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Dedicated to Professor Alina Skirgiełło
on the occasion of her ninety-fifth birthday

Wood-inhabiting fungi on pedunculate oak coarse woody debris in relation to substratum quantity and forest age

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Wood-inhabiting fungi on pedunculate oak (*Quercus robur*) coarse woody debris (CWD) was investigated in 50 plots of 0.1 ha in oak stands of different ages in Lithuania. In maturing stands (50-120 years) the average volume of oak CWD was 4.7 m^3/ha, and in mature stands (over 120 years) – 13.9 m^3/ha. Both in maturing and mature stands, the greatest fraction of CWD consisted of fallen oak branches (81 % and 84 % respectively), whereas fallen trunks comprised about 10 % of the total units of CWD. In total 1350 records of 203 species (49 ascomycetes and 154 basidiomycetes) were collected during 2 years of investigation. Species richness and abundance increased significantly with the increase of volume and abundance of CWD. Higher species richness was detected in mature stands than in maturing ones. Wood-inhabiting species composition varied greatly at stand scale, and one third of all detected species occurred only in one plot. Red-listed fungi were found only in mature stands. We conclude that, even in managed oak stands, oak CWD maintains a rather diverse species composition of ascomycetes and basidiomycetes. However, the current practice of forestry in Lithuania of removing dying or dead wood of large volume, e.g. standing and fallen trunks, reduce the distribution of highly specialized, usually rare, and endangered fungi.

Key words: Xylotrophic fungi, coarse woody debris, *Quercus robur,* fungal conservation

INTRODUCTION

Large pieces of dead rotting fallen trunks, branches and stumps, which characterize coarse woody debris (CWD), are substantial components in forest ecosystems (Harmon et al. 1986). There is no doubt that woody debris plays an essential role in creating habitats for many saproxylic organisms, including wood-inhabiting fungi (Boddy 2001; Siitonen 2001). The diversity and frequency of wood-inhabiting fungi depend on the stage of wood decay (Niemelä, Renvall, Pentillä 1995;

Renvall 1995; Lindblad 1998) and in general considered to be greater on large-diameter woody debris (Bader, Jansson, Jonsson 1995; Høiland, Bendiksen 1997; Kruys et al. 1999). Recent studies indicate that forest management and fragmentation in boreal coniferous forests have greatly affected the diversity of wood-inhabiting fungi, especially the occurrence of rare species (Sippola, Renvall 1999; Lindgren 2001; Penttilä, Siitonen, Kuusinen 2004). Studies dealing with temperate broadleaved forests have also analyzed the relationship between fungal species diversity (both basidiomycetes and ascomycetes) and woody debris quantity/quality (Runge 1975; Lange 1992; Heilmann-Clausen, Christensen 2004; Nordén et al. 2004), some environmental factors (Heilmann-Clausen 2001), and stand structure/age (Nordén, Paltto 2001).

As in most parts of Europe, the old-growth temperate broadleaved forests in Lithuania have been fragmented to rather small fractions (Peterken 1996; Kenstavičius 1997), and intensive forest management has endangered many organisms, including fungi, associated with oak (Sunhede, Vasiliauskas 1996, 2003). Out of total 40 red-listed wood-inhabiting fungi in Lithuania (Anonymous 2005), more than 10 species are confined to the pedunculate oak (*Quercus robur*), both ecologically and economically important tree species in Lithuania. *Quercus robur* stands occupy about 33600 ha, i.e. 1.8 % of the total forest area in Lithuania (Navasaitis et al. 2003), and they usually grow intermixed with other deciduous or coniferous trees.

The main focus of most mycological studies on oak wood in Lithuania has been species composition and distribution, and the quantity and quality of CWD has not usually been considered. Moreover, there is no up to date and generally available information on the amount of woody debris in Lithuanian forests. The first attempt to examine fungi and CWD in various coniferous and deciduous unmanaged stands of 40-130 years old is that of Vasiliauskas et al. (2004). They found the volume of CWD of different tree species to be larger in older stands than in younger ones, demonstrated the variation of structural characteristics of CWD, and recorded 41 species of wood-decomposing polypores. Nevertheless, their sampling of oak CWD was too limited to draw conclusions about distribution patterns, and the oak wood-decomposing fungi were not specified.

