Analysis of the species composition of epiphytic lichens in Central European oak forests

Analýza druhového složení epifytických lišejníků ve středoevropských doubravách

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This paper deals with the species composition of epiphytic lichens in Central European oak forests. A total of 192 oak trees at 48 localities in the Czech Republic, Slovakia and Hungary were investigated. In total, 104 lichen species were recorded and divided into three groups in accordance with their frequency of occurrence on trees within the area. The importance of abiotic factors affecting species composition was assessed by multivariate statistics. Principal component analysis illustrated that lichen assemblages reflected geographical distribution of localities and that the occurrence of many species is closely associated with several environmental factors. In particular there is a high negative association with pollution, and positive associations with precipitation, solar radiation and basic bedrock. The variation partitioning estimated the influence of environmental parameters, human impact and naturality factors on lichen composition. Cluster analysis recognized six communities of lichens, of which the members differed from those in the other communities in their autecological characteristics. Two of the communities can be assigned to *Parmelion caperatae* and *Pertusarion amarae* and seem to be similar to natural lichen communities of oak forests in Central Europe. Possible reasons for absence of several epiphytic lichen associations (*Lobarion pulmonariae*, *Pertusarion hemisphaericae*) in the forests studied is discussed and the species composition in Central Europe was compared with the lichen assemblages in oak forests in neighbouring regions (western Europe, Scandinavia). On the basis of these findings several indicative species of close to natural oak forest are suggested (*Acrocordia gemmata*, *Bacidia rubella*, *Calicium* spp., *Caloplaca lucifuga*, *Cetrelia olivetorum* s.l., *Chrysothrix candelaris*, *Flavoparmelia caperata*, *Melanelia subargentifera*).

Keywords: environmental factors, indicator species, lichen associations, Lichen Diversity Value, multivariate analyses, pollution, *Quercus petraea*, *Q. pubescens*, *Q. cerris*

Introduction

Oak forests and mixed deciduous forests with oaks are probably the most widespread forest types in the lowlands of Central Europe. From the Atlantic period, the major part of Europe was covered with different types of woodland (Godwin 1975). In the lowlands the forests were dominated by hardwoods with oak trees as the main component (Neuhäuslová et al. 1998). During medieval and modern period the majority of these forests have been changed. Until recently, only a few of the natural or semi natural ecosystems persisted in western Europe (Rose 1974, Bates 1992) and practically no primeval forest of this type exists now in the Central European region with almost all oak forests only “close to natural”.

Oak (*Quercus petraea*, *Q. robur*, *Q. pubescens*, *Q. cerris* and their hybrids) is the principal tree of several mixed deciduous forest alliances in the Czech Republic (Chytrý et al. 2001) and neighbouring European countries (Slovakia, Austria, Germany, Hungary). Generally, oak trees are very rich in epiphytic lichens (Hilitzer 1925, Rose 1974, Bates 1992, Svoboda et al. 2010). Unlike in some coastal regions of Europe (for example those sampled by Rose 1992, James et al. 1977, Bates 1992), the natural development of most Central European forests during the last two centuries has been adversely affected by pollution, tree cutting and other negative influences. Thus, many sensitive lichen alliances, such as *Lobarion pulmonariae,* have declined and persist only at several favourable sites, often as only partially developed associations (Liška 1996).

Rose (and several other authors) developed the methodology for estimating forest or landscape conditions, especially those favouring the long-term persistence of ancient woodlands (Rose 1974) and established the Index of Ecological Continuity (Rose 1976, 1992). This approach is based on the detection of specific epiphyte species that are considered as "old-forest indicators" for natural, long-persistent woodlands. It was proposed for the British Isles and similar climatic regions of Europe. The more continental climate of Central Europe (many indicative species described in the above mentioned studies prefer a humid climate) could therefore restrict the presence of such lichen communities and distort the results. The second important difference is the high level of background pollution, which is unfavourable for the development of the lichen assemblages cited in the original literature (Rose 1974, 1976) for unpolluted woodlands.

A large number of publications deal with investigations of epiphytes in untouched or not significantly affected forest communities, especially in western European countries and Scandinavia (e.g. Bates et al. 1981, 2001, Gauslaa 1985, Ranius et al. 2008). Of the studies on Central European oak forests only a few focus on the diversity and species preferences of lichens.

The objectives of the present study are to (i) determine the current composition of epiphytic lichens in selected oak forests in Central Europe; (ii) analyse the occurrence of the species recorded in relation to abiotic factors and epiphytic associations of the lichens; (iii) select possible indicator species of natural thermophilous and dry acidophilous oak forests in Central Europe.

Material and methods

Study area

In the temperate climatic zone of Central Europe, diverse types of oak forest can naturally occur in lowlands up to ca 600 m a.s.l., especially in semi-dry or sub-xerothermic habitats (Janssen & Seibert 1991, Neuhäuslová et al. 1997). Remnants of natural (or close to natural) oak forests occur at several sites. For this study the following biotopes (from NATURA 2000 programme, www.natura.org; Chytrý et al. 2001) were selected: thermophilous oak forests and dry acidophilous oak forests (for detailed information on these forest associations see Svoboda et al. 2010).

