Tuexenia 40: 33–52. Göttingen 2020.
doi: 10.14471/2020.40.010, available online at www.zobodat.at

Vegetation classification of acidophilous oak forests in Slovakia

Vegetationsklassifikation bodensaurer Eichenwälder in der Slowakei

Michal Slezák[1, 2, *], Milan Valachovič[3], Drahoš Blanár[4], František Máliš[5, 6], Dušan Senko[3] & Hubert Žarnovičan[7]

[1]Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, 950 53 Zvolen, Slovakia; [2]Podtatranské museum in Poprad, Vajanského 72/4, 058 01 Poprad, Slovakia; [3]Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Dúbravská cesta 9, 845 23 Bratislava, Slovakia; [4]Administration of the Muránska planina National Park, J, Kráľa 12, 050 01 Revúca, Slovakia; [5]Department of Phytology, Faculty of Forestry, Technical University in Zvolen, T. G. Masaryka 24, 960 01 Zvolen, Slovakia; [6]National Forest Centre, Forest Research Institute Zvolen, T. G. Masaryka 22, 960 01 Zvolen, Slovakia; [7]Department of Landscape Ecology, Faculty of Natural Sciences, Comenius University, Mlynská dolina, Ilkovičova 6, 842 15 Bratislava, Slovakia
**Corresponding author, e-mail: slezak.miso@gmail.com*

Abstract

Acidophilous oak forests are species-poor forest plant communities usually growing on mineral-poor geological and soil substrates. We compiled a large data set of 263 phytosociological relevés assigned to the *Quercion roboris* alliance in Slovakia to produce the first syntaxonomical revision at national level. Modified Twinspan algorithm was applied for numerical classification and identification of basic vegetation units. To find main environmental gradients governing species composition, unconstrained ordination method (Detrended Correspondence analysis; DCA) was used. Floristic differences were interpreted using ecological plant indicator values, altitude and climatic data. We have accepted five associations of the alliance *Quercion roboris*: *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967, *Vaccinio vitis-idaeae-Quercetum roboris* Oberdorfer 1957, *Festuco ovinae-Quercetum roboris* Šmarda 1961, *Viscario vulgaris-Quercetum petraeae* Stöcker 1965 and *Luzulo luzuloidis-Quercetum petraeae* Hilitzer 1932. Results of DCA suggested that species compositional variability follows mainly gradients of moisture and nutrients, but altitude and continentality are also important. The syntaxonomical scheme overlaps with the schemes used in other Central European regions, but it reflects local environmental and floristic patterns as well.

Keywords: modified TWINSPAN, phytosociological nomenclature, plant communities, *Quercion roboris*, syntaxonomy, Western Carpathians

Erweiterte deutsche Zusammenfassung am Ende des Artikels

Manuscript received 21 December 2019, accepted 17 July 2020
Co-ordinating Editor: Erwin Bergmeier

1. Introduction

Central European acidophilous oak forests typically occur on mineral-poor soils in lowlands and low mountain ranges (PALLAS 1996, 2000; HÄRDTLE 2004). They inhabit dry to intermittently wet sites at low altitudes, as they are usually substituted by acidophilous beech forests in submontane and montane regions. The species composition may considerably vary depending on the local site conditions, with soil moisture and soil chemistry being the most important predictors. However, the distribution pattern of acidophilous oak forests does not reflect only environmental factors, but also historical land use legacies (ROLEČEK 2013). Many of these stands are among the poorest in number of vascular plants in comparison with other forests in temperate regions. This is a result of a unique combination of evolutionary and historical processes controlling size and composition of the species pool (PÄRTEL 2002, EWALD 2003), and plant adaptations to extreme soil conditions (i.e. low nutrient availability, toxicity of released metal ions; TYLER 2003). These broadleaved deciduous forests with variable canopy closure are composed mainly of oligotrophic and acid-tolerant plant species originating from both forests and open habitats (HÄRDTLE 2004).

Acidophilous oak forests are usually assigned to the order *Quercetalia roboris*, which is commonly divided into geographically defined alliances throughout Europe (e.g. PALLAS 1996, 2003; MUCINA et al. 2016). In the Czech Republic and Slovakia, acidophilous oak forests were traditionally classified into the alliance *Genisto germanicae-Quercion* described by NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ (1967a). Its protologue comprised three validly published associations at that time (*Luzulo luzuloidis-Quercetum petraeae*, *Vaccinio vitis-idaeae-Quercetum*, *Molinio arundinaceae-Quercetum*), with the last one being lectotype for the alliance designated by PALLAS (1996). This alliance, widespread in Central and Eastern Europe, only slightly differs (presence/absence of some sub-oceanic vs. sub-continental species) from the nominate alliance *Quercion roboris* recognized by MALCUIT (1929). Although MUCINA et al. (2016) put the name *Genisto germanicae-Quercion* to the syntaxonomical synonyms of the *Agrostio-Quercion petraeae* and PALLAS (1996) considered this name as superfluous (*sensu* ICPN Art. 29c), it is usually placed as a synonym of the *Quercion roboris*, following floristic and ecological similarities (e.g. WILLNER & GRABHERR 2007, ROLEČEK 2013). Central European acidophilous oak forests with species-poor herb layer and with dominance of *Quercus petraea* agg. and/or *Q. robur*, typically without or with very rare occurrence of oceanic species, are thus classified into the *Quercion roboris* alliance. Numerous phytosociological syntheses and revisions were published over the last two decades supporting this assignment (e.g. KEVEY & BORHIDI 2005, KASPROVICZ 2010, INDREICA 2012, ROLEČEK 2013, RECZYŃSKA 2015).

Phytosociological research of oak-dominated forests using Braun-Blanquet methodology has a long tradition in Slovakia (e.g. KLIKA 1937, MIKYŠKA 1937, 1939; JURKO 1951). Although the oldest studies comprised some relevés of acidophilous oak forests with brief descriptions of their vegetation structure and ecological features, more intensive sampling of these stands has started in various regions of the country since 1960s (e.g. ŠOMŠÁK 1963, HUSOVÁ 1967, NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ 1967b, NEUHÄUSLOVÁ-NOVOTNÁ 1970, FRAŇO et al. 1971, JURKO 1975). The increasing number of vegetation data resulted in the first proposal of phytosociological scheme for acidophilous oak forests (MUCINA & MAGLOCKÝ 1985) and in the layout of their potential distribution pattern (MICHALKO et al. 1986). The syntaxonomical concept of the *Quercion roboris* was later slightly modified by JAROLÍMEK & ŠIBÍK (2008). Both national vegetation surveys (MUCINA & MAGLOCKÝ 1985, JAROLÍMEK & ŠIBÍK 2008) described units reported by local phytosociological studies, mostly using expert-based approaches, and combined them with published surveys from neighbouring countries. They comprised a considerable overlap of corresponding associations. Moreover, several recently published studies (e.g. SLEZÁK & PETRÁŠOVÁ 2010, KUNDRÁK et al. 2014) compiled sets of new phytosociological data and indicated the need of a broad syntaxonomical revision.

Acidophilous oak forest stands seem to be well documented in Slovakia, but a revision at the national level using representative data set and more formalized classification methods is still lacking. We aimed to delimit and describe main plant community types of acidophilous oak forests in Slovakia using numerical classification and to explore major ecological gradients responsible for their variation in species composition.

2. Material and Methods

Vegetation data of acidophilous oak forests were taken from the Slovak phytosociological database (Centrálna databáza fytocenologických zápisov [CDF] na Slovensku; http://ibot.sav.sk/cdf/index.html) and completed with authors' unpublished material. They were stored in Turboveg database software (HENNEKENS & SCHAMINÉE 2001) and exported into the Juice program (TICHÝ 2002). Initial data set was designed according to original relevé assignment to the target alliance *Quercion roboris* (*Genisto germanicae-Quercion*) or class *Quercetea robori-petraeae* by their authors and by the presence of diagnostic species, previously defined for acidophilous oak forests (JAROLÍMEK & ŠIBÍK 2008, ROLEČEK 2013). Only relevés with a plot size 100–600 m^2 and tree layer cover ≥ 25% were further processed. Relevés without any plot size reported in original publication or in header data within the database were also analysed, as we assumed that they fall within the defined range. Relevés with dominance of *Pinus sylvestris* in the tree layer were excluded. Finally, we obtained 263 phytosociological relevés. Species nomenclature for vascular plants and mosses were unified according to checklists by MARHOLD & HINDÁK (1998) and MIŠÍKOVÁ et al. (2020), respectively. The names of plant communities unified according to JAROLÍMEK & ŠIBÍK (2008) were checked for compliance with the International Code of Phytosociological Nomenclature (ICPN; WEBER et al. 2000). The soil nomenclature followed the World reference base for soil resources (IUSS Working Group WRB 2015).

Identical species occurring in different vegetation layers were merged into a single record and cryptogamic species (bryophytes and lichens) were removed prior to numerical classification, as they were recorded only for a subset of relevés. However, bryophytes were re-inserted in the next step to calculate the diagnostic species. Plant taxa determined only at the genus level were excluded prior to numerical classification. The data set was classified with modified TWINSPAN algorithm (ROLEČEK et al. 2009) using two pseudospecies cut levels (0%, 50%) and total inertia as a heterogeneity measure. Diagnostic species were defined as species with frequency ≥ 20%, fidelity ≥ 0.25 and a difference of two constancy classes or at least twice higher frequency compared to another cluster. However, they didn't have to be constant species (frequency ≥ 50%) in two or more clusters. Diagnostic species for two or more clusters (associations) were estimated individually in accordance with published expert knowledge or our field experience, but their diagnostic value was generally accepted if they reached frequency ≥ 20% at least in two clusters irrespective of the fidelity value and if their lowest frequency in a cluster for which they are diagnostic was at least twice as high as in any of the remaining clusters. Fidelity calculation followed presence/absence data with a standardization of relevé groups to an equal size. The Fisher's exact test ($p < 0.01$) was used to eliminate species with non-significant fidelity to a particular cluster (TICHÝ & CHYTRÝ 2006). Manual reassignment of some relevés was performed according to the prevalence of diagnostic species and our expert judgement.

To explain the floristic variability within the data set, we used unweighted means of the Ellenberg indicator values (EIV for light, moisture, reaction, nutrients) compiled for vascular plants of the Czech Republic (CHYTRÝ et al. 2018), continentality proposed by BERG et al. (2017), as well as altitude (m), mean annual temperature (°C) and precipitation (mm). Climatic data from the Slovak Hydrometeorological Institute for the period of 1981–2010 were derived from raster values using GRASS GIS (NETELER et al. 2012). Environmental differences among vegetation units were tested using ANOVA and post-hoc Tukey HSD test. They were illustrated with box and whiskers plots. Vegetation-environmental relationships were analysed using Detrended Correspondence Analysis (DCA). DCA was run with detrending by segments and square-root transformation of species cover values. Altitude was used as a proxy for climatic gradient in DCA, as it strongly correlated with both mean annual temperature (Spearmann correlation coefficient r = -0.69, $p < 0.001$) and mean annual precipitation ($r = 0.64$, $p < 0.001$). Environmental variables were plotted into DCA diagram only if they showed significant multiple linear regressions with the first two DCA axes ($p < 0.05$, 999 permutations; ZELENÝ & SCHAFFERS 2012). All the statistical analyses were performed in Canoco for Windows package (ver. 4.5) and R software ver. 3.0.3 (R CORE TEAM 2014) using MoPeT algorithm (ZELENÝ & SCHAFFERS 2012).

