Vegetation types of dry-mesic oak forests in Slovakia

Vegetační typy subtermofilních doubrav na Slovensku

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Typology of dry-mesic oak forest vegetation of Slovakia is presented. Seven vegetation types were distinguished based on a Braun-Blanquetian relevé data analysis using a TWINSPAN classification algorithm. The identified vegetation types are related to seven syntaxa traditionally used by Central European phytosociologists: dry-mesic oak forest on sandy soils – *Carici fritschii-Quercetum roboris*, dry-mesic oak forest on heavy soils – *Potentillo albae-Quercetum*, dry-mesic oak forest on basic rocky substrates – *Corno-Quercetum*, dry-mesic oak forest on acidic substrates – *Sorbo torminalis-Quercetum*, dry oak forest on loess – *Quercetum pubescenti-roboris*, dry-mesic oak forest on loess – *Convallario-Quercetum roboris*, dry-mesic forest of Turkey oak – *Quercetum petraeae-cerris*. Detrended correspondence analysis was used to visualize the similarity of vegetation types. Some aspects of dry-mesic oak forest ecology, distribution and dynamics in Slovakia are discussed; their general retreat due to mesophilous tree species expansion is stressed.

K e y w o r d s : classification, phytosociology, *Quercetalia pubescenti-petraeae, Quercus*, syntaxonomy, vegetation typology, vegetation survey

Introduction

Central European dry-mesic oak forests constitute a peculiar group of plant communities, occupying the niche between shady mesic mixed forests and dry thermophilous open oak forests. Compared to dry thermophilous oak forests they occur in flatter areas with deeper soils and also in colder regions. They are composed of a mixture of xerophilous and mesophilous species of both forest and open habitats. Many stands, and perhaps whole vegetation types, represent successionally unstable vegetation created by man from mixed mesic forests (Svoboda 1943, Kwiatkowska & Wyszomirski 1988, 1990, Jakubowska-Gabara 1996).

Central Europe maintains a considerable diversity of dry-mesic oak forests, as their species composition changes along several environmental and geographical gradients. The heterogeneity of landscapes, variety of bedrock and the mixture of biogeographic influences (Central European, boreal, Pontic-Pannonian, subatlantic, subcontinental and submediterranean), typical of this region, create opportunities for various oak forest communities to develop. Diversified and long-lasting human impact has also played an important role (Ložek 1973, Krippel 1986, Magic et al. 1986).

First detailed studies of Slovak dry and dry-mesic oak forest vegetation were conducted during the 1930s–1940s (Sillinger 1931, Dostál 1933, Klika 1938, Mikyška 1939, Futák 1947). Thorough descriptions of their diversity appeared in the second half of the 20th century, when numerous authors published phytosociological papers on local vegetation types. Some of them described new local syntaxa (Michalko 1957, Michalko & Džatko

1965, Šomšák & Háberová 1979, Miadok 1991, Michalko 1991, Chytrý 1994), and others tried to introduce syntaxa used in neighbouring countries (Jakucs 1961, Neuhäusl & Neuhäuslová-Novotná 1964, Neuhäuslová-Novotná & Neuhäusl 1965, Jurko 1965). The evaluation of relevé data was usually performed without explicit rules, either using phytosociological tables or completely arbitrarily.

The attempts to synthesize the knowledge on oak forest diversity in Slovakia were undertaken mainly by J. Michalko (Michalko in Mucina & Maglocký 1985, Michalko et al. 1986, Michalko 1991). His ecologically and geographically focused approach, which followed the tradition of Hungarian authors (Zólyomi 1957, Jakucs 1961), gained ground when the geobotanical map of Slovakia was compiled (Michalko et al. 1986). Extensive field experience enabled him to appreciate local vegetation peculiarities and simplify the classification scheme to meet the needs of a broad-scale vegetation map. In the syntaxonomic synopsis of oak forest vegetation of Slovakia (Michalko in Mucina & Maglocký 1985) he presented a simple hierarchical enumeration of hitherto known local and regional syntaxa, with little generalization. In a latter paper (Michalko 1991) he extensively discussed the syntaxonomy of the *Potentillo-Quercion* alliance in Slovakia.