In total, 48 localities were chosen for this study: 35 in the Czech Republic, 12 in Slovakia and one in Hungary (Fig. 1). Generally, the north-western part of the area investigated is more industrial and the south-eastern part less industrialized with a predominantly

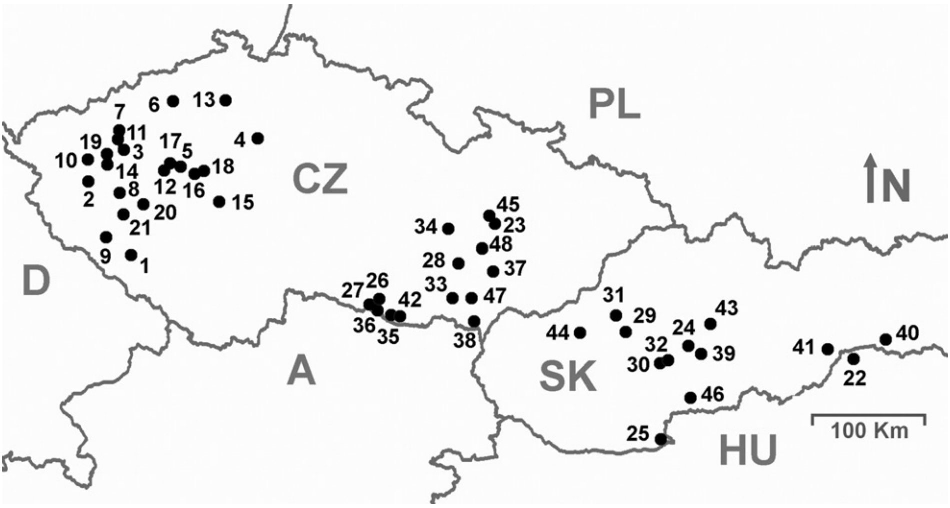

Fig. 1. – Map of Central Europe showing the localities sampled (numbered black circles). Abbreviations: A – Austria, CZ – Czech Republic, D – Germany, HU – Hungary, PL – Poland, SK – Slovakia. For detailed characteristics of each locality see Svoboda et al. (2010).

agricultural and forested landscape. The forests selected included 42 sites with *Quercus petraea* or mixture of *Q. petraea* and *Q. pubescens*, and six localities with *Q. cerris* or a mixture of *Q. cerris* and *Q. petraea/pubescens* (identification of oaks follows the key of Koblížek 1990). Forests of natural or seminatural status were chosen based on the literature and other authors' observations (Němec & Ložek 1996, Mackovčin & Sedláček 1999, 2002, Stanová & Valachovič 2002).

Sampling design

The selection of the sampling sites was based on the following criteria: inclination up to 35°; locality not directly affected by traffic, industry or other types of direct anthropogenic disturbance; minimal understory layer cover; oak canopy cover at least 75%; forest age at least 40 years. These types of localities were generally found on rocky escarpments, steep slopes and at other relatively inaccessible areas, because more accessible sites in Central Europe have been subjected over centuries to intensive use by man.

The 48 sites chosen were greater or equal in area to 1 ha (100 × 100 m). The areas sampled (50 × 50 m) within well-developed oak vegetation were as close to the centre of the locality as possible.

Lichen sampling

The lichen samples were treated using two different methods: the presence of all the lichen epiphytes, both macro- and micro-lichens, was recorded on all the oak trees (on tree trunks up to 2 m above the ground) in each plot.

Furthermore, measurements of the lichen diversity value (LDV) were made in accordance with the European Guideline for mapping lichen diversity as an indicator of environmental alteration (Asta et al. 2002) in each of the plots. The original guideline, however, was modified (see below). The LDV data record the frequencies of all the species of lichen in quadrate segments in a terrain grid placed at four cardinal points on selected trees. LDV measurements of four oak trees at each locality were taken. Following the recommendations of Asta et al. (2002) sampling was limited to vertical trees not directly influenced by the shrub layer and with a diameter greater than 20 cm. Lichen diversity value per plot was the mean of the LDV values obtained from individual trees (following protocol in Asta et al. 2002). Lichens were usually identified in the field, however, some were identified in the laboratory using standard techniques. Nomenclature of lichen species follows Liška et al. (2008).

Environmental data

Environmental data at tree- and plot-levels were collected for each sample. These included oak species; forest age (data from Forest Management Institute – www.uhul.cz, and historical maps from mid 19th century); forest cover (as % of forest per 10×10 km square in the neighbourhood of the locality); GPS-derived coordinates of latitude and longitude (north-GPS, east-GPS); altitude; mean annual potential direct radiation, calculated according to Herben (1987) as a function of slope, orientation and latitude of the site; mean annual precipitation (Veselský et al. 1958); general character of bedrock (acid-basic) and air pollution levels in 1996 and 2005: mean annual concentrations of SO_2 (SO_2-96, SO_2-05), NO_X (NO_X-96, NO_X-05) and particulate matter up to 10 μm in diameter (PM10s-96, PM10s-05), which were obtained from the Czech Hydrological and Meteorological Institute and Slovak Hydrological and Meteorological Institute. Air pollution at the sites in 1996 (2005) varied from 5–35 (0–10) $\mu g \cdot m^{-3}$ for SO_2, 10–35 (10–35) $\mu g \cdot m^{-3}$ for NO_X and 10–65 (10–35) $\mu g \cdot m^{-3}$ for PM10s.

Statistical analyses

Principal component analysis (PCA) was used to describe general patterns in lichen community structure (CANOCO for Windows ver. 4.5, ter Braak & Šmilauer 2002). The relationships among sites, factors and species were illustrated using an ordination diagram based on the presence/absence of lichen species at 48 sites (CanoDraw for Windows, ter Braak & Šmilauer 1998). The sizes of site symbols correspond to the species richness at each locality (Lepš & Šmilauer 2003). Ecological variation in species data (presence/absence of lichen species on 4 oak trees at 48 sites, i.e. 192 samples) was partitioned according to Borcard et al. (1992). Partialling of the ecological correlation was changed from two components to three: "naturality" factors (forest age, forest cover, tree diameter), anthropogenic impact (concentrations of air pollutants) and environmental parameters (precipitation, potential radiation, altitude, slope, GPS coordinates, tree species). Percentage of variation and covariance between variables were calculated using a series of canonical correspondence analyses (CCA) in CANOCO for Windows and illustrated using a Venn diagram obtained by using R ver. 2.10.1 (R Development Core Team 2010) and a venneuler package (Wilkinson 2008, 2010).