3. Results

According to the results of modified TWINSPAN algorithm, five groups of acidophilous oak forests were distinguished. These vegetation types were interpreted at the level of association and identified with associations previously described in Central Europe. They differ with respect to both species composition (Table 1) and environmental conditions (Fig. 1, 2). Four environmental gradients displayed in DCA ordination diagram (Fig. 1a) were found to be important for the floristic variability. Differences in species composition were mostly related to moisture gradient and nutrient availability (first DCA axis), but the effect of altitude and continentality (second DCA axis) played an important role as well. In our data set, plant species were distributed along a moisture gradient from moisture-demanding (*Betula pendula*, *Frangula alnus*, *Molinia caerulea* agg.) and mesophilous species (e.g. *Convallaria majalis*, *Melampyrum pratense*, *Vaccinium myrtillus*) to species of xerophilous sites (e.g. *Lembotropis nigricans*, *Steris viscaria*; Fig. 1b). The ecologically best-delimited associations were *Molinio arundinaceae-Quercetum roboris* and *Viscario vulgaris-Quercetum petraeae*, occurring on different ends of the moisture gradient. The well-defined habitat affinity was also found for the *Vaccinio vitis-idaeae-Quercetum roboris*, which prefers strongly acidic soils on mesic sites in submontane regions (Fig. 2).

Molinio arundinaceae-Quercetum roboris **Neuhäusl et Neuhäuslová-Novotná 1967** ***nom. cons. propos.*** **(cluster 1, Table 1)**

Original form of the name: NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ (1967a), *Molinio arundinaceae-Quercetum* ass. nova
Nomenclatural type: NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ (1967a), Tab. 2., rel. 11, lectotypus designated by PALLAS (1996)
Synonyms: *Luzulo pilosae-Quercetum roboris* Šomšák et al. 2002

Tree layer is usually dominated by *Quercus robur* agg., less frequently by *Betula pendula*, or *Quercus petraea* agg. Well-developed shrub layer is most often composed of *Frangula alnus*, accompanied by the tree layer juveniles and other species of acidic and moist sites (mainly *Sorbus aucuparia* and *Viburnum opulus*). These stands are characterized by a mosaic of species adapted to inter- and intra-annual fluctuations of groundwater level (i.e. wet from autumn to spring with temporary drying out in summer; *Deschampsia cespitosa*, *Lysimachia vulgaris*, *Molinia caerulea* agg., *Potentilla erecta*). Overall herb-layer composition is also enriched by indicators of air humidity (mainly ferns *Athyrium filix-femina*, *Dryopteris carthusiana* agg., *D. filix-mas*), boreal elements (*Luzula pilosa*, *Maianthemum bifolium*, *Senecio nemorensis* agg.) and other acidophilous and acidic-tolerant species of mesic sites (e.g. *Oxalis acetosella*, *Poa nemoralis*). In the moss layer, higher frequency was recorded for *Hypnum cupressiforme*, *Plagiomnium affine* and *Polytrichum formosum*.

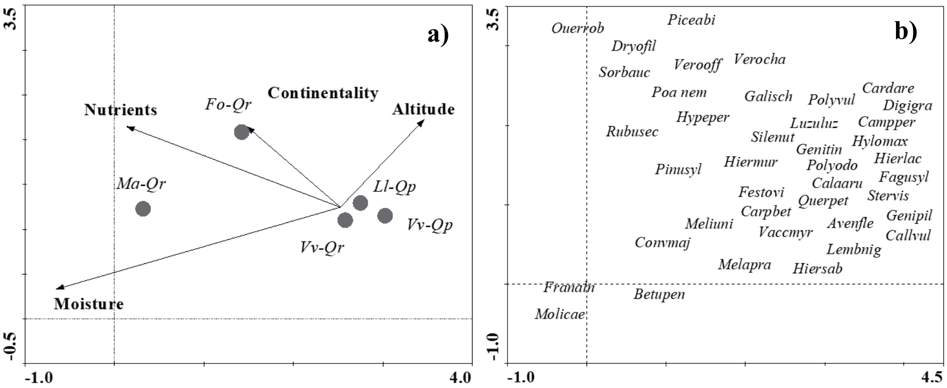

Fig. 1. DCA ordination diagrams of the acidophilous oak forests in Slovakia with first two ordination axes. **a)** Biplots with centroids of the vegetation plots assigned to the associations and variables with significant regression ($p < 0.05$) to ordination axes (*Ma-Qr – Molinio arundinaceae-Quercetum roboris*, *Vv-Qr – Vaccinio vitis-idaeae-Quercetum roboris*, *Fo-Qr – Festuco ovinae-Quercetum roboris*, *Vv-Qp – Viscario vulgaris-Quercetum petraeae* and *Ll-Qp – Luzulo luzuloidis-Quercetum petraeae*), and **b)** scatter plot showing species with weight range between 3–100%. Abbreviations of species names: Avenfle: *Avenella flexuosa*, Betupen: *Betula pendula*, Calaaru: *Calamagrostis arundinacea*, Callvul: *Calluna vulgaris*, Campper: *Campanula persicifolia*, Cardare: *Cardaminopsis arenosa*, Carpbet: *Carpinus betulus*, Convmaj: *Convallaria majalis*, Digigra: *Digitalis grandiflora*, Dryofil: *Dryopteris filix-mas*, Fagusyl: *Fagus sylvatica*, Festovi: *Festuca ovina* agg., Fraaln: *Frangula alnus*, Galisch: *Galium schultesii*, Genipil: *Genista pilosa*, Genitin: *Genista tinctoria*, Hierlac: *Hieracium lachenalii*, Hiermur: *Hieracium murorum*, Hiersab: *Hieracium sabaudum*, Hylomax: *Hylotelephium maximum*, Hypeper: *Hypericum perforatum*, Lembnig: *Lembotropis nigricans*, Luzuluz: *Luzula luzuloides*, Melapra: *Melampyrum pratense*, Molicae: *Molina caerulea* agg., Piceabi: *Picea abies*, Pinusyl: *Pinus sylvestris*, Poanem: *Poa nemoralis*, Polyodo: *Polygonatum odoratum*, Polyvul: *Polypodium vulgare*, Querpet: *Quercus petraea* agg., Querrob: *Quercus robur* agg., Rubusec: *Rubus* sect. *Rubus*, Silenut: *Silene nutans*, Sorbauc: *Sorbus aucuparia*, Stervis: *Steris viscaria*, Vaccmyr: *Vaccinium myrtillus*, Verocha: *Veronica chamaedrys*, Verooff: *Veronica officinalis*.

Abb. 1. DCA-Diagramme mit den ersten beiden Ordinationsachsen der bodensauren Eichenwälder der Slowakei. **a)** Biplot mit Zentroiden der Vegetationsaufnahmen, die zu den angegebenen Assoziationen gehören (Abkürzungen der Assoziationen siehe oben). Vektoren bezeichnen Variablen mit signifikanter Regression ($p < 0,05$) zu den Ordinationsachsen. **b)** Scatter plot der wichtigsten Arten (Wichtungsbereich 3–100 %); Abkürzungen der Artnamen siehe oben.

This community prefers seasonally moist sites at lower-altitudes (75% of the plots have an altitude < 500 m a.s.l.; Fig. 2). Soils are usually loamy and silty (Umbrisol, Stagnic Albic Luvisol), located in flat terrains or depressions, frequently related to old river terraces. It was found in the Záhorská nižina Lowland, Nitrianska pahorkatina Upland and few relevés were recorded in submontane areas of the Turčianska kotlina Basin, as well (Fig. 3).

Vaccinio vitis-idaeae-Quercetum roboris Oberdorfer 1957 (cluster 2, Table 1)

Original form of the name: OBERDORFER (1957), *Vaccinio vitis-idaeo-Quercetum* ass. nov.
Nomenclatural type: PALLAS (1996), p. 32, rel. 1, neotypus designated by Oberdorfer in PALLAS (1996)

The tree layer with dominant *Quercus petraea* agg. is admixed especially by *Betula pendula* on strongly acidic and shallow soils. At higher altitudes, the overstorey can be enriched by *Fagus sylvatica*. The poorly developed shrub layer is composed of young individuals

Table 1. Shortened synoptic table with frequency and fidelity (phi coefficient × 100 in the upper indices) for acidophilous oak forests in Slovakia. Diagnostic species of the associations in the herb layer are sorted according to decreasing frequency and other species according to decreasing absolute frequency (AF). Plant species with frequency > 10% in the particular cluster are shown.

Tabelle 1. Gekürzte synoptische Tabelle der bodensauren Eichenwälder der Slowakei mit Stetigkeit und Treuegrad (phi-Koeffizient, hochgesetzt). Werte der diagnostischen Arten der Assoziationen sind grau hinterlegt; diagnostische Arten in der Krautschicht sind in ihrer Gruppe nach abnehmender Stetigkeit angeordnet, andere Arten gemäß abnehmender absoluter Stetigkeit (AF). Gezeigt sind Pflanzenarten mit Stetigkeit von > 10 % in einer der fünf Gruppen.