In summary, all hitherto used classifications of oak forests in Slovakia are traditional, based mainly on arbitrary decisions, local rules and sometimes on mere dominance of species. This is not necessarily wrong, as all these criteria may relate to vegetation per se but it can be useful to compare them with vegetation classification based on an evaluation of overall species composition. Therefore, the goal of the present paper is to describe the diversity of dry-mesic oak forests[1] in Slovakia in terms of vegetation types, based on numerical analysis of a large number of relevés originating from the whole of Slovakia. Identified vegetation types are characterized by their species composition, ecology and distribution.

Material and methods

The study is based on the analysis of original and excerpted phytosociological relevés recorded according to Braun-Branquet approach (Westhoff & van der Maarel 1978) and stored in a TURBOVEG database (Hennekens & Schaminée 2001, Chytrý & Rafajová 2003). From the total of more than 1100 relevés of oak, oak-hornbeam and oak-Scots pine forests gathered for the pilot analysis, 309 relevés of dry-mesic oak forests were selected on the basis of TWINSPAN classification (Hill 1979), carried out by using JUICE software (Tichý 2002). Of them, about 130 relevés originated from the Central Database of the Phytosociological Relevés in Slovakia (Valachovič 1999; most of these relevés came from Mikyška 1939, Michalko 1957, Neuhäusl & Neuhäuslová-Novotná 1964, Michalko & Džatko 1965, Šomšák & Háberová 1979, Michalko 1991), about 50 were retrieved from the literature (Dvořák 1960, Jurko 1965, Neuhäuslová-Novotná & Neuhäusl 1965, Michalko & Plesník 1982, Chytrý 1994, Šomšák & Kubíček 2000), 70 came from the author's field research and another 60 unpublished relevés were kindly provided by

[1] The term "dry-mesic oak forests", as used in the present paper, includes all kinds of open canopy subthermophilous oak forests and thermophilous oak forests on deep soils. On the other hand, neither dry thermophilous oak forests on shallow rocky soils (syntaxonomically treated as e.g. *Pruno mahaleb-Quercetum pubescentis*, *Seslerio albicantis-Quercetum pubescentis*, *Cotino-Quercetum pubescentis*, *Genisto pilosae-Quercetum petraeae*) nor species-poor acidophilous oak forests and oak-Scots pine forests are considered in the present paper. A complete synthesis of Slovak oak forest vegetation requires further field sampling.

J. Ružičková, M. Valachovič and M. Hájek. Before the analysis, the data on the moss layer were excluded because of their incompleteness and taxonomic concepts were unified using broader species aggregates.

A comment on the taxonomical concept of *Quercus* species used in this paper is necessary. The genus *Quercus* is taxonomically complicated and very different numbers of species are recognized by different authors within this genus (Gömöry et al. 2001). While *Q. cerris* from the section *Cerris* is a well-defined species, the relation between taxa of the section *Robur* (in Slovakia occur *Q. robur*, *Q. pedunculiflora*, *Q. petraea*, *Q. dalechampii*, *Q. polycarpa*, *Q. pubescens*, *Q. virgiliana* and *Q. frainetto*) is unclear and even the treatment of the two most widespread taxa, *Q. robur* and *Q. petraea*, as separate species has been challenged (Kleinschmit et al. 1995). The splitter approach prevails in Slovak taxonomic tradition and all the taxa mentioned above are treated as species (Magic 1975, Požgaj & Horváthová 1986). Nevertheless, because of the minute morphological differences between the taxa and the extensive morphological plasticity, it is impossible to distinguish between them during routine phytosociological research. In a synthetic study like this, it is also necessary to unify the taxonomic concepts of different authors of relevés, therefore I lumped the data on the occurrence of *Quercus* species as follows: *Quercus robur* agg. (incl. *Quercus robur* s. str., *Q. pedunculiflora*), *Quercus petraea* agg. (incl. *Q. petraea* s. str., *Q. dalechampii*, *Q. polycarpa*), *Q. pubescens* agg. (incl. *Q. pubescens* s. str., *Q. virgiliana*), *Q. frainetto*, *Q. cerris* and the introduced *Q. rubra*.