Therefore, in this study we examined the present status of CWD of oak and the diversity of fungi associated with it. The study focuses on wood-inhabiting ascomycetes and basidiomycetes on coarse woody debris in managed oak dominated stands of different age. The list of recorded species and the analysis of fungal composition on wood of different decay stage are presented in separate paper (Iršėnaitė, Kutorga 2006). The aim of this paper was to analyse the species richness of oak wood-inhabiting fungi with respect to quantitative and structural features of CWD in maturing and mature oak stands.

MATERIAL AND METHODS

Study sites and plots. Ten study sites were selected in different parts of Lithuania (Fig. 1) according to the forest management documents and maps. Study sites 1-2, 5-8 and 10 comprised of forests growing on mezotrophic humid soil and dominated by pedunculate oak (*Quercus robur*). The co-existing tree species are *Picea abies*,

Fig. 1. The location of the study sites in Lithuania: 1, Kreiviškės; 2, Plikoji sala; 3, Minijos kilpa; 4, Šilas; 5, Gojus; 6, Drausgiris; 7, Subartonys; 8, Ąžuolija; 9, Ginučiai; and 10, Dūkštos.

Populus tremula, *Tilia cordata* and *Fraxinus excelsior*. The bush layer is moderately thick and consists mainly of *Corylus avellana*, *Lonicera xylosteum*, *Frangula alnus* and *Sorbus aucuparia*. Sites 3 and 4 comprised forests on mezotrophic dry soil, dominated by both *Quercus robur* and *Pinus sylvestris*, and with a sparse shrub layer of *Corylus avellana* and *Sorbus aucuparia*. Site 9 is an abandoned oak-wood pasture with solitary *Corylus avellana*. Local foresters´ information and cut stumps we observed indicate that all sites were more or less managed during the last 50 years, mostly by thinning or removing dead trees.

The study comprised two oak stand age groups: I, – maturing (50–120 years); and II, – mature (over 120 years). According to the study site size, from one to nine circular study plots of 0.1 ha were randomly selected. In total, we surveyed 50 plots (25 in each age group).

Examination of CWD. The method for the examination of CWD was prepared according to Kruys et al. (1999). Within each plot, all fallen and standing dead oak wood with the base 5 cm in diameter and more and over 30 cm in length was investigated. The following characteristics were recorded for each unit of dead wood that harboured a fungus: category of CWD (lying trunk, snag, stump, branch), maximum (base) and minimum (top) diameter (m), length (m), and decay stage (DS). Five CWD decay stages were defined following a modified classification of Renvall (1995). If the stage of decomposition varied in different parts of a trunk, an average decay stage was considered. CWD volume was calculated by the Smalian's formula (Petterson, Wiant, Wood 1993).

Sampling and identification of fungi. The fieldwork was undertaken in 2001–2002 during the main period of fruit body production (August–October) in both those years, with a single visit at each plot (up to 3 hours). Both basidiomycetes and ascomycetes were inventoried. Recorded species were arranged into these fungal groups: discomycetes, pyrenomycetes and loculoascomycetes, agarics (including cyphelloid fungi), corticioid fungi (including thelephoroid fungi), gasteromycetes, heterobasidiomycetes, polypores (including *Ramaria*). These commonly used fungal groups are based on fruit body types, and are not taxonomical groups reflecting phylogenetic relationships. A species found on a single unit of wood was considered as one record, regardless of the number of observed fruit bodies. Easily recognizable species were identified in the field, and about 1000 specimens were collected for microscopic examination. Voucher specimens are preserved in the Herbarium of the Institute of Botany, Vilnius (BILAS).

Data analysis. Differences in number of species and abundance and the amount and volume of CWD in different age stands were tested for significance using a non-parametric Mann-Whitney U-test. CWD profile was quantified by summarizing the volume of CWD in a 2-way cross-table of maximum diameter and decay stages (Stokland 2001). The Chi-squared test was used to examine differences in the distribution of fungal groups and CWD decay stages. The Shannon diversity index (H') was used to evaluate the diversity of decay stages of CWD in the study plots. The first-order jackknife estimator was used to calculate true species richness (Zar 1999). Dissimilarity in species composition between study plots in one study site was calculated with the Sørensen distance measure, and Spearman's rank correlation coefficient (r_s) was used to express the correlation between different variables. All statistical analyses were run using STATISTICA 6.0 (StatSoft Inc 2001) and PC-ORD 4.0 software (McCune, Mefford 1999).