Correlation between species occurrence and environmental variables was tested by using Spearman's rank correlation coefficient, based on 192 samples (PAST ver. 1.74, Hammer et al. 2001). The following categories of variables were used: geographic positions (north-west1, north-west2, south-east1, south-east2), lichen diversity values (6–19, 20–29, 30–39, 40–49, 50–59, 60–72, 78–107) and tree diameters (12–19, 20–29, 30–39, 40–49, 50–59, 60–90 cm). Preference for a particular geographic region (north-west or south-east) was assigned to species that were significantly positively correlated with one region and negatively correlated with another ($P < 0.01$). Groups of lichen species that occurred together were assessed by cluster analysis using Spearman's coefficient (Legendre 2005). Groups containing at least five species were selected on the basis of their autecological characteristics (e.g. Hilitzer 1925, Barkman 1958, Wirth 1995). Species with similar ecological preferences occur inside the same group.

Results

Lichen species

A total of 104 species of epiphytic lichens were recorded at the 48 localities (plots). Species richness varied from three to 46 taxa per locality. The minimum number of species recorded on a tree trunk was one and the maximum number 22. The average number was almost nine species per tree. Eleven species were recorded only once. Among them, several "incidental" species, which grow commonly on other substrates, such as woodland floors or bryophytes, were identified.

Recorded lichens can be placed into one of three groups based on the frequencies of their presence (Table 1):

(1) The following nine common abundant epiphytes were found on more than 50% of the trees sampled: *Amandinea punctata*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Lecanora conizaeoides*, *L. expallens*, *Lepraria incana*, *Melanelia fuliginosa*, *Parmelia sulcata* and *Phlyctis argena*.

(2) The following 13 less common species occurred on 20–50% of the trees sampled: *Candelariella reflexa*, *C. xanthostigma*, *Cladonia coniocraea, C. fimbriata, Evernia prunastri*, *Flavoparmelia caperata*, *Lecanora chlarotera*, *Pertusaria albescens*, *P. amara, Physconia enteroxantha*, *Punctelia jeckeri*, *Ramalina pollinaria* and *Scoliciosporum chlorococcum.*

(3) A total of 82 infrequent species, including rare species with an occurrence below 20%, were recorded. There were also 64 taxa with occurrences below 10%, e.g. *Acrocordia gemmata*, *Anaptychia ciliaris*, *Bacidia rubella*, *Buellia griseovirens, Calicium glaucellum*, *C. salicinum, Caloplaca cerina, C. lucifuga, Cetrelia olivetorum* s. l., *Flavopunctelia flaventior*, *Chaenotheca phaeocephala*, *Chrysothrix candelaris*, *Melanelia glabra*, *M. subargentifera*, *Parmelina quercina*, *Pertusaria coccodes*, *P. flavida*, *P. hemisphaerica*, *Phaeophyscia endophoenicea*, *Ramalina fastigiata*, *R. fraxinea*, *Rinodina exigua*, *Scoliciosporum sarothamni*, *Tuckermanopsis chlorophylla*, *Usnea filipendula*, *U. hirta* and *Xanthoria candelaria*.

Besides species richness, the Lichen diversity value (LDV) was used as an indicator of lichen diversity. The LD values for particular localities ranged from 17 to 88 and those for individual trees between 6 and 107.

Table 1. – List of lichen species recorded in the study, with the frequency of occurrence; values are percentages of the 192 oak trees on which the species occurred.

Species	Frequency (%)	Species	Frequency (%)
Acrocordia gemmata	12	*Melanelia glabra*	6
Agonimia tristicula	1	*Melanelia subargentifera*	11
Amandinea punctata	73	*Melanelia subaurifea*	4
Anaptychia ciliaris	10	*Micarea peliocarpa*	1
Bacidia egenula	1	*Micarea prasina* s.l.	1
Bacidia rubella	10	*Parmelia ernstiae*	1
Bryoria fuscescens	3	*Parmelia saxatilis*	19
Buellia griseovirens	6	*Parmelia submontana*	1
Calicium glaucellum	3	*Parmelia sulcata*	63
Calicium salicinum	2	*Parmelina quercina*	3
Caloplaca cerina	3	*Parmelina tiliacea*	17
Caloplaca ferruginea	1	*Parmeliopsis ambigua*	17
Caloplaca lucifuga	2	*Pertusaria albescens*	28
Candelariella reflexa	21	*Pertusaria amara*	26
Candelariella xanthostigma	39	*Pertusaria coccodes*	2
Catillaria globulosa	2	*Pertusaria flavida*	2
Cetrelia olivetorum s.l.[1]	2	*Pertusaria hemisphaerica*	1
Chaenotheca ferruginea	15	*Phaeophyscia endophoenicea*	1
Chaenotheca furfuracea	1	*Phaeophyscia nigricans*	2
Chaenotheca chrysocephala	18	*Phaeophyscia orbicularis*	3
Chaenotheca phaeocephala	4	*Phlyctis argena*	66
Chaenotheca trichialis	1	*Physcia adscendens*	17
Chrysothrix candelaris	1	*Physcia aipolia*	1
Cladonia coniocraea	41	*Physcia biziana*	1
Cladonia digitata	3	*Physcia stellaris*	2
Cladonia fimbriata	40	*Physcia tenella*	17
Cladonia ochrochlora	1	*Physconia enteroxantha*	22
Cladonia pyxidata	3	*Physconia grisea*	2
Coenogonium pineti	1	*Physconia perisidiosa*	8
Diploschistes muscorum	1	*Placynthiella icmalea*	2
Evernia prunastri	43	*Platismatia glauca*	9
Flavoparmelia caperata	27	*Pleurosticta acetabulum*	6
Flavopunctelia flaventior	2	*Pseudevernia furfuracea*	11
Hypocenomyce caradocensis	17	*Punctelia jeckeri*	22
Hypocenomyce scalaris	52	*Ramalina farinacea*	18
Hypogymnia physodes	78	*Ramalina fastigiata*	7
Hypogymnia tubulosa	10	*Ramalina fraxinea*	4
Imshaugia aleurites	1	*Ramalina pollinaria*	34
Lecanora albella	1	*Rinodina exigua*	1
Lecanora carpinea	8	*Scoliciosporum chlorococcum*	33
Lecanora conizaeiodes	71	*Scoliciosporum sarothamni*	1
Lecanora expallens	93	*Scoliciosporum umbrinum*	3
Lecanora chlarotera	31	*Strangospora* sp.	2
Lecanora saligna	3	*Trapeliopsis flexuosa*	2
Lecidella elaeochroma	11	*Trapeliopsis granulosa*	2
Lecidella euphorea	2	*Tuckermanopsis chlorophylla*	4
Lepraria sp.	19	*Usnea filipendula*	2
Lepraria incana	81	*Usnea hirta*	2
Lepraria membranacea	1	*Usnea sp.*	6
Leprocaulon microscopicum	4	*Xanthoria candelaria*	3
Melanelia exasperatula	5	*Xanthoria parietina*	12
Melanelia fuliginosa	71	*Xanthoria polycarpa*	3