Group No.	1	2	3	4	5	AF
No. of relevés	15	56	9	42	141	
No. of relevés with determined E_0	7	32	9	33	83	
Mean no. of vascular plants	29	17	13	21	20	
Mean no. of bryophytes	5	3	6	3	3	
Trees in tree (E_3) and shrub (E_2) layer						
Quercus petraea agg. (E_3)	20^{---}	98^{---}	89^{---}	95^{---}	$96^{20.0}$	241
Quercus petraea agg. (E_2)	7^{---}	50^{---}	44^{---}	43^{---}	48^{---}	118
Fagus sylvatica (E_3)	$.^{---}$	$55^{34.7}$	$.^{---}$	31^{---}	40^{---}	100
Fagus sylvatica (E_2)	$.^{---}$	$57^{37.5}$	$.^{---}$	33^{---}	33^{---}	93
Betula pendula (E_3)	$67^{39.3}$	$52^{23.1}$	$.^{---}$	19^{---}	15^{---}	68
Betula pendula (E_2)	13^{---}	$21^{18.0}$	$.^{---}$	10^{---}	8^{---}	29
Pinus sylvestris (E_3)	33^{---}	9^{---}	$89^{60.8}$	17^{---}	13^{---}	43
Pinus sylvestris (E_2)	7^{---}	5^{---}	22^{---}	10^{---}	2^{---}	13
Carpinus betulus (E_3)	20^{---}	11^{---}	$.^{---}$	10^{---}	18^{---}	38
Carpinus betulus (E_2)	13^{---}	16^{---}	$.^{---}$	12^{---}	$31^{23.7}$	60
Quercus robur agg. (E_3)	$87^{58.2}$	4^{---}	$67^{36.8}$	2^{---}	2^{---}	25
Quercus robur agg. (E_2)	7^{---}	4^{---}	$33^{43.6}$	$.^{---}$	$.^{---}$	6
Sorbus aucuparia (E_3)	27^{---}	5^{---}	$.^{---}$	2^{---}	2^{---}	11
Sorbus aucuparia (E_2)	$47^{35.3}$	$32^{16.8}$	11^{---}	$.^{---}$	5^{---}	33
Picea abies (E_3)	20^{---}	5^{---}	$.^{---}$	2^{---}	3^{---}	11
Picea abies (E_2)	13^{---}	4^{---}	$.^{---}$	$.^{---}$	4^{---}	9
Alnus glutinosa (E_3)	$27^{47.5}$	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$	4
Populus tremula (E_3)	13^{---}	4^{---}	$.^{---}$	$.^{---}$	$.^{---}$	4
Populus tremula (E_2)	20^{---}	7^{---}	$.^{---}$	$.^{---}$	3^{---}	11
Tilia cordata (E_2)	20^{---}	4^{---}	$.^{---}$	$.^{---}$	6^{---}	14
Sorbus aria agg. (E_2)	$.^{---}$	$12^{24.2}$	$.^{---}$	2^{---}	3^{---}	12
Fraxinus excelsior (E_2)	13^{---}	$.^{---}$	$.^{---}$	$.^{---}$	1^{---}	3
Shrub layer (E_2)						
Frangula alnus	$87^{82.4}$	11^{---}	$.^{---}$	$.^{---}$	4^{---}	25
Corylus avellana	13^{---}	5^{---}	$.^{---}$	2^{---}	11^{---}	22
Viburnum opulus	$27^{46.6}$	$.^{---}$	$.^{---}$	$.^{---}$	1^{---}	5
Sambucus racemosa	$20^{39.8}$	$.^{---}$	$.^{---}$	$.^{---}$	1^{---}	4
Diagnostic species of herb layer (E_1)						
***Molinio arundinaceae-Quercetum roboris* (cluster 1)**						
Deschampsia cespitosa	$93^{95.4}$	$.^{---}$	$.^{---}$	$.^{---}$	1^{---}	15
Rubus sect. *Rubus*	$80^{71.9}$	7^{---}	$.^{---}$	5^{---}	14^{---}	38
Molinia caerulea agg.	$67^{68.7}$	12^{---}	$.^{---}$	$.^{---}$	1^{---}	19
Dryopteris carthusiana agg.	$67^{76.0}$	2^{---}	$.^{---}$	$.^{---}$	1^{---}	13
Lysimachia vulgaris	$60^{73.9}$	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$	9
Dryopteris filix-mas	$53^{44.6}$	$27^{10.5}$	$.^{---}$	2^{---}	11^{---}	39
Maianthemum bifolium	$53^{56.0}$	14^{---}	$.^{---}$	$.^{---}$	4^{---}	21
Oxalis acetosella	$53^{66.1}$	4^{---}	$.^{---}$	$.^{---}$	$.^{---}$	10
Mycelis muralis	$47^{48.4}$	9^{---}	$.^{---}$	$.^{---}$	12^{---}	29
Viola reichenbachiana	$47^{57.7}$	2^{---}	$.^{---}$	$.^{---}$	6^{---}	16
Melica nutans	$47^{61.2}$	2^{---}	$.^{---}$	$.^{---}$	1^{---}	10

Group No.	1	2	3	4	5	AF
Fragaria vesca	40 $^{36.4}$	11 $^{---}$	. $^{---}$	7 $^{---}$	14 $^{---}$	35
Moehringia trinervia	40 $^{51.3}$	2 $^{---}$	. $^{---}$	2 $^{---}$	4 $^{---}$	14
Scrophularia nodosa	40 $^{53.2}$	2 $^{---}$	. $^{---}$	. $^{---}$	4 $^{---}$	13
Athyrium filix-femina	40 $^{53.5}$	4 $^{---}$	. $^{---}$	. $^{---}$	2 $^{---}$	11
Luzula pilosa	33 $^{51.1}$	. $^{---}$	. $^{---}$	. $^{---}$	2 $^{---}$	8
Senecio nemorensis agg.	33 $^{50.7}$	2 $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	7
Potentilla erecta	33 $^{49.6}$	4 $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	7
Carex acutiformis	33 $^{53.5}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	5
Ajuga reptans	27 $^{37.3}$	. $^{---}$	. $^{---}$	5 $^{---}$	5 $^{---}$	13
Brachypodium sylvaticum	27 $^{40.1}$	4 $^{---}$	. $^{---}$	2 $^{---}$	1 $^{---}$	8
Chamerion angustifolium	27 $^{43.7}$	2 $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	7
Carex pallescens	27 $^{46.6}$	. $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	5
Anemone nemorosa	27 $^{47.5}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	4
Festuca gigantea	27 $^{47.5}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	4
Angelica sylvestris	20 $^{40.8}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	3
Carex remota	20 $^{40.8}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	3
***Vaccinio vitis-idaeae-Quercetum roboris* (cluster 2)**						
Vaccinium myrtillus	. $^{---}$	100 $^{84.4}$	. $^{---}$	14 $^{---}$	16 $^{---}$	84
***Festuco ovinae-Quercetum roboris* (cluster 3)**						
Festuca dominii	. $^{---}$	. $^{---}$	100 ^{100}	. $^{---}$	. $^{---}$	9
Luzula campestris agg.	20 $^{---}$	2 $^{---}$	56 $^{43.6}$	19 $^{---}$	6 $^{---}$	25
Tithymalus cyparissias	. $^{---}$	4 $^{---}$	56 $^{57.9}$	12 $^{---}$	2 $^{---}$	15
Peucedanum oreoselinum	. $^{---}$	2 $^{---}$	56 $^{68.0}$	. $^{---}$	1 $^{---}$	8
Linaria genistifolia	. $^{---}$	. $^{---}$	33 $^{45.2}$	5 $^{---}$	4 $^{---}$	10
Campanula rotundifolia agg.	. $^{---}$	5 $^{---}$	33 $^{45.7}$	2 $^{---}$	. $^{---}$	7
Teucrium chamaedrys	7 $^{---}$	. $^{---}$	22 $^{32.3}$	2 $^{---}$	1 $^{---}$	5
Senecio viscosus	. $^{---}$	2 $^{---}$	22 $^{40.7}$	. $^{---}$	. $^{---}$	3
Thymus serpyllum	. $^{---}$	. $^{---}$	22 $^{43.1}$	. $^{---}$	. $^{---}$	2
***Viscario vulgaris-Quercetum petraeae* (cluster 4)**						
Festuca ovina agg.	13 $^{---}$	12 $^{---}$	11 $^{---}$	52 $^{41.4}$	9 $^{---}$	44
Pilosella officinarum	. $^{---}$	5 $^{---}$	. $^{---}$	50 $^{58.8}$	4 $^{---}$	30
Steris viscaria	. $^{---}$	12 $^{---}$	. $^{---}$	45 $^{40.0}$	22 $^{---}$	57
Hieracium umbellatum	. $^{---}$	9 $^{---}$	. $^{---}$	33 $^{37.0}$	11 $^{---}$	34
Acetosella multifida agg.	. $^{---}$	7 $^{---}$	11 $^{---}$	26 $^{28.6}$	3 $^{---}$	20
Anthericum ramosum	. $^{---}$	2 $^{---}$	. $^{---}$	24 $^{33.1}$	9 $^{---}$	24
***Luzulo luzuloidis-Quercetum petraeae* (cluster 5)**						
Hieracium sabaudum	20 $^{---}$	12 $^{---}$	. $^{---}$	21 $^{---}$	45 $^{32.0}$	83
Galium schultesii	13 $^{---}$	14 $^{---}$	. $^{---}$	17 $^{---}$	40 $^{30.6}$	73
Diagnostic species for two or more clusters						
Luzula luzuloides	40 $^{---}$	95 $^{---}$	. $^{---}$	81 $^{---}$	94 $^{33.3}$	226
Avenella flexuosa	7 $^{---}$	89 $^{35.5}$	. $^{---}$	100 $^{46.2}$	74 $^{---}$	197
Hieracium lachenalii	. $^{---}$	34 $^{---}$	. $^{---}$	60 $^{---}$	54 $^{26.8}$	120
Genista pilosa	. $^{---}$	27 $^{---}$	. $^{---}$	69 $^{46.0}$	43 $^{---}$	105
Lembotropis nigricans	. $^{---}$	29 $^{---}$	11 $^{---}$	38 $^{---}$	31 $^{---}$	77
Calamagrostis arundinacea	. $^{---}$	27 $^{---}$	. $^{---}$	19 $^{---}$	23 $^{---}$	56
Campanula persicifolia	. $^{---}$	14 $^{---}$	. $^{---}$	40 $^{---}$	39 $^{25.9}$	80
Genista tinctoria	. $^{---}$	12 $^{---}$	. $^{---}$	31 $^{---}$	39 $^{30.3}$	75
Silene nutans	. $^{---}$	2 $^{---}$	44 $^{---}$	48 $^{28.7}$	23 $^{---}$	57
Polygonatum odoratum	7 $^{---}$	5 $^{---}$	22 $^{---}$	24 $^{---}$	16 $^{---}$	39
Hypericum perforatum	13 $^{---}$	14 $^{---}$	67 $^{39.7}$	40 $^{11.2}$	16 $^{---}$	56
Agrostis capillaris	20 $^{---}$	2 $^{---}$	33 $^{---}$	19 $^{5.1}$	3 $^{---}$	19
Calamagrostis epigejos	20 $^{---}$	2 $^{---}$	33 $^{33.8}$	2 $^{---}$	1 $^{---}$	9
Calluna vulgaris	. $^{---}$	46 $^{21.6}$	11 $^{---}$	64 $^{41.7}$	14 $^{---}$	74
Polypodium vulgare	. $^{---}$	36 $^{---}$	. $^{---}$	14 $^{---}$	28 $^{---}$	65
Poa nemoralis	60 $^{---}$	21 $^{---}$	. $^{---}$	26 $^{---}$	52 $^{21.9}$	106
Melica uniflora	20 $^{---}$	9 $^{---}$	. $^{---}$	2 $^{---}$	24 $^{20.8}$	43