The data set of 309 relevés was classified using TWINSPAN (pseudospecies cut levels 0, 5 and 25, layers merged). The assignment of the Twinspan groups to the final vegetation types was made subjectively in order to obtain units approximately as broad as traditional phytosociological associations, sufficiently homogeneous and ecologically interpretable. Detrended correspondence analysis (DCA) from the CANOCO software (ter Braak & Šmilauer 2002) and CanoDraw 4.1 software were used to visualize the similarity of the identified vegetation types. Default options and logarithmic transformation of percentage species cover data were used in DCA. A synoptic table was created and indicator species were determined using the fidelity calculation within the JUICE software. As a measure of fidelity, the Dufręne-Legendre indicator value index (Dufręne & Legendre 1997) was used and species with values higher than 30 in one or two columns were designated as indicator species. In comparison with some other measures of indicator/diagnostic species, the Dufręne-Legendre indicator value index emphasizes the importance of the more frequent species (Chytrý et al. 2002).

The method of classification described above is subjective and imperfectly formalized sensu Chytrý (2000) because subjective a posteriori decisions (dividing and merging of TWINSPAN groups) were made during classification. The symbols E_3, E_2, E_1 are used for tree, shrub and herb layer respectively. The nomenclature of plant species follows Marhold & Hindák (1998). The names of identified vegetation types conform partly to the Slovak tradition, and partly to accepted standards in neighbouring countries (Chytrý 1997, Moravec 1998, Moravec et al. 2000, Matuszkiewicz 2001a, Borhidi 2003). The International Code of Phytosociological Nomenclature (Weber et al. 2000) was not strictly followed and the nomenclature of the types has to be treated as provisional. The relation of the identified types to higher syntaxa was not considered, as both nomenclature and syntaxonomy at higher levels of hierarchy require a large-scale synthesis and international agreement.

Results and discussion

Seven types of dry-mesic oak forests were identified in Slovakia. A dendrogram is presented to illustrate the subjective assignment of relevé groups identified by TWINSPAN to the final vegetation types (Fig. 1).

The following descriptions of structure, species composition and ecology relate to the types as they were defined during this particular classification and hold only for Slovakia. Any generalization concerning the distribution of types outside Slovakia is of limited relevance unless the relevés are compared.

Dry-mesic oak forest on sandy soils: *Carici fritschii-Quercetum roboris* type (Fig. 2a)

Species-rich open-canopy oak forest dominated by *Quercus robur* in the tree layer, in places with *Quercus petraea* agg. and *Pinus sylvestris* admixed. The shrub layer is usually poorly developed, typically with *Frangula alnus*, *Crataegus* spp., *Rhamnus cathartica*, *Ligustrum vulgare* and juveniles of *Quercus robur*, *Tilia cordata* or *Pinus sylvestris*. The composition of the herb layer varies according to soil humidity. The xerophytic variant with *Festuca ovina* is confined to depressions in sand dunes and gravel sand terraces. It is rich in drought-tolerant species of dry grasslands and forest edges (*Teucrium chamaedrys*, *Carex humilis*, *C. caryophyllea*, *Peucedanum oreoselinum*, *Cerastium arvense*, *Iris variegata*, *Vincetoxicum hirundinaria*) and acidophytes (*Festuca ovina*, *Genista tinctoria, Luzula divulgata*). It represents a transition to xeric acidophilous oak forests of the association *Festuco ovinae-Quercetum roboris* F. Šmarda 1961, from which it differs in the reduced occurrence of acidophytes and psammophytes (*Festuca vaginata*, *Carex ericetorum*, *Thymus serpyllum*, *Jasione montana*, *Acetosella multifida* agg., *Dianthus serotinus*). The variant with *Molinia caerulea* s.l. occurs at more humid sites. It includes more mesophilous species (*Brachypodium pinnatum*, *Serratula tinctoria*, *Lysimachia vulgaris*, *Carex brizoides*) and represents a transition to the *Potentillo-Quercetum* type. Common forest species (*Dactylis polygama*, *Convallaria majalis*), common heliophilous species (*Festuca rubra*, *Poa angustifolia*, *Arrhenatherum elatius*, *Clinopodium vulgare*) and species of intermittently wet soils (*Potentilla alba, Betonica officinalis*) are a constant feature. Abundant occurrence of *Carex fritschii* is characteristic – a tussocky sedge species with a scattered and probably relic Central European distribution (Holub & Moravec 1964).