[1]After Smith et al. (2009)

Whether the lichen frequencies on different species of oak (*Quercus petraea, Q. pubescens*, *Q. cerris*) differed was tested. The LDV calculated for individual trees did not significantly differ among oak species (Kruskal-Wallis test, $P > 0.05$). Furthermore, there was not a significant difference in the species composition of the lichens on the different species of oak.

Lichens and environmental factors

In the PCA of localities, factors and species (Fig. 2), most of the north-western sites (Bohemia) were separated from the south-eastern stands (Moravia, Slovakia, Hungary) along the first ordination axis (22.5% of the explained variation); consequently GPS coordinates were found to be highly correlated with the first axis. Air pollution values were higher in the north-west. The species richness and LDV evidently changed with respect to the geographic position of sites, with species diversity increasing from north-west to south-east. Detailed analyses of correlations between lichen diversity (LDV, species richness), human factors and natural parameters are presented in a previous study of Svoboda et al. (2010).

The majority of species are negatively correlated with the north-GPS and air pollution. Some species are strongly positively correlated with high values of precipitation and potential radiation (e.g. *Anaptychia ciliaris*, *Flavoparmelia caperata*, *Pertusaria albescens*, *Ramalina* spp.) and others are associated with oak forests growing on basic bedrocks (e.g. *Acrocordia gemmata*, *Candelariella reflexa*, *Lecanora chlarotera*, *Xanthoria parietina*). Several species, such as *Parmelia saxatilis*, *Pertusaria amara* and *Platismatia glauca*, seem to be associated with old forests and areas with high forest cover. However, these relationships were not tested.

The variation in species composition that can be explained by the three groups of abiotic factors is depicted in the Venn diagram in Fig. 3. All factors together explained 26.5% of total variation in species composition. The factors forest age, forest continuity and tree diameter contribute, independently of the influence of other two groups, 3.6% of total variation, the environmental/natural parameters (precipitation, potential radiation, altitude, slope, GPS-coordinates, tree species) explained 10.2% and the anthropogenic factors (concentration of air pollutants) 6.2% of the total variation. These three groups of parameters covariate with each other and the highest amount of shared variability is between anthropogenic factors and environmental parameters.

Cluster analysis

Cluster analysis, using Spearman's correlation coefficient as a distance metrics, was used to reveal the co-occurrence of lichen species (i.e. species associations; Table 2). Small groups formed early in the hierarchy were rejected and six groups were finally recognized (Fig. 2, Table 2).

Group 1 includes acidophytic crustose ombrophobic species (e.g. *Calicium glaucellum*, *C. salicinum*, *Chaenotheca ferruginea*, *Lepraria incana*). Group 2 is distinctive in including acidophytic crustose species (e.g. *Hypocenomyce caradocensis*, *H. scalaris*, *Chaenotheca chrysocephala*, *Lecanora conizaeoides*) that were found especially in the north-western part of the study area, characterized by high levels of air pollution (with the exception of the strongly adidophytic but toxic intolerant *Caloplaca lucifuga*). *Lecanora*