Group No.	1	2	3	4	5	AF
Constant and other species						
Hieracium murorum	27 $^{---}$	43 $^{---}$	11 $^{---}$	69 $^{---}$	73 $^{28.7}$	161
Melampyrum pratense	27 $^{---}$	61 $^{---}$	33 $^{---}$	40 $^{---}$	50 $^{---}$	129
Hylotelephium maximum	. $^{---}$	34 $^{---}$	33 $^{---}$	40 $^{---}$	38 $^{---}$	92
Veronica officinalis	27 $^{---}$	14 $^{---}$	44 $^{---}$	43 $^{---}$	31 $^{---}$	78
Veronica chamaedrys	33 $^{---}$	9 $^{---}$	22 $^{---}$	14 $^{---}$	34 $^{13.7}$	66
Digitalis grandiflora	. $^{---}$	12 $^{---}$	. $^{---}$	19 $^{---}$	23 $^{---}$	48
Cardaminopsis arenosa	. $^{---}$	12 $^{---}$	. $^{---}$	12 $^{---}$	22 $^{21.9}$	43
Convallaria majalis	20 $^{---}$	20 $^{---}$	11 $^{---}$	10 $^{---}$	14 $^{---}$	39
Galium mollugo agg.	7 $^{---}$	5 $^{---}$	. $^{---}$	19 $^{---}$	13 $^{---}$	31
Cruciata glabra	7 $^{---}$	7 $^{---}$	. $^{---}$	. $^{---}$	18 $^{23.5}$	30
Solidago virgaurea	7 $^{---}$	20 $^{---}$	. $^{---}$	7 $^{---}$	9 $^{---}$	27
Galeopsis pubescens	. $^{---}$	11 $^{---}$	. $^{---}$	21 $^{---}$	9 $^{---}$	27
Fallopia convolvulus	. $^{---}$	5 $^{---}$	22 $^{---}$	14 $^{---}$	11 $^{---}$	26
Hieracium racemosum	. $^{---}$	4 $^{---}$	. $^{---}$	5 $^{---}$	13 $^{22.3}$	23
Galium odoratum	20 $^{---}$	4 $^{---}$	. $^{---}$	5 $^{---}$	10 $^{---}$	21
Melampyrum nemorosum	7 $^{---}$	11 $^{---}$	. $^{---}$	5 $^{---}$	8 $^{---}$	20
Dactylis glomerata agg.	7 $^{---}$	2 $^{---}$	. $^{---}$	2 $^{---}$	11 $^{15.6}$	18
Vincetoxicum hirundinaria	. $^{---}$	5 $^{---}$	11 $^{---}$	10 $^{---}$	7 $^{---}$	18
Rubus idaeus	20 $^{---}$	14 $^{---}$	. $^{---}$	2 $^{---}$	4 $^{---}$	17
Anthoxanthum odoratum	13 $^{---}$	5 $^{---}$	. $^{---}$	10 $^{---}$	6 $^{---}$	17
Pteridium aquilinum	13 $^{---}$	11 $^{---}$	. $^{---}$	2 $^{---}$	4 $^{---}$	14
Dianthus carthusianorum	. $^{---}$	2 $^{---}$	. $^{---}$	12 $^{---}$	5 $^{---}$	13
Symphytum tuberosum	13 $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	6 $^{---}$	11
Pilosella bauhinii	. $^{---}$	. $^{---}$	. $^{---}$	17 $^{33.0}$	3 $^{---}$	11
Stellaria holostea	13 $^{---}$	4 $^{---}$	. $^{---}$	2 $^{---}$	4 $^{---}$	10
Senecio sylvaticus	. $^{---}$	4 $^{---}$	. $^{---}$	14 $^{27.1}$	1 $^{---}$	10
Sedum sexangulare	. $^{---}$	. $^{---}$	. $^{---}$	19 $^{38.7}$	1 $^{---}$	9
Geranium robertianum	13 $^{---}$	5 $^{---}$	11 $^{---}$	. $^{---}$	1 $^{---}$	8
Melampyrum sylvaticum	13 $^{---}$	5 $^{---}$	. $^{---}$	2 $^{---}$	1 $^{---}$	8
Leucanthemum vulgare agg.	. $^{---}$	. $^{---}$	. $^{---}$	14 $^{31.9}$	1 $^{---}$	8
Vaccinium vitis-idaea	. $^{---}$	11 $^{25.3}$	. $^{---}$	2 $^{---}$	. $^{---}$	7
Viola riviniana	13 $^{---}$	. $^{---}$	. $^{---}$	2 $^{---}$	2 $^{---}$	6
Achillea millefolium agg.	. $^{---}$	2 $^{---}$	11 $^{---}$	2 $^{---}$	2 $^{---}$	6
Jasione montana	. $^{---}$	. $^{---}$	11 $^{---}$	10 $^{13.0}$	1 $^{---}$	6
Poa pratensis agg.	. $^{---}$	. $^{---}$	11 $^{---}$	5 $^{---}$	2 $^{---}$	6
Trifolium alpestre	. $^{---}$	. $^{---}$	11 $^{---}$	2 $^{---}$	3 $^{---}$	6
Poa compressa	7 $^{---}$	. $^{---}$	11 $^{---}$	2 $^{---}$	1 $^{---}$	5
Prenanthes purpurea	13 $^{---}$	2 $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	4
Carex hirta	13 $^{19.6}$	. $^{---}$	11 $^{---}$	. $^{---}$	. $^{---}$	3
Rubus caesius	13 $^{29.2}$	. $^{---}$	. $^{---}$	2 $^{---}$	. $^{---}$	3
Pulmonaria mollis	13 $^{31.9}$	. $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	3
Hieracium bifidum	13 $^{31.9}$	. $^{---}$	. $^{---}$	. $^{---}$	1 $^{---}$	3
Pimpinella saxifraga	. $^{---}$	. $^{---}$	11 $^{---}$	2 $^{---}$	1 $^{---}$	3
Juncus effusus	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Veratrum album ssp. *lobelianum*	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Lycopus europaeus	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Peucedanum palustre	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Lythrum salicaria	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Scutellaria galericulata	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Carex brizoides	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Paris quadrifolia	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Holcus lanatus	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Equisetum arvense	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Ranunculus repens	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2
Epilobium collinum	13 $^{33.1}$	. $^{---}$	. $^{---}$	. $^{---}$	. $^{---}$	2

Group No.	1	2	3	4	5	AF
Viola rupestris	. ---	. ---	11 ---	. ---	. ---	1
Asperula cynanchica	. ---	. ---	11 ---	. ---	. ---	1
Betonica officinalis	. ---	. ---	11 ---	. ---	. ---	1
Carex supina	. ---	. ---	11 ---	. ---	. ---	1
Solidago canadensis	. ---	. ---	11 ---	. ---	. ---	1
Convolvulus arvensis	. ---	. ---	11 ---	. ---	. ---	1
Carex fritschii	. ---	. ---	11 ---	. ---	. ---	1
Cerastium arvense	. ---	. ---	11 ---	. ---	. ---	1
Juvenile woody species						
Quercus petraea agg.	33 ---	86 ---	78 ---	90 ---	87 ---	220
Fagus sylvatica	. ---	52 ---	. ---	62 ---	57 ---	136
Carpinus betulus	20 ---	21 ---	. ---	40 ---	45 $^{22.9}$	96
Sorbus aucuparia	67 $^{31.3}$	48 $^{12.1}$	33 ---	17 ---	18 ---	72
Betula pendula	13 ---	30 $^{24.1}$	. ---	17 ---	9 ---	38
Pinus sylvestris	20 ---	9 ---	44 ---	19 ---	11 ---	35
Rosa canina agg.	7 ---	5 ---	. ---	14 ---	17 ---	34
Frangula alnus	93 $^{74.4}$	11 ---	22 ---	2 ---	7 ---	33
Acer pseudoplatanus	13 ---	14 ---	. ---	17 ---	7 ---	27
Picea abies	13 ---	16 ---	. ---	10 ---	7 ---	25
Sorbus aria agg.	. ---	14 ---	. ---	10 ---	9 ---	25
Abies alba	. ---	9 ---	. ---	7 ---	11 ---	24
Cerasus avium	. ---	2 ---	. ---	10 ---	13 ---	23
Tilia cordata	13 ---	2 ---	. ---	7 ---	8 ---	17
Viburnum opulus	40 $^{51.5}$	4 ---	. ---	2 ---	2 ---	12
Fraxinus excelsior	20 ---	4 ---	. ---	. ---	5 ---	12
Quercus robur agg.	33 $^{31.6}$	4 ---	22 ---	2 ---	1 ---	11
Populus tremula	. ---	11 $^{25.7}$	. ---	. ---	2 ---	9
Moss layer (E_0)						
Hypnum cupressiforme	71 ---	59 ---	78 ---	94 ---	81 ---	129
Dicranum scoparium	14 ---	41 ---	22 ---	42 ---	52 ---	73
Polytrichum formosum	57 ---	38 ---	11 ---	33 ---	47 ---	67
Pleurozium schreberi	14 ---	25 ---	56 ---	6 ---	18 ---	31
Leucobryum glaucum	43 ---	41 $^{16.5}$	33 ---	3 ---	11 ---	29
Polytrichum piliferum	. ---	6 ---	33 ---	33 ---	16 ---	29
Ceratodon purpureus	. ---	12 ---	33 ---	30 ---	13 ---	28
Dicranella heteromalla	. ---	19 ---	. ---	18 ---	11 ---	21
Dicranum polysetum	. ---	9 ---	89 $^{81.8}$	. ---	10 ---	19
Polytrichum juniperinum	. ---	12 ---	44 $^{42.4}$	6 ---	10 ---	18
Brachytheciastrum velutinum	14 ---	6 ---	44 $^{39.3}$	3 ---	11 ---	17
Atrichum undulatum	29 ---	. ---	. ---	3 ---	17 $^{12.1}$	17
Plagiomnium affine	43 ---	. ---	78 $^{60.8}$	. ---	5 ---	14
Hylocomium splendens	14 ---	12 ---	22 ---	. ---	5 ---	11
Plagiothecium denticulatum	14 ---	9 ---	. ---	. ---	1 ---	5
Bryum capillare	. ---	. ---	22 ---	. ---	4 ---	5
Plagiomnium cuspidatum	14 ---	3 ---	. ---	6 ---	. ---	4
Pseudoscleropodium purum	14 ---	3 ---	11 ---	. ---	. ---	3
Pohlia cruda	14 ---	. ---	. ---	. ---	2 ---	3
Plagiomnium undulatum	. ---	3 ---	11 ---	. ---	1 ---	3
Dicranum montanum	14 ---	. ---	. ---	. ---	1 ---	2
Lepidozia reptans	14 ---	. ---	. ---	. ---	1 ---	2
Brachythecium rutabulum	. ---	. ---	11 ---	. ---	1 ---	2
Campylopus pyriformis	14 ---	. ---	. ---	. ---	. ---	1
Calypogeia suecica	14 ---	. ---	. ---	. ---	. ---	1
Tetraphis pellucida	14 ---	. ---	. ---	. ---	. ---	1
Blepharostoma trichophyllum	14 ---	. ---	. ---	. ---	. ---	1
Sphagnum palustre	14 ---	. ---	. ---	. ---	. ---	1

of tree layer species. Physiognomy of herb layer is determined by dominance of dwarf shrubs *Vaccinium myrtillus* and *Calluna vulgaris*, rarely with co-dominance of *V. vitis-idaea* or *Avenella flexuosa*. The species-poor herb layer consists also of common acidophilous species such as *Hieracium murorum*, *Luzula luzuloides*, *Melampyrum pratense*. In the moss layer grow mainly generalists of nutrient-poor substrates (e.g. *Dicranum scoparium*, *Hypnum cupressiforme*, *Leucobryum glaucum*). Floristic delimitation against the *Viscario vulgaris-Quercetum petraeae* (cluster 4) and *Luzulo luzuloidis-Quercetum petraeae* (cluster 5) is well supported by the presence of some forest overstorey trees (mainly *Betula pendula*, *Sorbus aucuparia*) accompanied by higher frequency of *Vaccinium myrtillus*, *Drypteris filix-mas*, *Convallaria majalis*, *Solidago virgaurea* and the moss *Leucobryum glaucum*.