In Slovakia, *Carici fritschii-Quercetum roboris* is confined to Záhorská nížina lowland, a region of blown sands and sandy gravel terraces of the river Morava. Probably it was more widespread there (Ružička 1960, Michalko & Plesník 1982) but now only a few well-preserved stands remain, mostly in the surroundings of the town of Gbely, where it grows exclusively on a sandy gravel substrate (Roleček 2004).

Carici fritschii-Quercetum roboris belongs to a group of oak forest types on intermittently wet soils, which is sometimes treated within ass. *Potentillo albae-Quercetum* Libbert 1933 sensu lato, or within *Potentillo albae-Quercion* alliance (Michalko et al. 1986, Michalko 1991, Šomšák & Kubíček 2000). My results accord with this (Fig. 3), nevertheless it seems to be useful to distinguish *Carici fritschii-Quercetum* from *Potentillo albae-Quercetum* sensu stricto as a separate type (Roleček 2004).

This distinctive vegetation type occurs also in S Moravia (Šmarda 1961, Chytrý 1997) from where it was formally described as an association for the first time (*Carici fritschii-Quercetum roboris* Chytrý et Horák 1997). Similar oak forests on sandy substrates are

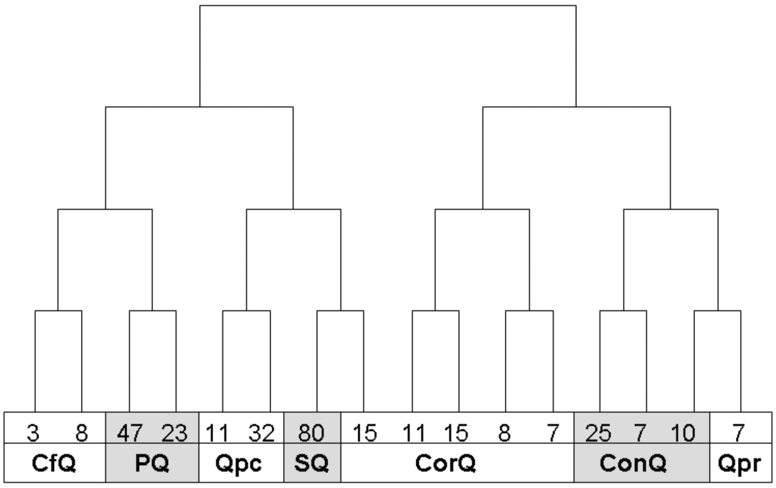

Fig. 1. – Dendrogram illustrating the subjective assignment of relevé groups identified by TWINSPAN to particular vegetation types. Numbers indicate the number of relevés belonging to a particular relevé group. Abbreviations of the names of the vegetation types: CfQ – *Carici fritschii-Quercetum roboris*, PQ – *Potentillo albae-Quercetum*, Qpc – *Quercetum petraeae-cerris*, SQ – *Sorbo torminalis-Quercetum*, CorQ – *Corno-Quercetum*, ConQ – *Convallario-Quercetum*, Qpr – *Quercetum pubescenti-roboris.*

known also from E Hungary under the name *Festuco rupicolae-Quercetum roboris* Soó (1934) 1957 (Soó 1963, Borhidi 2003). However, a comparison of relevés is necessary before synonymization.