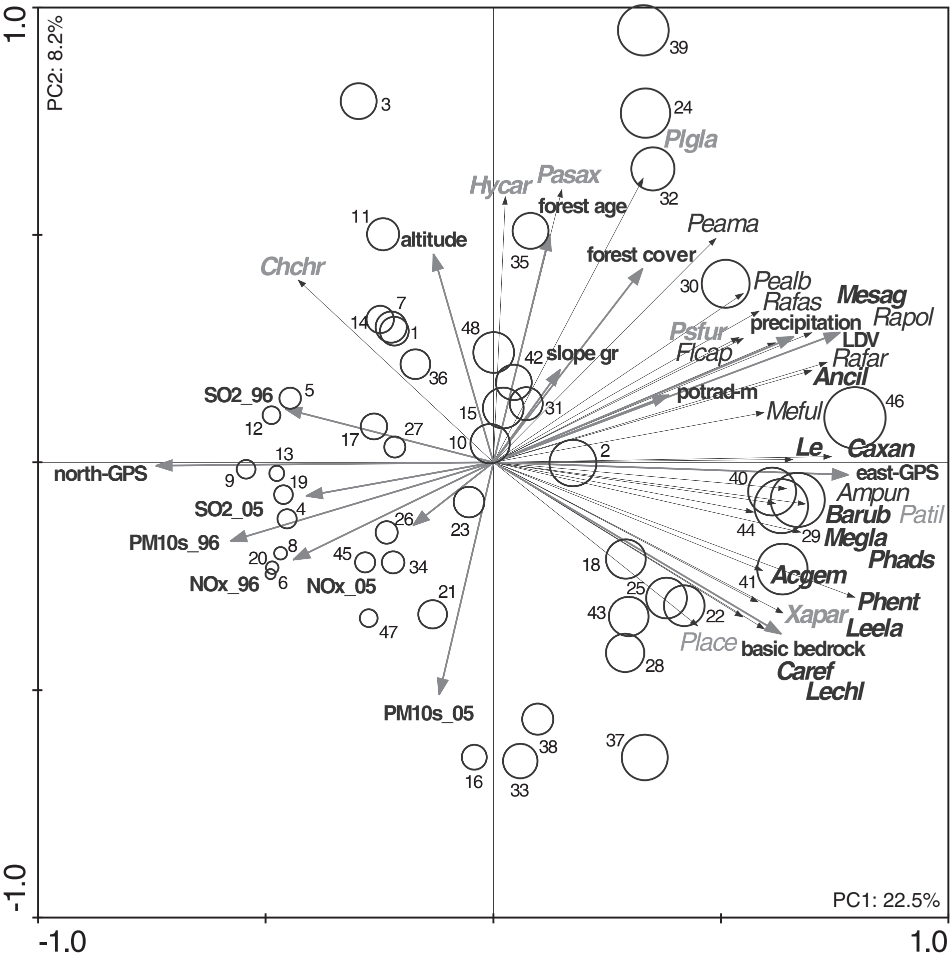

Fig. 2. – Ordination of localities, factors and species (PCA). The sizes of site symbols (circles) correspond to the species richness at each locality. For the description of localities see Svoboda et al. (2010). Abbreviations: NOx_96, NOx_05, PM10s_96, PM10s_05, SO2_96, SO2_05 – mean annual concentrations of air pollutants in 1996 and 2005; potrad-m – mean annual potential direct solar radiation; slope_gr – slope inclination. Species codes: Acgem – *Acrocordia gemmata*, Ampun – *Amandinea punctata*, Ancil – *Anaptychia ciliaris*, Barub – *Bacidia rubella*, Caref – *Candelariella reflexa*, Caxan – *Candelariella xanthostigma*, Chchr – *Chaenotheca chrysocephala*, Flcap – *Flavoparmelia caperata*, Hycar – *Hypocenomyce caradocensis*, Le – *Lepraria* sp. non *incana*, Lechl – *Lecanora chlarotera*, Leela – *Lecidella elaeochroma*, Meful – *Melanelia fuliginosa*, Megla – *Melanelia glabra*, Mesag – *Melanelia subargentifera*, Pasax – *Parmelia saxatilis*, Patil – *Parmelina tiliacea*, Pealb – *Pertusaria albescens*, Peama – *Pertusaria amara*, Phads – *Physcia adscendens*, Phent – *Physconia enteroxantha*, Place – *Pleurosticta acetabulum*, Plgla – *Platismatia glauca*, Psfur – *Pseudevernia furfuracea*, Rafar – *Ramalina farinacea*, Rafas – *Ramalina fastigiata*, Rapol – *Ramalina pollinaria*, Xapar – *Xanthoria parietina.* Species names in different colours and fonts correspond to groups identified by cluster analysis. Group 6 – bold black; group 5 – black; groups 3 and 4 – bold grey; not clustered species – grey.

conizaeoides is closely associated with a low LDV. Group 3 includes foliose acidophytes (e.g. *Hypogymnia tubulosa*, *Parmelia saxatilis*, *Platismatia glauca*, *Pseudevernia furfuracea*). Groups 1–3 are positioned close to each other and have a joint root.

Table 2. – The results of cluster analysis and correlation analyses using Spearman's coefficients. Six clusters of species associations (1–6) contained species that occur together and have similar ecological preferences. Data in brackets are the significant correlations between species (Spearman's rho, $P < 0.01$) and the parameters associated with species diversity recorded in the study area. The additional group at the bottom of the table is composed of species that do not form a cluster and are significantly correlated with at least one parameter. Geographical area studied (NW – north-west, SE – south-east), significant interval of tree diameter categories, and significant range of Lichen Diversity Values are indicated.

1	***Calicium glaucellum***, ***Calicium salicinum***, ***Chaenotheca ferruginea*** (NW, diameter 30–39 and 60–90), ***Lepraria incana*** (SE, diameter 20–29), ***Scoliciosporum umbrinum*** (diameter 60–90)
2	***Caloplaca lucifuga***, ***Hypocenomyce caradocensis*** (NW, diameter 40–49), ***Hypocenomyce scalaris***, ***Chaenotheca chrysocephala*** (NW, diameter 40–49 and 60–90), ***Lecanora conizaeoides*** (NW, LDV 20–29)
3	***Hypogymnia tubulosa***, ***Parmelia saxatilis*** (LDV 78–107), ***Parmeliopsis ambigua*** (NW), ***Platismatia glauca***, ***Pseudevernia furfuracea***
4	***Lecanora saligna*** (LDV 60–72), ***Melanelia subaurifea***, ***Physcia tenella***, ***Tuckermanopsis chlorophylla***, ***Usnea* sp.** (NW, LDV 60–72), ***Xanthoria candelaria***, ***Xanthoria parietina*** (LDV 60–107), ***Xanthoria polycarpa*** (LDV 60–72)
5	***Amandinea punctata*** (SE, LDV 78–107, diameter 10–19), ***Evernia prunastri*** (SE, LDV 78–107), ***Flavoparmelia caperata*** (SE, LDV 78–107), ***Hypogymnia physodes***, ***Lecanora expallens*** (SE), ***Melanelia fuliginosa*** (SE, LDV 60–107), ***Parmelia sulcata*** (SE, LDV 60–107, diameter 12–19), ***Pertusaria albescens*** (SE, LDV 78–107, diameter 12–19), ***Pertusaria amara***, ***Phlyctis argena*** (SE, LDV 78–107, diameter 12–19), ***Ramalina farinacea*** (SE, LDV 78–107), ***Ramalina fastigiata*** (LDV 78–107), ***Ramalina pollinaria*** (SE, LDV 78–107)
6	***Acrocordia gemmata*** (SE, LDV 78–107), ***Anaptychia ciliaris*** (SE, LDV 78–107, diameter 12–19), ***Bacidia rubella*** (SE, diameter 12–19), ***Caloplaca cerina***, ***Candelariella reflexa*** (LDV 50–59 and 78–107), ***Candelariella xanthostigma*** (SE, LDV 78–107), ***Lecanora chlarotera*** (SE, LDV 78–107), ***Lecidella elaeochroma*** (LDV 78–107), ***Lepraria* sp. non *incana*** (LDV 60–107), ***Melanelia glabra*** (LDV 78–107), ***Melanelia subargentifera*** (LDV 78–107), ***Physcia adscendens***, ***Physcia stellaris***, ***Physconia enteroxantha*** (LDV 78–107), ***Ramalina fraxinea*** (LDV 78–107)
–	[***Buellia griseovirens*** (SE, LDV 78–107), ***Catillaria globulosa*** (diameter 50–59), ***Chaenotheca phaeocephala*** (LDV 78–107), ***Parmelina tiliacea*** (SE, LDV 60–107)]