RESULTS

Characteristics of CWD. In total 321 units (46.5 m^3) of oak coarse woody debris were recorded across all study plots, taking both years together. The mature stands had significantly more CWD (203 units; 34.8 m^3) than the maturing ones (118 units; 11.7 m^3) (Mann-Whitney U-test; $p<0.001$). There was large variation in CWD volume within plots, from 0.01 m^3 to 5.61 m^3 in maturing stands, and from 0.25 m^3 to 7.12 m^3 in mature stands. Data on average characteristics of CWD are given in Table 1.

The Chi-squared test indicates that volume of CWD of different decay stage is distributed in the same proportions in maturing and mature stands ($\chi^2 = 4.62$; df = 4; $\alpha = 0.05$). The CWD patterns with respect to dimensions and decay stages shown in Table 2, 3.

Fallen branches comprised the largest proportion of the total units of CWD, both in maturing (81 %) and in mature stands (84 %). The proportion of lying oak trunks was respectively only 9 % and 10 %. Stumps and snags formed the minority of all recorded CWD.

Species richness. In total 1350 records of 203 species (49 ascomycetes and 154 basidiomycetes) were collected over the period of investigation. Four species (2 %)

Table 1

Characteristics of the CWD, the number of records and fungal species (mean ± standard deviation) in study plots

Stand age group	n	No. of CWD units per ha	Diam[c] of CWD (m)	Volume of CWD (m^3/ha)	No. of records per ha	No. of species per ha
I [a]	25	47.2 (±17.7)	0.17 (±0.12)	4.7 (±11.4)	199.6 (±98.1)	157.2 (±73.7)
II[b]	25	81.2 (±27.1)	0.22 (±0.07)	13.9 (±15.8)	338.0 (±107.2)	262.8 (±81.8)

Explanations: [a] maturing stands; [b] mature stands; [c] base diameter of the CWD unit.

Table 2

The volume of CWD (m^3 per ha) in maturing stands in a CWD profile based on their maximum (base) diameter and decay stage

Decay stage	5–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120
I	-	0.05	-	-	-	-	-	-	-	-	-	-
II	0.02	0.14	0.03	0.02	0.09	-	0.02	-	-	-	-	-
III	0.04	0.16	0.10	0.15	-	-	0.15	-	-	-	-	-
IV	0.06	0.35	0.38	0.19	-	0.58	-	0.05	1.95	-	-	-
V	0.01	0.03	-	-	0.02	-	-	-	-	-	-	-

Base diameter (cm)

Table 3

The volume of CWD (m^3 per ha) in mature stands in a CWD profile based on their maximum (base) diameter and decay stage

Decay stage	5–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120
I	-	0.02	0.03	-	-	-	-	-	-	-	-	-
II	0.01	0.07	0.16	0.07	0.02	-	-	-	-	-	-	-
III	0.08	0.88	0.64	0.31	1.66	0.21	1.61	0.09	-	0.09	-	-
IV	0.09	0.74	0.62	1.33	2.01	0.99	0.92	0.05	-	-	-	0.39
V	0.01	0.50	0.09	0.03	-	-	0.11	0.12	-	-	-	-

Base diameter (cm)

were found in more than half of the study plots, while 67 species (33 %) were found only in one. The most frequently encountered species (more than 30 records) were *Eriopezia caesia*, *Humaria hemisphaerica*, *Hyphodontia quercina*, *Hymenochaete rubiginosa*, *Mollisia cinerea*, *Nemania serpens, Phanerochaete velutina* and *Schizopora paradoxa*. Two species, *Fistulina hepatica* and *Xylobolus frustulatus*, listed in the Lithuanian Red Data Book (Anonymous 2005) were also found.

There was large variation in species numbers within plots in maturing stands (range 7 to 37 species) and in mature stands (range 11 to 43), but the number of species in mature stands (167) was significantly higher than in the maturing ones (134) (Mann-Whitney U-test; $p = 0.001$). The mean number of species and records per ha in study plots are shown in Table 1. Thirty-six species were exclusive to maturing stands, and 69 to mature stands. Nearly half (48 %) of all species were common to stands of both age groups. The total number of records made was significantly greater in mature stands than in maturing ones (Mann-Whitney U-test; $p<0.001$), but a comparison of distribution proportions of the species in the different fungal groups in maturing and mature stands revealed similar patterns of occurrence ($\chi^2 = 11.5$; df = 6; $\alpha = 0.05$). The number of records of corticioid fungi and discomycetes in mature stands were almost twice as high as that in maturing ones, although the number of species in both stands were nearly the same (Tab. 4). Polypores, gasteromycetes and heterobasidiomycetes were much less abundant in comparison with other fungal groups. As shown in Table 5, species composition varied greatly between plots even within a single study site (Dūkštos forest), but it was more similar in plots of the same age group.