This community was mostly recorded in the foothills of the Western Carpathians (Považský Inovec Mts., Tríbeč Mts., Štiavnické vrchy Mts., Čierna hora Mts.) and in the northern edge of the Pannonian Basin (Malé Karpaty Mts., Volovské vrchy Mts., Zemplínske vrchy Mts.). Some isolated localities were found in northern Slovakia (Malá Fatra Mts.), as well. These stands usually occur on strongly acidic soils (Dystric Cambisol) in submontane areas (75% of the plots occur at altitudes from 400 to 753 m a.s.l.; Fig. 2, 3) with crystalline bedrock.

***Festuco ovinae-Quercetum roboris* Šmarda 1961 (cluster 3, Table 1)**

Original form of the name: ŠMARDA (1961), *Quercetum roboris-Festucetum ovinae*

Dominant tree species of the forest overstorey are *Quercus petraea* agg. or *Q. robur* agg., with admixture of *Pinus sylvestris*. A shrub layer composed of oak species is present in most stands, but it usually doesn't exceed 5–10% cover. Species-poor herb layer consists of psammophilous and thermophilous herbs or graminoids (e.g. *Festuca dominii*, *Linaria genistifolia*, *Peucedanum oreoselinum*, *Tithymalus cyparissias*), which are accompanied by species of acidic sites (*Luzula campestris* agg., *Melampyrum pratense*, *Veronica officinalis*) and rock outcrops (*Campanula rotundifolia* agg.). The moss layer is usually very well developed and encompasses various acrocarpous and pleurocarpous mosses (e.g. *Brachytheciastrum velutinum*, *Dicranum polysetum*, *Hypnum cupressiforme*, *Plagiomnium affine*, *Pleurozium schreberi*, *Polytrichum juniperinum*).

These stands were found only in the Záhorská nížina Lowland, where they grow on nutrient-poor sandy soils (Dystric Regosol, Arenic) at altitudes from 170 to 222 m a.s.l. (Fig. 2, 3).

***Viscario vulgaris-Quercetum petraeae* Stöcker 1965 (cluster 4, Table 1)**

Original form of the name: STÖCKER (1965), *Viscario-Quercetum* ass. nov.
Nomenclatural type: BLAŽKOVÁ (1989), p. 99–100, Tab. 5, rel. 6, neotypus designated by MORAVEC (1998)

The tree layer is almost exclusively formed by *Quercus petraea* agg., with occasional admixture of *Fagus sylvatica* or *Pinus sylvestris*. These forests usually form low stands with rather open canopies. A shrub layer is either absent or composed of tree layer species. The most dominant species of the herb layer is *Avenella flexuosa*. Forest understorey is well characterized by presence of drought-adapted and partially thermophilous plants (*Festuca ovina* agg., *Genista pilosa*, *Lembotropis nigricans*, *Silene nutans*, *Steris viscaria*), which grow in combination with oligotrophic and acidic-tolerant species (*Acetosella multifida* agg., *Calluna vulgaris*, *Genista tinctoria*, *Luzula luzuloides*, *Pilosella officinarum*). Higher frequencies in the moss layer reach various species, such as *Dicranum scoparium*, *Hypnum cupressiforme*, *Polytrichum formosum* and *P. piliferum*. This community is floristically

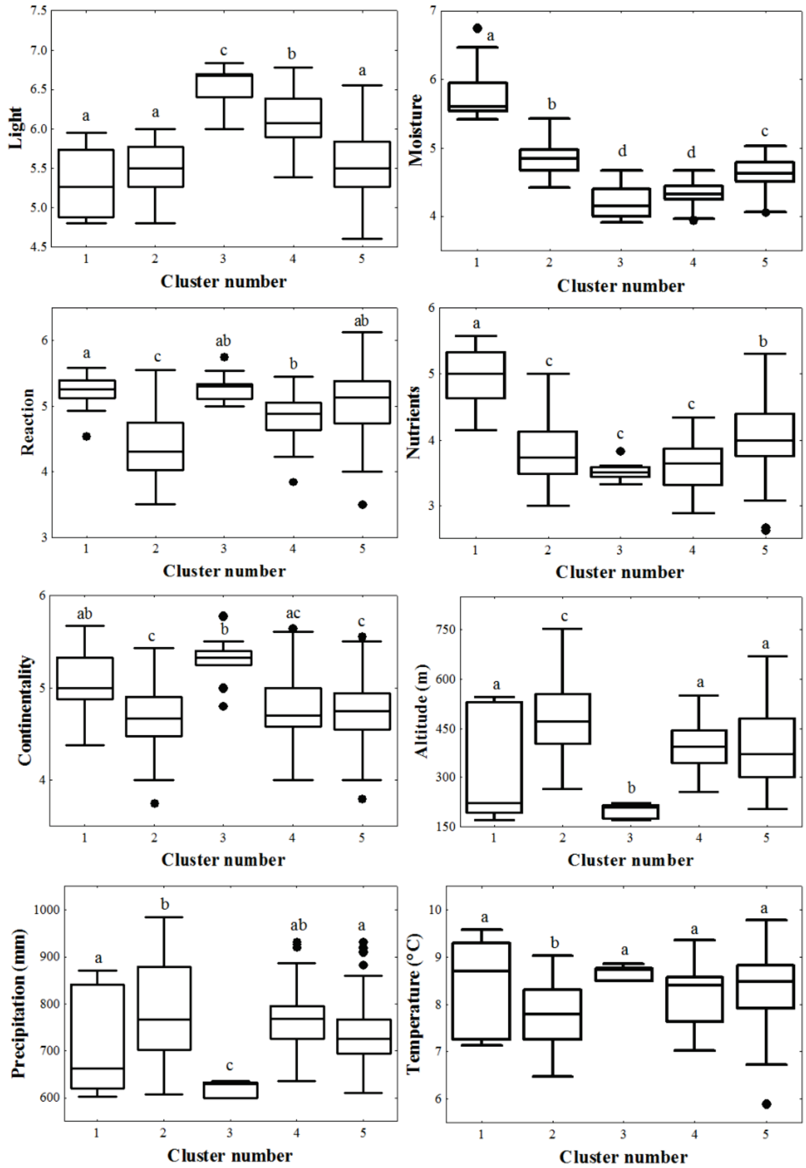

Fig. 2. Multiple comparisons of environmental variables (EIVs, altitude, mean annual precipitation and temperature) among acidic oak forests. Significant differences in one-way ANOVA and post-hoc Tukey HSD test ($p < 0.05$) are indicated by different letters. Boxes display interquartile range (25–75% values), central line median value and whiskers refers to range of values without outliers (black dots). For interpretation of individual clusters see Table 1.

Abb. 2. Box-Whisker-Diagramme zur Ausprägung der Umweltvariablen (Ellenberg-Zeigerwerte, Meereshöhe, Niederschlags- und Temperatur-Jahresmittel) bei den bodensauren Eichenwäldern. Nach ANOVA und Post-hoc-Tukey-HSD-Test signifikante Unterschiede ($p < 0{,}05$) zwischen den Assoziationen 1–5 (Reihenfolge wie im Text) sind durch unterschiedliche Buchstaben gekennzeichnet. Die Kästchen geben Interquartilsabstände zwischen 25% und 75% an, die Horizontallinie im Kästchen den Median, und die Whisker beziehen sich auf die Wertebereiche, bei denen die durch schwarze Punkte gekennzeichneten Ausreißer ausgenommen sind.

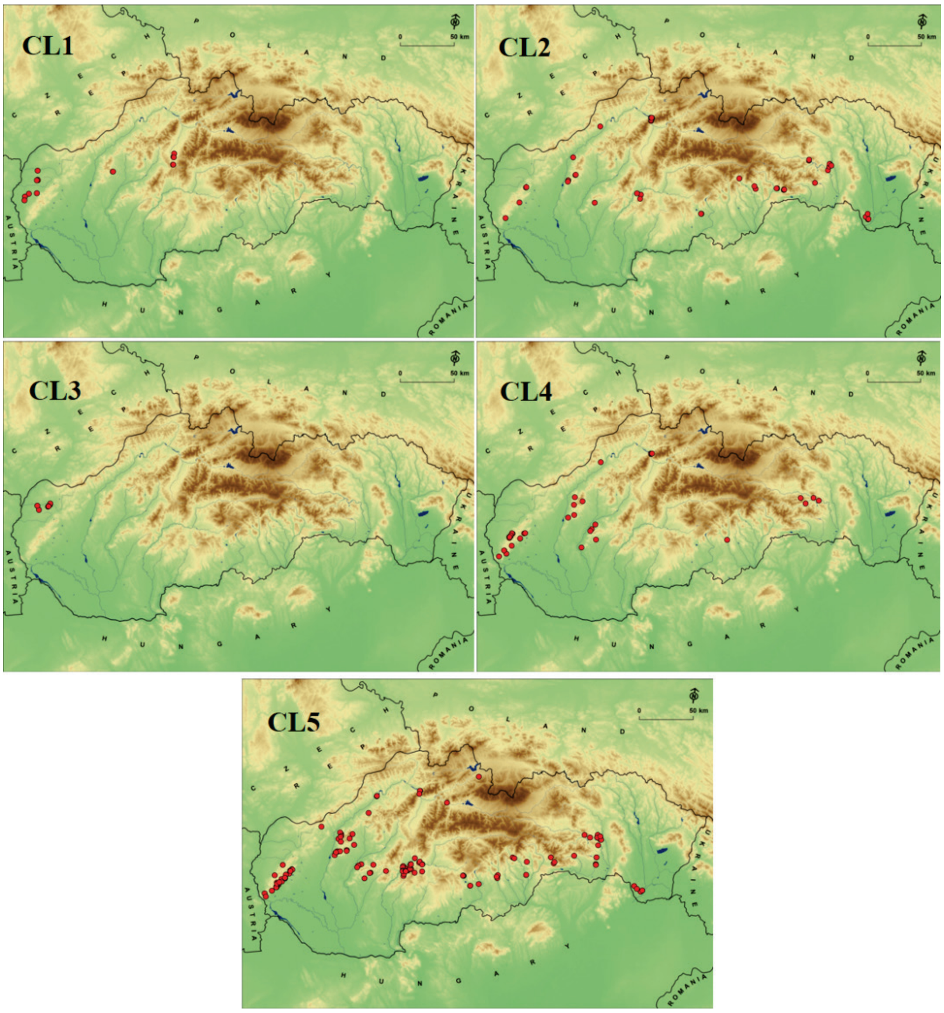

Fig. 3. Red dots indicate distribution pattern of acidophilous oak forests in Slovakia on separate map for each association (CL1 – *Molinio arundinaceae-Quercetum roboris*, CL2 – *Vaccinio vitis-idaeae-Quercetum roboris*, CL3 – *Festuco ovinae-Quercetum roboris*, CL4 – *Viscario vulgaris-Quercetum petraeae*, CL5 – *Luzulo luzuloidis-Quercetum petraeae*).