Group 4 includes species associated with a rather high LDV. It includes acidophytes (*Melanelia subaurifera*, *Tuckermanopsis chlorophylla*) and nitrophytes (*Physcia tenella*, *Xanthoria* spp.), growing often on young stems or horizontal twigs of oak. The majority of the lichens in this group are abundant or less frequent species (Table 1).

Group 5 includes neutrophytic or slightly acidophytic species. Some of these lichens may be abundant (e.g. *Amandinea punctata*, *Hypogymnia physodes*, *Lecanora expallens*, *Parmelia sulcata*) or less frequent (*Flavoparmelia caperata*, *Pertusaria amara*, *Ramalina pollinaria*; Table 1). The majority of them occur in the south-east of the area and are associated with a high LDV.

Group 6 includes lichens that occur at south-eastern localities with high LD values. The occurrence of these species is associated also with basic bedrock (e.g. *Acrocordia gemmata*, *Anaptychia ciliaris*, *Bacidia rubella*, *Lecanora chlarotera*, *Lecidella elaeochroma*, *Melanelia glabra*, *M. subargentifera*, *Physconia enteroxantha*, *Ramalina fraxinea*).

Besides cluster analysis the associations of individual lichen species with variables associated with species diversity (LDV, geographic position, tree diameter) were tested. Thirty-nine of the epiphytic lichens are significantly associated ($P \leq 0.01$) with at least one of the above variables (Table 2). The majority of these species tended to occur on trees

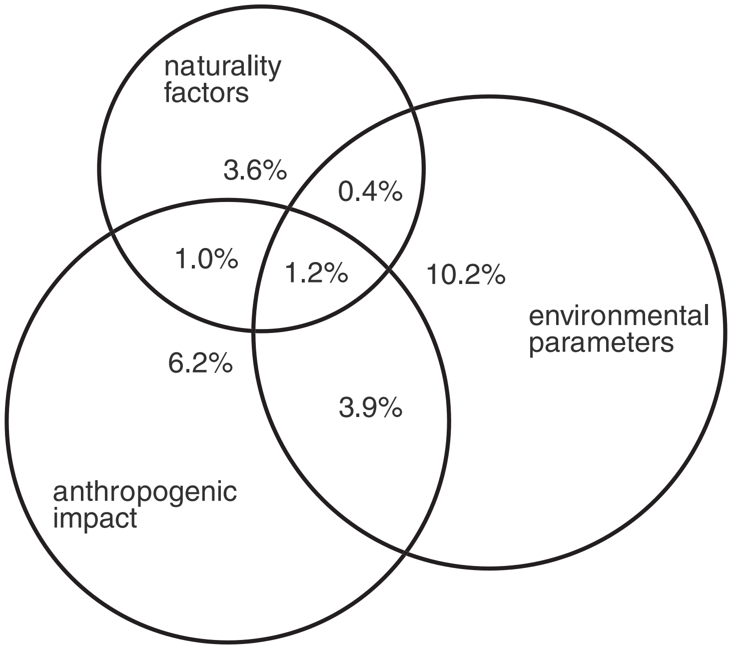

Fig. 3. – Variation in species composition as explained by the three groups of abiotic factors, using a series of canonical correspondence analyses. Modified method of Borcard et al. (1992) was used to separate the variation and covariation in species data explained by three environmental components: naturality factors (forest age, forest continuity, tree diameter), anthropogenic effects (concentrations of air pollutants) and environmental/natural parameters (precipitation, potential radiation, altitude, slope, GPS coordinates, tree species). Variation in these parameters accounted for 26.5% of the total variability in species composition. The three rings of the Venn diagram demonstrate the contribution of each group to total variation and covariance of groups with each other (overlaps between circles with indicated percentage).

with high lichen diversities, only *Lecanora conizaeoides*, *Lecanora saligna* and *Xanthoria polycarpa* are associated with low LDVs. The acidophytic species *Chaenotheca ferruginea*, *C. phaeocephalla*, *Hypocenomyce caradocensis*, *Lecanora conizaeoides*, *Parmeliopsis ambigua* and *Usnea* spp. occurred significantly more frequently in the polluted north-western part of the study area. The occurrence of only a few lichens was significantly associated with a certain tree diameter. Although found on oaks with narrow trunks, they all occurred in the south-eastern part of the study area (e.g. *Amandinea punctata*, *Bacidia rubella*, *Parmelia sulcata*). Ombrophobic lichens (*Chaenotheca chrysocephala*, *C. ferruginea*) are mainly associated with oak trees with wide trunks.