Table 4

The number of species and records of fungal groups in oak stands of different age

Fungal group	Maturing stands		Mature stands	
	No. of species	No. of records	No. of species	No. of records
Ascomycetes				
discomycetes	17	119	23	207
pyrenomycetes and loculoascomycetes	14	52	22	109
Basidiomycetes				
agarics	17	37	25	101
corticioid fungi	72	267	76	404
gasteromycetes	2	4	2	3
heterobasidiomycetes	6	9	7	11
polypores	6	10	12	19
Total	134	496	167	854

Table 5

Sørensen dissimilarity distance coefficients of species composition between study plots in site No. 10 (Dūkštos forest)

	Iag2	Iag4	Iag6	Iag7	Iag10	IIag1	IIag3	IIag5	IIag8
Iag[a]2[b]									
Iag4	0.79								
Iag6	0.53	0.80							
Iag7	0.76	0.76	0.64						
Iag10	0.86	0.86	0.96	0.75					
IIag[a]1	0.67	0.92	0.73	0.84	0.88				
IIag3	0.82	0.91	0.82	0.79	0.83	0.78			
IIag5	0.75	0.92	0.64	0.81	0.93	0.74	0.53		
IIag8	0.86	0.86	0.78	0.79	0.79	0.81	0.76	0.68	
IIag9	0.76	0.88	0.81	0.78	0.69	0.75	0.73	0.71	0.69

Explanations:[a]Iag, maturing stand; IIag, mature stand; [b]number of study plot.

Table 6

Coefficients of the Spearman rank correlation (r_s) and significant level (p) between plot variables and number and records of fungal species and between the DBH of living oaks per study plot

Variables	No. of species		No. of records		DBH of living oaks	
	r_s	p	r_s	p	r_s	p
No. of CWD units	0.651	0.000	0.746	0.000	0.559	0.000
Volume of CWD (m^3)	0.840	0.000	0.819	0.000	0.764	0.000
Diam. of CWD	0.506	0.000	0.495	0.000	0.440	0.001
DS[a] diversity (H')[b]	0.213	0.137	0.170	0.237	0.344	0.014
DBH of living oaks	0.614	0.000	0.604	0.000	-	-

Explanations:[a]Decay stage (from I to V); [b]the Shannon diversity index (H') is used as an expression of CWD decay stage heterogeneity in the study plot.

The estimation of species richness by the jackknife estimator indicated that the actual number of species present should be higher than those recorded. In plots of age group I and II, 70 % and 73 % respectively of the estimated number of species were recorded.

Patterns of relationships. Significant positive correlations were found between the abundance and richness of fungal species and CWD variables (Tab. 6). The number of species and records showed a higher correlation with the volume of CWD than with the number and average diameter of CWD units. No significant correlation between diversity of decay stages in the study plots and species abundance was revealed. However, there was a significant correlation between the mean DBH of living oaks, an expression of the oak's age, and the variables measured.

DISCUSSION

Coarse woody debris of pedunculate oak. In Lithuania the average volume of *Quercus robur* CWD in mature oak stands (13.9 m^3/ha) is three times higher than in maturing ones (4.7 m^3/ha). This corresponds closely with the volume of CWD in Switzerland: 13.8 m^3/ha in natural oak forests, and 5.3 m^3/ha in managed ones (Bretz, Guby and Dobbertin 1996). Abandoned oak wood-pastures with high biodiversity conservation value in Sweden are on average 100-160 years old and contain only 5 m^3/ha of coarse and 1.9 m^3/ha of fine oak woody debris (Nordén et al. 2004). The average volume of CWD of managed mature deciduous forests in England (12–23 m^3/ha) and Poland (10 m^3/ha) is comparable to that of mature forests in Lithuania, but the calculated average volume of wood debris of natural deciduous forests in Poland is several times higher (94 m^3/ha) (Kirby, Webster, Antckzak 1991). Comparison of these data shows that different amounts of CWD are affected by forest type, age, and management intensity. The important feature of our study plots was the abundance of fallen oak branches and the lack of large dead trunks. The volume of CWD of various decay stages was distributed in the same proportions in mature and maturing stands, and in both stands low CWD abundance and multiply gaps were observed from CWD profile. The extremely small amount of recently fallen woody debris (< 1 m^3/ha) and very small amount of large diameter and strongly decayed wood indicates constant management in oak stands.