Abb. 3. Verbreitung der Assoziationen der bodensauren Eichenwälder der Slowakei. Vorkommen der Assoziationen (Namen siehe oben) sind durch rote Punkte gekennzeichnet.

well-differentiated (Table 1). Major differences against the *Vaccinio vitis-idaeae-Quercetum roboris* (cluster 2) and *Luzulo luzuloidis-Quercetum petraeae* (cluster 5) refer to the group of diagnostic species and to the higher frequency of some other thermophilous plants, such as *Hypericum perforatum* and *Silene nutans*. Numerous acidic-tolerant species (mainly *Genista pilosa*, *G. tinctoria*, *Veronica officinalis*) play an important role by differentiation against the acidophilous oak forests dominated by *Vaccinium* dwarf shrubs (cluster 2), as well.

This association was documented mainly in the lower mountain ranges (Čierna hora Mts., Malé Karpaty Mts., Považský Inovec Mts., Tríbeč Mts.) with scattered occurrence in Malá Fatra Mts. (Fig. 3). It prefers dry, stony and shallow soils (Leptic Dystric Cambisol) with low cation exchange capacity. This community was found at lower altitudes (75% of the plots show altitudes < 440 m a.s.l.; Fig. 2), frequently on south exposed steep slopes on crystalline bedrock.

Luzulo luzuloidis-Quercetum petraeae **Hilitzer 1932 (cluster 5, Table 1)**

Original form of the name: HILITZER (1932), asociace *Quercus sessilis-Luzula nemorosa* (*albida*) (*Quercus sessilis* = *Quercus petraea*, *Luzula nemorosa* (*albida*) = *Luzula luzuloides*)

Nomenclatural type: HILITZER (1932), p. 9–10, rel. 1, holotypus

Synonyms: *Quercetum medioeuropaeum* Br.-Bl. 1932, com. *Quercus sessilis-Genista tinctoria* Klika 1932

The tree layer is dominated by *Quercus petraea* agg., with admixture of *Fagus sylvatica* and *Carpinus betulus*. The shrub layer is usually sparse, with the presence of younger tree layer species. The herb layer is dense and dominated by *Luzula luzuloides*, rarely by *Avenella flexuosa* or *Melampyrum pratense*. Many mesophilous acidophytes (*Genista tinctoria*, *Hieracium lachenalii*, *H. murorum*, *H. sabaudum*,) occur together with acidic-tolerant forest plants with higher light requirements (*Campanula persicifolia*, *Veronica chamaedrys*) and with species of oak-hornbeam forests (*Galium schultesii*, *Poa nemoralis*). The most frequent mosses are *Dicranum scoparium*, *Hypnum cupressiforme* and *Polytrichum formosum*. This community is well-differentiated compared to *Vaccinio vitis-idaeae-Quercetum roboris* (cluster 2) and *Viscario vulgaris-Quercetum petraeae* (cluster 4) primarily by higher frequency of numerous acidic-tolerant species of mesic sites (e.g. *Carpinus betulus* in shrub layer, *Galium schultesii*, *Hieracium sabaudum*, *Melica uniflora*, *Poa nemoralis*, *Veronica chamaedrys*).

This vegetation type occupies deeper and slightly acidic to acidic soils (mostly Cambisols). It was documented throughout the northern edge of the Pannonian Basin with lower mountain ranges and uplands, which are accompanied by scattered localities in the Inner-Western Carpathians (e.g. Malá Fatra Mts., Čierna hora Mts.). These stands are commonly developed in submontane areas (75% of the plots is situated > 300 m a.s.l.; Fig. 2, 3) on steep convex slopes and ridges, where tree litter is blown away. Presence of the community could be associated also with historical litter raking.

4. Discussion

In spite of floristic poverty observed in acidophilous oak forests, we identified five associations within the alliance *Quercion roboris* in Slovakia. More formalized classification approach allowed the revision of acidophilous oak forests (MUCINA & MAGLOCKÝ 1985, JAROLÍMEK & ŠIBÍK 2008). These two vegetation synopses showed a considerable overlap with four identical and traditionally delimited associations (*Luzulo luzuloidis-Quercetum petraeae*, *Viscario vulgaris-Quercetum petraeae*, *Vaccinio vitis-idaeae-Quercetum roboris*, *Molinio arundinaceae-Quercetum roboris*), although the last one was formerly classified within the alliance *Potentillo albae-Quercion petraeae*. Phytosociological scheme of the alliance *Quercion roboris* seems to be strongly driven by the syntaxonomical concept of the association *Luzulo luzuloidis-Quercetum petraeae*, which has been reported in many vegetation syntheses and overviews across the Central European regions (e.g. PALLAS 1996, MORAVEC 1998, WILLNER & GRABHERR 2007, RECZYŃSKA 2015). Although it was originally proposed for mesic types, following the nomenclatural type relevé (HILITZER 1932, see also WILLNER et al. 2011), a broadly conceived concept unifying acidophilous oak forests on mesic and xeric sites has also been used. Our TWINSPAN results indicate its division into three units, i.e. rather mesic vegetation on moderately acidic sites (*Luzulo luzuloidis-Quercetum petraeae*), more xeric vegetation (*Viscario vulgaris-Quercetum petraeae*) and strongly acidic, oligotrophic oak forests with dwarf shrubs (*Vaccinio vitis-idaeae-Quercetum roboris*). However, we admit that they can slightly overlap with each other. This pattern is indicated by presence of either constant species or some other shared floristic elements growing in all three units (e.g. *Avenella flexuosa*, *Calamagrostis arundinacea*, *Fagus sylvatica*, *Lembotropis nigricans*). In Slovakia, the last two association names were almost completely lacking in literature sources, because many authors (e.g. ŠOMŠÁK 1963, FRAŇO et al. 1971, SLEZÁK & PETRÁŠOVÁ 2010) did not previously recognise these stands as distinct associations. They were most often assigned to the broadly defined *Luzulo luzuloidis-Quercetum petraeae*, which typically occurs on slopes and flatlands in southern and eastern parts of the Central Europe (PALLAS 2003). This vegetation was found to be the most common type of acidophilous oak forests in the study area. Our conceptual definition for this association is consistent with ecological and floristical patterns observed in the Czech Republic (MORAVEC 1998, ROLEČEK 2013). Acidophilous oakwoods with dominance of *Vaccinium* dwarf shrubs (*Vaccinio vitis-idaeae-Quercetum roboris*) are mainly distributed in northern temperate regions (PALLAS 2003), but they can also occur in southern temperate territories (e.g. NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ 1967a, ROLEČEK 2013). Our results indicate its submontane character in Slovakia. These forest stands are generally less common at low altitudes up to 400 m a.s.l., where they are often confined to north-facing slopes while more xeric oak forests (mainly *Viscario vulgaris-Quercetum petraeae*) replace them on shallow soils on sunny south-facing slopes. The concept with three associations was re-introduced by ROLEČEK (2013) in contemporary vegetation synopsis of the Czech Republic and was adopted by RECZYŃSKA (2015) in vegetation classification of oak forests in Sudetes Mts. (Poland), as well.

The acidophilous oak forests of hygrophilous sites were traditionally assigned to the association *Molinio arundinaceae-Quercetum*, which was described for the first time by SAMEK (1962) from the Czech Republic. However, the lectotype designated by MORAVEC (1998) for this association actually represents thermophilous oak forests of the *Melico pictae-Quercetum roboris* (alliance *Quercion petraeae*; cf. ROLEČEK 2013). The inappropriate lectotype selection (ICPN Art. 19) causes that the association name *Molinio arundinaceae-Quercetum* Samek 1962 should not be used for the vegetation of acidophilous oak forests on wet habitats. As a later homonym (Art. 31 ICPN), the *Molinio arundinaceae-Quercetum roboris* Neuhäusl & Neuhäuslová-Novotná 1967 was subsequently published. The lectotypification performed by PALLAS (1996) is in accordance with the core character of this syntaxon. The name was accepted in most vegetation surveys across the eastern part of Central Europe (e.g. MUCINA & MAGLOCKÝ 1985, JAROLÍMEK & ŠIBÍK 2008, MATUSZKIEWICZ 2012, MATUSZKIEWICZ et al. 2018, see also MORAVEC 1998). In western and northern part of the Central Europe, seasonally wet acidic oak-birch forests with higher constancy of boreal species are usually classified in the alliance *Molinio caeruleae-Quercion roboris* (e.g. PALLAS 1996, 2003), but its associations include several oceanic or sub-oceanic species (e.g. *Lonicera periclymenum*) and our stands are thus situated beyond their eastern distributional limits. Some authors (e.g. ROLEČEK 2013) prefer a broadly conceived concept of the association *Holco mollis-Quercetum roboris* for classification of similar stands, but the protologue (SCAMONI 1935), as well as the neotypus relevé (PASSARGE in PALLAS 1996) does not fully match their species composition. Consequently, to avoid changes in a commonly used name, we propose to conserve the name *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967 against the antedating name *Molinio arundinaceae-Quercetum* Samek 1962 (ICPN Art. 52).

For species-poor acidophilous mixed pine-oak forests developed on aeolian sands or strongly sandy soils, we propose to use the name *Festuco ovinae-Quercetum roboris*. We have accepted previously suggested syntaxonomical affiliation of this association to acidophilous oak forests reported by NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ (1967a) and MORAVEC (1998), although some other authors consider them transitional between acidophilous and thermophilous oak forests (e.g. ROLEČEK 2013). In Slovakia, species composition of these stands was documented by RUŽIČKA (1964) and KRIPPEL (1965) in detail, with many relevés containing planted *Pinus sylvestris* in forest overstorey. They were classified as *Pino-Quercetum zahoricum* (an illegitimate name according to ICPN Art. 34a) or *Pineto-Quercetum festucetosum*. Similar stands in adjacent southern Moravia region (Czech Republic) were described by ŠMARDA (1961) as *Quercetum roboris-Festucetum ovinae*. We inverted this name to the *Festuco ovinae-Quercetum roboris* (ICPN Art. 10b). Phytosociological material from both nearby regions showed high similarity in floristic composition, physiognomy and ecology. They share numerous frequent species (e.g. *Hypericum perforatum*, *Luzula campestris* agg., *Pleurozium schreberi*, *Quercus robur*, *Tithymalus cyparissias*, *Veronica officinalis*), including those suggesting human impact on vegetation structure (*Calamagrostis epigejos*, *Pinus sylvestris*). We identified several other species in common as well (e.g. *Carex ericetorum*, *Cerastium arvense*, *Teucrium chamaedrys*, *Thymus serpyllum*), mainly in stands dominated by *Pinus sylvestris* (cf. RUŽIČKA 1964, KRIPPEL 1965). Only higher frequency of the species *Festuca ovina* in Moravian relevés in comparison with Slovak ones and vice versa for the species *Festuca dominii* was observed. A lectotypification is not possible because the protologue of the association (ŠMARDA 1961) does not contain single relevés or a reference to an effectively published relevé but only two synoptic columns with typical (six relevés) and cultural (ten relevés) variants. However, we did not designate here the neotype (ICPN Art. 21) for two reasons. Firstly, most of the original sites were replaced by cultivated pine plantations many years ago and secondly, there are potential taxonomic uncertainties by determination of *Festuca* species in original vegetation relevés.