Discussion

The cluster analysis delimited six distinct groups of lichen associations in oak forests in the areas studied. The first three groups comprise mainly very common species with a high affinity for acid bark. They occur in oak stands strongly affected by human activity. Group 2, in particular, is composed mainly of the highly toxic tolerant crustose species *Lecanora* *conizaeoides*. This community is very common in the north-western part of the study area, which is characterized by intensive human exploitation and high levels of pollutants. The third group consists mainly of associations of the foliose acidophytic species *Parmeliopsis ambigua* and *Pseudevernia furfuracea* (sensu Hilitzer 1925 and Barkman 1958), which are also highly tolerant of air pollution (Barkman 1958).

Group 4 includes an interesting mixture of lichens. Some of them are nitrophytes belonging to *Xanthorion* (*Physcia tenella, Xanthoria candelaria*, *X. parietina*, *X. polycarpa*). Their presence on oak trees indicates eutrophication, because oak has naturally subneutral bark (Barkman 1958, Bates 1992). The other species are acidophytic lichens (*Usnea* sp., *Melanelia subaurifera* and *Tuckermanopsis chlorophylla*) and early colonizers of previously polluted areas in Central Europe (Svoboda & Peksa 2008). Thus, this group includes lichen species that indicate human influence.

Groups 5 and 6, the most species-rich groups, seem to be the close-to-final communities in oak forests in the area studied. These groups occur at localities with relatively well conserved forests in the south-eastern part of the area studied, which is characterized by high values of LDV, species richness and precipitation. Group 5 is dominated by species belonging to *Parmelion caperatae* (*Parmelietum revolutae* var. *caperatosum* Barkman 1958) and lichens of the related association, *Pertusarietum amarae*. Barkman (1958) describes var. *caperatosum* as the most xerophytic and nitrophobic variant of *Parmelietum revolutae*. This characteristic is in accordance with that recorded. Furthermore, Barkman also considers this association to be the most toxic tolerant variant of *Parmelietum revolutae*. However, in the context of the current levels of air pollutants, *F. caperata* has a limited distribution in the study area (it occurs at 19 of the 48 localities). It is practically absent in the north-western part, although in the first half of 20th century it was the most typical macrolichen on oaks in Central Europe (Suza 1925a, Černohorský et al. 1956; A. Vězda, pers. comm.). On the other hand, the association with *P. revoluta* (species currently known only from five localities in the Czech Republic; Vondrák & Liška 2010) is uncommon in Central Europe; occurring only in humid valleys and especially on *Alnus* sp. rather than oak in drier areas (Suza 1925b, 1944).

Ramalina pollinaria and *R. farinacea* are included in group 5. Suza (1925a, 1944) records that in the former Czechoslovakia these two *Ramalina* species occurred commonly on rough bark of oaks. According to Hilitzer (1925), the species of *Pertusarion amarae* (*P. amara*, *P. albescens*, *Phlyctis argena*) occur only on isolated and old trees in oak forests. The results of the field investigations confirm his observations. Barkman (1958) and James et al. (1977) combine *Pertusarietum amarae* and *Pertusarietum hemisphaericae* with several variants of this association. Other authors (Ritschel 1977, Neuwirt & Türk 1993) distinguish the association *Pertusarietum amarae* from that of *Pertusarietum hemisphaericae* because species of the latter prefer a higher rainfall and more open stands. Prigodina Lukošienė & Naujalis (2009), who studied the lichen communities on *Quercus robur* in more oceanic Lithuania, recorded *Pertusarietum hemisphaericae* mostly on mature oaks and less frequently on beech. The species of *Pertusarietum hemisphaericae* (*Pertusaria hemisphaerica*, *P. coccodes*, *P. flavida*) were recorded only rarely in this study and always in mature oak forests in areas with high precipitation (about 900 mm/yr), particularly in Central Slovakia. In the Czech Republic, this community is predominantly associated with beech forests at altitudes above 800 m a.s.l., subject to high levels of precipitation (D. Svoboda, unpublished observation).

Group 6, the most species numerous group differentiated by cluster analysis, corresponds to natural oak stands with the most developed lichen diversity. This community occurs especially in regions where there is little human impact (low pollution levels, high forest cover, no clear cutting), and high values of environmental factors important for development of natural lichen associations, i.e. the age of the trees and forest continuity. Moreover, many of the sites with this lichen composition are on basic bedrock. This suggests that group 6 could be treated as a close-to-natural lichen community. Nevertheless, it is difficult to differentiate this phytosociological association, because the clustered species belong to a mixture of associations (e.g. *Physcietum adscendentis*, *Ramalinetum fastigiatae*, *Parmelietum acetabuli*). Therefore, the observations and analyses are used only to compare the general characteristics of these species. All are associated with the bark of mature oak trees that has a neutral reaction. These lichens occur mainly in central Slovakia where there are large forests that have a prolonged ecological continuity. Many stands with these species occur on exposed slopes, or are in old "pasture woodlands" (sensu Rose 1976). Furthermore, Rose (1976) characterized well developed forests with a long ecological continuity by a high diversity of species growing in the forests. The authors of LDV methodology and the "naturality" approach (Asta et al. 2002, Loppi et al. 2002) also assume that a high diversity of lichens (i.e. number of species per stand) indicates a less disturbed biotope.

The results indicate that the species in groups 5 and 6 are characteristic of communities occurring in well developed oak forests in Central Europe. However, group 5 includes more acidophytic, xerophytic and toxic tolerant species than group 6, which are associated with bark with a high pH and a more stable forest microclimate.

