatyta mišriuose miškuose (13 rūšių), pušynuose (10) ir eglynuose (10).
4. Žemaitijos NP skirtingos sudėties medynuose (tyrimo laukeliai Ž1–Ž5) atlikto tyrimo metu vidutiniškai viename tyrimo laukelyje rasta po 4 rūšis požeminių grybų ir po 30 rūšių antžeminių grybų. Didžiausia požeminių ir antžeminių grybų įvairovė nustatyta mišriame medyne, mažiausia – ažuolyne. Panašiausios grybijos (rūšys ir jų vaisiakūnių gausumas) buvo dviejuose eglynuose (Ž1 ir Ž2), o labiausiai skyrėsi ažuolyno grybija.
5. Požeminių ir antžeminių grybų rūšių sudėtis ir fruktifikacija priklausė nuo biotinių veiksnių (medynų tipo ir augmenijos, dirvožemio dangos pažaidų, atsiradusių dėl šernų knisimo). Statistiškai patikima abiotinių veiksnių (dirvožemio cheminė sudėtis, kritulių kiekis ir oro temperatūra) įtaka požeminių grybų sudėčiai ir fruktifikacijai nenustatyta.
6. Kai kurie peliniai graužikai (*Apodemus* spp., *Myodes glareolus*) ir vabzdžiaėdžiai gyvūnai (*Sorex araneus* ir *S. minutus*) skirtingo tipo medynuose mito požeminiais ir antžeminiais grybais pavasarį, vasarą ir rudenį. Šių smulkiųjų žinduolių ekskrementuose nustatyti 22 grybų taksonai, iš jų dažniausiai nustatytos *Elaphomyces* ir *Endogone* genčių požeminių grybų sporos. Didžiausia požeminių grybų įvairovė smulkiųjų žinduolių ekskrementuose nustatyta mišriame medyne.
7. *Myodes glareolus* individų ekskrementuose nustatytas didžiausias požeminių grybų taksonų skaičius ir juose dažniausiai rastos požeminių grybų sporos. Manome, kad *M. glareolus* individai yra svarbesni požeminių grybų sporų platinime tirtuose medynuose nei *Apodemus* spp. individai.
8. Pritaikius smulkiųjų žinduolių mikofagijos tyrimo metodą, gautos papildomos žinios apie požeminių grybų įvairovę. Ištyrus smulkiųjų žinduolių ekskrementus, išaiškinta beveik du kartus daugiau požeminių grybų genčių (9 gentys) nei požeminių grybų vaisiakūnių paieškos metodu (5 gentys).

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