Main environmental drivers shaping the variability of acidophilous oak forests were moisture conditions and availability of nutrients, but species composition also varied along the altitudinal gradient. This finding is consistent with previous studies (e.g. ROLEČEK 2013). The important role of soil moisture is clearly indicated by the length of a moisture gradient with seasonally wet communities on one side (*Molinio arundinaceae-Quercetum roboris*) and xeric vegetation on the other (*Viscario vulgaris-Quercetum petraeae*). The variability of species composition was also driven by nutrient availability. This could be explained by the importance of even small deviation in nutrient supply within the narrow range of pH values of acidic substrates. Strongly acidic soils are characterized by a decline of nutrient availability and a rising solubility of toxic metals, whereas slightly acidic soils show an increase of nutrient uptake by plants, accompanied by neutralisation of metal toxicity (TYLER 2003). In our study, the strongly acidic soils (e.g. topsoil horizon pH_{H2O} 4.0, FRAŇO et al. 1971) were documented for example within the stands of *Vaccinio vitis-idaeae-Quercetum roboris*, whereas several habitats of the *Luzulo luzuloidis-Quercetum petraeae* were recorded on soils with topsoil horizon pH_{H2O} values higher than 5.0 (e.g. SLEZÁK & AXMANOVÁ 2016).

Our results further suggest that acidophilous oak forests share a group of oligotrophic and acidic-tolerant plant species able to grow on suitable habitats irrespective of altitude (e.g. *Avenella flexuosa*, *Luzula luzuloides*, *Vaccinium myrtillus*, *Veronica officinalis*). However, overall plant species assemblages respond to the recorded altitudinal gradient (170 to 753 m a.s.l.) with a continuous species turnover. In submontane areas at the same altitudes, these plant communities usually prefer south-facings slopes because on more humid north-facing slopes (or towards higher altitudes) they are competed by acidophilous beech forests (SLEZÁK et al. 2016).

Erweiterte deutsche Zusammenfassung

Einleitung – Zentraleuropäische bodensaure Eichenwälder kommen auf basenarmen Böden in Tief- und Mittelgebirgslagen vor (PALLAS 1996, 2003; HÄRDTLE 2004). In höheren Lagen können noch relativ trockene Standorte mit flachgründigen oder steinigen Böden besiedelt werden, wo die Konkurrenzkraft der Buche reduziert ist. Die Pflanzengesellschaften sind relativ artenarm, doch trotz der harten Umweltbedingungen variabel in ihrer Artenzusammensetzung. In der Slowakei sind bodensaure Eichenwälder (Ordnung der *Quercetalia roboris*, Verband *Quercion roboris*) seit den 1960er Jahren genauer pflanzensoziologisch untersucht worden (u. a. ŠOMŠÁK 1963, HUSOVÁ 1967, NEUHÄUSLOVÁ-NOVOTNÁ 1970, JURKO 1975), obwohl die ersten Vegetationsaufnahmen länger zurückliegen (u. a. MIKYŠKA 1939, JURKO 1951). Mit der vorliegenden Arbeit präsentieren wir die erste syntaxonomische Revision der bodensauren Eichenwälder in der Slowakei. Dazu verwenden wir einen repräsentativen Datensatz und benutzen formal verbindliche Klassifikationsmethoden sowie die nomenklatorischen Regeln des ICPN (WEBER et al. 2000). Wir analysieren (1) die floristische Variabilität und Syntaxonomie der bodensauren Eichenwälder der Slowakei und beschreiben (2) die hauptsächlichen Umweltgradienten, die der Variabilität zugrunde liegen.

Methoden – Die verfügbaren Vegetationsaufnahmen des *Quercion roboris* aus der Slowakei wurden in einer Turboveg-Datei (HENNEKENS & SCHAMINÉE 2001) zusammengetellt und weiter in Juice (TICHÝ 2002) verarbeitet. Der Datensatz wurde mittels TWINSPAN, in der durch ROLEČEK et al. (2009) modifizierten Version, klassifiziert. Die Auswirkungen von Umweltfaktoren auf die Artenzusammensetzung wurden mit dem Ordinationsverfahren Detrended Correspondence Analysis (DCA) veranschaulicht. Die wichtigsten Umweltgradienten wurden mit den Ellenberg-Zeigerwerten für Gefäßpflanzen Tschechiens (CHYTRÝ et al. 2018), Kontinentalitätswerten (BERG et al. 2017), der Lage über Meereshöhe und den Jahresmittelwerten für Temperatur und Niederschlag interpretiert.

Ergebnisse – Der Datensatz von 263 Aufnahmen wurde in fünf Cluster gruppiert und auf Assoziationsebene interpretiert (Tab. 1). Die klassifizierten Einheiten wurden im Verband *Quercion roboris* den Assoziationen *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967, *Vaccinio vitis-idaeae-Quercetum roboris* Oberdorfer 1957, *Festuco ovinae-Quercetum roboris* Šmarda 1961, *Viscario vulgaris-Quercetum petraeae* Stöcker 1965 und *Luzulo luzuloidis-Quercetum petraeae* Hilitzer 1932 zugeordnet. Die DCA ließ erkennen, dass Bodenfeuchte, Nährstoffgehalt, Höhenlage (stellvertretend für Temperatur und Niederschlag) und Kontinentalität zu den wichtigsten Umweltfaktoren für die Differenzierung der Eichenwälder gehören (Abb. 1, 2). Das *Molinio arundinaceae-Quercetum roboris* kommt in wechselfeuchtem flachen Gelände auf lehmig-schluffigen Böden vor. Es handelt sich gewöhnlich um Stieleichen-Wälder (*Quercus robur* agg.) mit azidophytischem Unterwuchs sowie mit Arten wie *Deschampsia cespitosa*, *Lysimachia vulgaris* oder *Molinia caerulea* agg., die an im Jahresverlauf wechselnde Grundwasserstände angepasst sind. Das *Vaccinio vitis-idaeae-Quercetum roboris* kommt vor allem im Vorland der Westkarpaten auf stark sauren Böden vor. Die Baumschicht wird dominiert von *Quercus petraea* agg., der Unterwuchs durch Zwergsträucher wie *Calluna vulgaris* und *Vaccinium myrtillus*, begleitet von *Avenella flexuosa*. Das *Festuco ovinae-Quercetum roboris* wächst auf trockenen, nährstoffarmen sandigen Böden im Tiefland (Abb. 2, 3). Im Kronenraum dominieren *Quercus petraea* agg. oder *Q. robur* agg. Die artenarme Krautschicht wird bestimmt von sandbewohnenden und wärmeliebenden Pflanzen mit hohem Anteil von Grasartigen. Eine Moosschicht ist gewöhnlich gut entwickelt. Das *Viscario vulgaris-Quercetum petraeae* bevorzugt trockene, steinige und flachgründige Böden über Silikatgestein in Südhanglage. *Quercus petraea* agg. dominiert die Baumschicht. Die Krautschicht wird bestimmt von trockenheits- und hitzeangepassten Arten mit Beteiligung von Azidophyten. Die Bestände des *Luzulo luzuloidis-Quercetum petraeae* kommen auf relativ tiefgründigen und weniger sauren Böden vor. Ihr Vorkommen könnte mit der früheren Waldnutzungsform des Streurechens in Verbindung gebracht werden. Dominante Baumart ist *Quercus petraea* agg., begleitet von *Fagus sylvatica* und *Carpinus betulus*. Die Krautschicht ist typischerweise dominiert von *Luzula luzuloides*, beigemischt sind relativ lichtbedürftige mesophile Arten wie *Poa nemoralis, Galium schultesii* und *Campanula persicifolia* (Tab. 1).

Diskussion – Der Verband *Quercion roboris* umfasst verschiedene Typen azidophytischer Eichen- und Eichenmischwälder, wobei das *Luzulo luzuloidis-Quercetum petraeae* weit oder eng ausgelegt werden kann. Unsere Ergebnisse, basierend auf numerischer Klassifikation, unterstützen eine Unterteilung des *Luzulo luzuloidis-Quercetum petraeae* sensu lato in drei Assoziationen – eher frische Eichenwälder an mäßig sauren Standorten (*Luzulo luzuloidis-Quercetum petraeae* sensu stricto), eher trockene Eichenwälder des *Viscario vulgaris-Quercetum petraeae*, und stark saure oligotrophe zwergstrauch-reiche Eichenwälder des *Vaccinio vitis-idaeae-Quercetum roboris*. Für artenarme Kiefern-Eichen-Mischwälder auf sauren Flugsandböden im Tiefland von Záhorská nížina schlagen wir den Namen *Festuco ovinae-Quercetum roboris* vor.

Acknowledgements

We thank I. Svitková for language improvement, J. Pallas and two other anonymous reviewers for their constructive and helpful comments on the manuscript. This research was supported by the Science Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences VEGA (grant number 1/0639/17 and 2/0031/17).

Author contribution statement

M.S. and M.V. conceived the idea of the research and led the writing. All authors participated in field sampling, discussed the results and contributed to the manuscript.

ORCIDs

Michal Slezák https://orcid.org/0000-0002-6926-7139
Milan Valachovič https://orcid.org/0000-0001-5296-5240
František Máliš https://orcid.org/0000-0003-2760-6988
Dušan Senko https://orcid.org/0000-0002-0630-043X
Hubert Žarnovičan https://orcid.org/0000-0002-5107-0151

References

BERG, C., WELK, E. & JÄGER, E.J. (2017): Revising Ellenberg's indicator values for continentality based on global vascular plant species distribution. – Appl. Veg. Sci. 20: 482–493.

BLAŽKOVÁ, D. (1989): Vegetace chráněného území Staňkovka (Vegetation des Naturschutzgebietes Staňkovka) [in Czech, with German summary]. – Bohm. Centr. 18: 77–103.

CHYTRÝ, M., TICHÝ, L., DŘEVOJAN, P., SÁDLO, J. & ZELENÝ, D. (2018): Ellenberg-type indicator values for the Czech flora. – Preslia 90: 83–103.

EWALD, J. (2003): The calcareous riddle: why are there so many calciphilous species in the central European flora? – Folia Geobot. 38: 357–366.

FRAŇO, A., JURKO, A. & ŠOMŠÁK, L. (1971): Böden und Wälder der Zemplíner Hügel (Slowakei). – Acta Fac. Rerum Natur. Univ. Comen., Botanica 17: 1–60.

HÄRDTLE, W. (2004): Bodensaure Eichen- und Eichenmischwälder Europas. – Tuexenia 24: 57–72.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. – J. Veg. Sci. 12: 589–591.

HILITZER, A. (1932): Bory na Horšovotýnsku (Pine-oak forests in der Region Horšovotýnsko) [in Czech]. – Čas. Nár. Mus. 106: 1–12.

HUSOVÁ, M. (1967): Azidophile Eichenwälder auf Quarziten im Tribeč-Gebirge, Slowakei. – Folia Geobot. Phytotax. 2: 121–136.