Unfortunately, practically none of the indicator species listed by Rose (1974, 1976) or Johansson et al. (2003), especially epiphytic cyanolichens, were found. Several studies describe associations of epiphytic cyanolichens with old forests, where these species form a substantial part of the associations with *Lobaria* and *Sticta* (Rose 1976, Gauslaa 1985, Goward & Arsenault 2000, Hedenås & Ericson 2008). It is likely that pollution and forest degradation during the last century is the main reason for the absence of such species. However, Stofer et al. (2006) record that not every old forest is a suitable habitat for cyanolichens. Other factors such as climatic conditions, isolation of forest stands or species composition of forest trees may affect the presence of these lichens in forest ecosystems (Hedenås & Ericson 2000). Climatic factors are more important in Central Europe than in oceanic regions (Hilitzer 1925). Ellis & Coppins (2007) demonstrate that the continental-oceanic geographic gradient is associated with a decrease in the frequencies of green-algal and crustose lichens and a concomitant increase in the frequencies of bryophytes, tripartite and foliose cyanolichens. They also suggest that in more continental climatic conditions, the lower photosynthetic efficiency of cyanolichens compared with green-algal photobionts may limit cyanolichen establishment and growth, despite N_2 fixation. The tree species composition of oak dominated stands may also affect the occurrence of epiphytes (Stofer et al. 2006). However, it is unknown whether in these types of central European oak forests epiphytic cyanolichens occurred or could occur in the past.

The lack of the *Lobarion* association and predominant presence of the *Parmelion caperatae* or the *Parmelia sulcata* association (Hilitzer 1925) in old growth lowland oak forests with a long continuity in Central Europe indicates another difference from the results of similar studies in Scandinavia and the British Isles (Rose 1976, Bates et al. 1981, Gauslaa 1985, Bates 1992). There are several explanations for this phenomenon. *Lobarion* usually occurs at altitudes higher than 900 m a.s.l. in Central Europe, as precipitation is higher there (Hilitzer 1925, Suza 1925b), but the altitudinal limit for oak forests in Central Europe is, in most cases, below 900 m. This hypothesis is supported by observations of remnants of *Lobarion* associations in Muráň National Park in Slovakia, where azonal oak forest grows on limestone at an altitude of 800–900 m (Guttová & Palice 2005). Another reason is surely the effect of atmospheric pollution on *Lobarion* species (Hawksworth & Rose 1970, Ekman 1989). Since *Lobarion* is restricted to bark that is not strongly buffered with a relatively high pH (5.0–6.0, Gauslaa 1985, Rose 1988), acid rain has a negative effect (Gilbert 1986, Farmer et al. 1992). Furthermore, fragmentation of forests has a negative influence on species richness and especially on the presence of sensitive lichens with limited dispersal ability, including the *Lobarion* species (Hilitzer 1925, Löbel et al. 2006, Hedenås & Ericson 2008, Svoboda et al. 2010). Drier continental climatic conditions amplify the effect of fragmentation (Gauslaa 1985). In addition to pollution and forest degradation, the climatic conditions probably have the most important effect on *Lobarion* occurrence in oak forests in Central Europe as this association occurs more frequently in montane (beech) forests, which have a more suitable climate, than in lowland forests.

The indicator species were those associated with the predictive variables historical landscape and age of stand, i. e. forest age, tree diameter and forest continuity (Rose 1976, Uliczka & Angelstam 1999, Johansson et al. 2003, Nitare 2005). Based on field observations and statistical analyses, it is suggested that the following lichens are indicators of old natural oak growths that have existed continuously over a long period in Central Europe [indication in accordance with the Red List of lichens of Czech Republic (Liška et al. 2008) is marked in parenthesis where available (EN – endangered species, VU – vulnerable species, DD – data deficient): *Acrocordia gemmata* (EN)*, Bacidia rubella* (VU)*, Calicium* spp., *Caloplaca lucifuga* (EN)*, Cetrelia olivetorum* s.l. (DD)*, Chaenotheca* spp. (except from *Chaenotheca ferruginea* and *C. chrysocephala*), *Chrysothrix candelaris* (VU), *Flavoparmelia caperata* (EN), *Melanelia subargentifera* (VU).

A detailed account of the life strategies of these indicator species (cf. Nordén & Appelqvist 2001) is not provided as further research on the dispersal traits of these species is required.

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Souhrn

Studovali jsme lišejníky dubových lesů (doubrav) Střední Evropy se snahou postihnout jejich současné druhové složení a nalézt druhy a společenstva typická pro tento lesní typ. Na 48 lokalitách (192 dubech) v České republice, na Slovensku a v Maďarsku jsme kromě celkové druhové skladby zjišťovali také index LDV (dle Asta et al. 2002) a významnost působení přirozených i antropogenních faktorů prostředí na lišejníková společenstva. Celkově jsme zjistili 104 druhů lišejníků, které byly rozděleny do 3 skupin podle frekvence výskytu. Analýza hlavních komponent (PCA) ukázala, že variabilita společenstev odráží především geografickou polohu lokalit a většina druhů je negativně korelována se znečištěním ovzduší, zatímco pozitivně s vyššími hodnotami srážek a s bazickým základním charakterem matečné horniny. Pomocí metody pro rozdělení variability byl odhadnut podíl vlivu

parametů prostředí, antropogenního působení a faktorů pro určení naturality na druhové složení lišejníků. Shluková analýza rozdělila druhy do šesti dobře ohraničených skupin ve spojitosti s jejich autekologickými charakteristikami. Dvě skupiny se vztahem ke svazům *Parmelion caperatae*, *Pertusarion amarae* a k několika dalším epifytickým společenstvům se zdají být blízko přirozeným lišejníkovým společenstvům středoevropských doubrav. V práci diskutujeme důvody výskytu či naopak absence některých společenstev lišejníků ve středoevropských doubravách (např. *Lobarion pulmonariae*, *Pertusarion hemisphaericae*) a další odlišnosti ve složení epifytických lišejníků ve vztahu k dubovým lesům jiných regionů (západní, severní Evropa). Na základě získaných znalostí navrhujeme několik druhů indikujících přirozené porosty daného typu (*Acrocordia gemmata*, *Bacidia rubella*, *Calicium* spp., *Caloplaca lucifuga*, *Cetrelia olivetorum* s.l., *Chrysothrix candelaris*, *Flavoparmelia caperata*, *Melanelia subargentifera*).

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