Fungal species richness and composition. The diversity of wood-inhabiting species on oak CWD in our study plots was high, and according to jackknife estimator it could be one third more in stands of both age group. Tofts and Orton (1998) stated that investigation of all species is hardly achievable in mycological inventories, unless the investigated community is very homogenous, as in the corticioid fungal community on *Alnus glutinosa* (Küffer, Senn-Irlet 2000). Most recorded species are not confined to oak wood, but can also fructify on wood of other deciduous trees, and to a lesser extent also on wood of coniferous trees. Some of them, like tomentelloid fungi, are not saprotrophs but ectomycorrhizal species, using oaks wood only as living habitat. Comparison of taxonomical structure of fungi on oak debris detected in this study with other related data is difficult because different sampling methods. Lindhe, Åsenblad and Toresson (2004) investigated only cut *Quercus robur* logs and reported that the logs harboured 53 fungal species, where the agarics comprised 45 %, corticioid fungi 13 %, and polypores 11 %. Our results (47 % of corticioid) are consistent with the data on fungi on coarse and fine woody debris in Sweden (Nordén et al. 2004), where the corticoid fungi also predominated (50 %).

Comparison of maturing and mature stands. The number of species and occurrence rate of wood-inhabiting fungi correlated positively not only with the CWD amount and volume, but also with DBH of living oak, as expression of stand age. Therefore, significantly more abundance of species was recorded in mature stands than in maturing ones. With a larger volume of CWD, higher numbers of wood-inhabiting fungal species could be expected. Thus, if in maturing stands the volume of CWD was larger the greater species richness of wood-inhabiting fungi would be expected. Despite the proportions of fungal groups being similar in stands of different age groups, the differences in species composition between mature and maturing plots as well as between plots of same age group were obvious. The number of unique species in mature stands was twice as high as in maturing ones, and red-listed species were found only in mature stands, an observation consistent with other studies showing that the red-listed wood-inhabiting fungi prefer old-growth forests (Sippola, Renvall 1999; Penttilä et al. 2004; Vasiliauskas et al. 2004) and woody debris of large diameter (Renvall 1995; Kruys et al. 1999; Lindhe et al. 2004). In our study the occurrence of two red-listed species only in mature stands can be explained by the preference of *Fistulina hepatica* to large trunks or stumps, and of *Xylobolus frustulatus* to coarse branches or fallen trunks of old oaks. Other red-listed species, such as *Inonotus dryadeus*, *I. dryophilus*, *Piptoporus quercinus*, *Grifola frondosa* and *Hapalopilus croceus*, not found during our research are mostly confined to large old living oak trunks or recently fallen ones. *Perenniporia medulla-panis,* specific to old oak stumps or snags, was also not recorded in study plots. This large diameter woody debris was remarkably scarce in both maturing and mature stands, which may have determined the low proportion of not only red-listed species, but of common polypores detected.

CONCLUSIONS

Our results confirm that wood-inhabiting fungal species richness depends on the amount of CWD. The average amount of CWD in managed mature oak stands in Lithuania is 13.9 m^3/ha. In accordance with similar studies (Kirby et al. 1991) it is evidently advisable to maintain not less than 20 m^3/ha of woody debris in temperate broadleaved stands.

Fallen branches comprise the largest fraction of oak CWD and greatest diversity of fungi species. However, large fallen trunks should be maintained in stands as well, because this valuable substrate is usually heterogeneous and comprises less or more decayed parts, and remnants of bark and branches; such substrate is especially important for rare polypores.

We conclude that, even in managed oak stands, oak CWD maintains a rather diverse species composition of ascomycetes and basidiomycetes. Although in general the highest species richness was detected in mature stands in our study, the species richness more correlated with the amount of CWD then with stand age itself.

Some maturing stands with a high amount of CWD, there were nearly as many or even more fungi than in particular mature stands. However, a very small amount of freshly fallen wood and strongly decayed woody debris, especially of large diameter trunks, and gaps in CWD continuity both in mature and maturing stands indicates long lasting management practices in Lithuanian oak stands, which reduce the distribution of highly specialized, usually rare, and endangered fungi.

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