INDREICA, A. (2012): Vegetation classification of acidophytic oak forests of Romania. – Phytocoenologia 42: 221–230.

IUSS Working Group WRB (2015): World reference base for soil resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome.

JAROLÍMEK, I. & ŠIBÍK, J. (Eds.) (2008): Diagnostic, constant and dominant species of the higher vegetation units of Slovakia. – Veda, Bratislava: 332 pp.

JURKO, A. (1951): Vegetácia stredného Pohornádia (Vegetation of the central Pohornádie region) [in Slovak, with Russian and French summary]. – Vydavatelstvo SAVU, Bratislava: 109 pp.

JURKO, A. (1975): Waldgesellschaften des Zentralteiles der Ostslowakei und einige Fragen ihrer Syntaxonomie. – Biol. Práce 21: 9–81.

KASPROVICZ, M. (2010): Acidophilous oak forests of the Wielkopolska region (West Poland) against the background of Central Europe. – Biodiv. Res. Conserv. 20: 1–138.

KEVEY, B. & BORHIDI, A. (2005): The acidophilous forests of the Mecsek and their relationship with the Balkan-Pannonian acidophilous forests. – Acta Bot. Hung. 47: 273–368.

KLIKA, J. (1937): Xerotherme und Waldgesellschaften der Westkarpathen (Brezover Berge). – Beih. Bot. Cbl. 57B: 295–342.

KRIPPEL, E. (1965): Postglaciálny vývoj lesov Záhorskej nížiny (historicko-geobotanická štúdia) (Postglacial forest development of the Záhorská nížina Lowland (historical-geobotanical study)) [in Slovak, with German summary]. – Biol. Práce 11 (3): 1–100.

KUNDRÁK, B., KOLLÁR, J., BALKOVIČ, J., ŽARNOVIČAN, H. & ÁBRAHÁMOVÁ, A. (2014): Fytocenologická a pôdno-ekologická charakteristika kyslomilných dúbrav Malých Karpát (Phytocoenological and soil-ecological characteristics of the acidophilous oak forest in the Malé Karpaty Mts.) [in Slovak, with English abstract]. – Phytopedon (Bratislava) 13: 54–65.

MALCUIT, G. (1929): Contribution à l'étude phytosociologique des Vosges méridionales saônoises. Les associations végétales de la vallée de la Lanterne (Contribution to phytosociological research of the southern Vosges region. Vegetation associations of the Lanterne valley) [in French]. – Arch. Bot. (Caen) 2: 1–211.

MARHOLD, K. & HINDÁK, F. (Eds.) (1998): Checklist of non-vascular and vascular plants of Slovakia. – Veda, Bratislava: 687 pp.

MATUSZKIEWICZ, W. (2012): Przewodnik do oznaczania zbiorowisk roślinnych Polski (Guidebook for determination of plant communities in Poland) [in Polish]. – Wydawnictwo Naukowe PWN, Warszawa: 537 pp.

MATUSZKIEWICZ, W., SIKORSKI, P., SZWED, W. & WIERZBA, M. (Eds.) (2018): Zbiorowiska roślinne Polski. Lasy i zarośla. (Plant communities of Poland. Forests and scrubs.) [in Polish]. – Wydawnictwo Naukowe PWN, Warszawa: 518 pp.

MICHALKO, J., BERTA, J. & MAGIC, D. (1986): Geobotanická mapa ČSSR (Geobotanical map of the CSSR) [in Slovak, with Russian and German summary]. – Veda, Bratislava: 168 pp.

MIKYŠKA, R. (1937): Přehled přirozených lesních společenstev ve Slovenském středohoří (Synopsis of natural forest communities in central Slovakia) [in Czech, with French and German summary]. – Lesn. Práce 16: 259–266.

MIKYŠKA, R. (1939): Studie über die natürlichen Waldbestände im Slowakischen Mittelgebirge (Slovenské stredohorie). Ein Beitrag zur Soziologie der Karpatenwälder. – Beih. Bot. Cbl. 59B: 169–244.

MIŠÍKOVÁ, K., GODOVIČOVÁ, K., ŠIRKA, P. & ŠOLTÉS, R. (2020): Checklist and red list of mosses (Bryophyta) of Slovakia. – Biologia 75: 21–37.

MORAVEC, J. (1998): Přehled vegetace České republiky. Svazek 1 Acidofilné doubravy (Acidophilous oak forests) [in Czech, with English summary]. – Academia, Praha, 64 pp.

MUCINA, L., BÜLTMANN, H., DIERßEN, K. … TICHÝ, L. (2016): Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Appl. Veg. Sci. 19: 3–264.

MUCINA, L. & MAGLOCKÝ, Š. (Eds.) (1985): A list of vegetation units of Slovakia. – Doc. Phytosociol. 9: 175–200.

NETELER, M., BOWMAN, M.H., LANDA, M. & METZ, M. (2012): GRASS GIS: A multiple-purpose open source GIS. – Environ. Modell. Soft. 31: 124–130.

NEUHÄUSL, R. & NEUHÄUSLOVÁ-NOVOTNÁ, Z. (1967a): Syntaxonomische Revision der azidophilen Eichen- und Eichenmischwälder im westlichen Teile der Tschechoslowakei. – Folia Geobot. Phytotax. 2: 1–41.

NEUHÄUSL, R. & NEUHÄUSLOVÁ-NOVOTNÁ, Z. (1967b): Die Waldgesellschaften der Zemplíner Hügel (SO-Slowakei). – Grad. Bot. (Cluj) 589: 247–262.

NEUHÄUSLOVÁ-NOVOTNÁ, Z. (1970): Beitrag zur Kenntnis der Waldgesellschaften der Kleinen Karpaten, Slowakei. I. Phytozönologische Verhältnisse. – Folia Geobot. Phytotax. 5: 265–306.

OBERDORFER, E. (1957): Süddeutsche Pflanzengesellschaften. – Pflanzensoziologie 10: 1–564.

PÄRTEL, M. (2002): Local and diversity patterns and evolutionary history at regional scale. – Ecology 83: 2361–2366.

PALLAS, J. (1996): Beitrag zur Syntaxonomie und Nomenklatur der bodensauren Eichenmischwälder in Mitteleuropa. – Phytocoenologia 26: 1–79.

PALLAS, J. (2000): Zur Systematik und Verbreitung der europäischen bodensauren Eichenmischwälder (*Quercetalia roboris* Tüxen 1931). – Abh. Westfälischen Mus. Naturkd. 62 (3): 1–125.

PALLAS, J. (2003): *Quercetea robori-petraeae* Braun-Blanquet et Tüxen 1943. – In: BOHN, U., NEUHÄUSL, R., GOLLUB, G., HETTWER, C., NEUHÄUSLOVÁ, Z., RAUS, T., SCHLÜTER, H. & WEBER, H. (Eds.): Karte der natürlichen Vegetation Europas / Map of the natural vegetation of Europe. Maßstab / Scale 1: 2 500 000. Erläuterungstext / Explanatory Text: 251–270. Landwirtschaftsverlag, Münster.

R CORE TEAM (2014): R: A language and environment for statistical computing. Version 3.0.3. – R Foundation for Statistical Computing, Vienna. – URL http://www.R-project.org.

RECZYŃSKA, K. (2015): Diversity and ecology of oak forests in SW Poland (Sudetes Mts.). – Phytocoenologia 45: 85–106.

ROLEČEK, J. (2013): Acidofilní doubravy (*Quercetea robori-petraeae*) (Acidophilous oak forests). – In: CHYTRÝ, M. (Ed.): Vegetace České republiky. 4. Lesní a křovinná vegetace (Vegetation of Czech Republic 4. Forest and scrub vegetation) [in Czech, with English summary]: 347–365. Academia, Praha.

ROLEČEK, J., TICHÝ, L., ZELENÝ, D. & CHYTRÝ, M. (2009): Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. – J. Veg. Sci. 20: 596–602.

RUŽIČKA, M. (1964): Geobotanische Verhältnisse der Wälder im Sandgebiete der Tiefebene Záhorská nížina (südwestslowakei). – Biol. Práce 10 (1): 1–124.

SAMEK, V. (1962): Lesy severovýchodního výběžku Brdských hřebenů (Forest of northeastern foothills of the Brdské hřebene Mts.) [in Czech]. – Pr. Výzk. Úst. Lesn. ČSSR 24: 107–168.

SCAMONI, A. (1935): Vegetationstudien im Sarnow. – Z. Forst-Jagdwes. 11–12: 561–600, 625–648.

SLEZÁK, M. & AXMANOVÁ, I. (2016): Patterns of plant species richness and composition in deciduous oak forests in relation to environmental drivers. – Comm. Ecol. 17: 61–70.

SLEZÁK, M., HRIVNÁK, R., UJHÁZY, K., UJHÁZYOVÁ, M., MÁLIŠ, F. & PETRÁŠOVÁ, A. (2016): Syntaxonomy and ecology of acidophilous beech forest vegetation in Slovakia. – Phytocoenologia 46: 69–88.

SLEZÁK, M. & PETRÁŠOVÁ, A. (2010): Oak forest vegetation in the northern part of the Štiavnické vrchy Mts (central Slovakia). – Hacquetia 9: 221–238.

ŠMARDA, F. (1961): Rostlinná spoločenstva území přesypových písků lesa Doubravy u Hodonína (Die Pflanzengesellschaften der Flugsandgebiete des Waldes Doubrava bei Göding in Südmähren) [in Czech, with German summary]. – Pr. Brněn. Zákl. Čs. Akad. Věd 33(1): 1–56.

ŠOMŠÁK, L. (1963): Dubiny južnej časti Malej Fatry a ich ochrana (Oak forests in southern part of Malá Fatra Mts and their protection) [in Slovak, with Russian and German summary]. – Čs. Ochr. Přír. 1: 146–164.

STÖCKER, G. (1965): Vorarbeit zu einer Vegetationsmonographie des Naturschutzgebietes Bodetal. II. Waldgesellschaften. – Wiss. Z. Univ. Halle, ser. math.-natur. 14: 505–561.

TICHÝ, L. (2002): JUICE, software for vegetation classification. – J. Veg. Sci. 13: 451–453.

TICHÝ, L. & CHYTRÝ, M. (2006): Statistical determination of diagnostic species for site groups of unequal size. – J. Veg. Sci. 17: 809–818.

TYLER, G. (2003): Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour – contribution to a debate. – Folia Geobot. 38: 419–428.

WEBER, H.E., MORAVEC, J. & THEURILLAT, J.-P. (2000): International Code of Phytosociological Nomenclature. 3rd ed. – J. Veg. Sci. 11: 739–768.

WILLNER, W. & GRABHERR, G. (2007): Die Wälder und Gebüsche Österreichs. Ein Bestimmungswerk mit Tabellen. – Spektrum Akademischer Verlag, Heidelberg: 302 pp.

WILLNER, W., GRABHERR, G., PALLAS, J. & WEBER, H.E. (2011): Report of the Committee for Nomina Conservanda, Ambigua, Inversa and Mutata: 1. – Phytocoenologia 41: 59–70.

ZELENÝ, D. & SCHAFFERS, A.P. (2012): Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. – J. Veg. Sci. 23: 419–431.