Dry-mesic oak forest on heavy soils: *Potentillo albae-Quercetum* type (Fig. 2b)

Moderately thermophilous open-canopy oak forest dominated by *Quercus robur* or *Q. petraea* agg. in the tree layer, growing predominantly on heavy substrates. *Carpinus betulus*, *Betula pendula*, *Populus tremula* and *Pinus sylvestris* (the latter mostly planted) are often admixed. Mesophilous and moderately thermophilous shrubs occur in the shrub layer, including *Frangula alnus*, *Crataegus laevigata*, *Ligustrum vulgare*, *Swida sanguinea*, *Corylus avellana*, *Rosa canina* agg. and saplings of *Carpinus betulus*, *Prunus avium* and *Quercus robur*. The development of the shrub layer greatly depends on the methods and intensity of forest management. The herb layer is mostly dominated by *Carex montana*, *Fragaria vesca*, *Poa nemoralis* or *Melica nutans*. Typical components of *Potentillo albae-Quercetum* understorey include mesic open forest and non-forest species (*Veronica chamaedrys* s. str.*, Ajuga reptans, Lysimachia nummularia*, *Cruciata glabra*, *Symphytum tuberosum* agg., *Viola riviniana*), acidophilous species (*Hieracium sabaudum*, *H. murorum*, *Veronica officinalis*, *Melampyrum pratense*, *Solidago virgaurea*, *Luzula luzuloides*), dry-mesic forest species (*Lathyrus niger, Campanula persicifolia, Melittis melissophyllum*, *Festuca heterophylla*) and species of intermittently wet soils (*Potentilla alba*, *Serratula tinctoria*, *Betonica officinalis*, *Pulmonaria mollis* agg., *Selinum carvifolia*, *Potentilla erecta*, *Deschampsia caespitosa*, *Molinia caerulea* s.l.). *Betula pendula*, *Populus tremula*, *Maianthemum bifolium* or *Luzula pilosa* represent subboreal elements in this vegetation type and even *Picea abies* rejuvenates occasionally. A distinctive local variant with *Molinia caerulea* s.l. occurs in Záhorská nížina lowland, where it occupies wet interdune depressions; species of intermittently wet soils frequently occur there (*Molinia caerulea* s.l., *Deschampsia cespitosa*, *Potentilla alba*, *Selinum carvifolia*), while thermophilous species of the *Carici fritschii-Quercetum* (*Carex fritschii*, *Pulmonaria angustifolia*, *Valeriana stolonifera*) are absent.

In contrast to other dry-mesic oak forest types in Slovakia, the distribution of *Potentillo albae-Quercetum* is concentrated in moderately warm regions, mainly basins (Hornonitrianská, Žilinská, Zvolenská, Hornádská, Košická kotlina basins), less often lower uplands (Nitrianská pahorkatina hills, Krupinská vrchovina uplands, Spišsko-šarišské mezihorie region); marginally it occurs also in the Nízké Beskydy mountains. There are only a few stands in the warm and dry regions of Slovakia (Záhorská nížina lowland, Východoslovenská nížina lowland). It mostly develops on heavy illimerized and pseudogleyic soils on the Neogene sediments and Carpathian flysch, less often on loess loams and other substrates.

Potentillo albae-Quercetum type is close to association *Frangulo alni-Quercetum* Michalko 1986 (see Michalko 1991 and Table 2). The occurrence of subboreal species and rather sparse presence of thermophytes distinguish it from *Carici fritschii-Quercetum* type and *Sorbo torminalis-Quercetum* type, variant with *Betonica officinalis*.

Generally, *Potentillo albae-Quercetum* is considered as a sarmatic community. In Central Europe it is common in Poland (Matuszkiewicz 2001a), where it was formally described for the first time (*Potentillo albae-Quercetum* Libbert 1933). It is recorded also from Germany (Pott 1995) and the Czech Republic (Chytrý 1997). Similar vegetation occurring in Austria and Hungary requires further study.

Dry-mesic oak forest on basic rocky substrates: *Corno-Quercetum* type (Fig. 2a)

Thermophilous oak forest growing on deeper soils on eutrophic rocky substrates (limestones, dolomites, calcareous flysch, volcanic formations) with *Quercus petraea* agg., *Q. pubescens*, *Acer campestre*, *Sorbus torminalis* and *Sorbus aria* dominant, and often some mesophilous tree species admixed (*Carpinus betulus*, *Tilia cordata*) in the tree layer. The shrub layer is species-rich, composed of thermophilous and mesophilous species (*Cornus mas*, *Swida sanguinea*, *Euonymus verrucosus*, *E. europaeus*, *Viburnum lantana*, *Ligustrum vulgare*, *Rosa canina* agg., *Lonicera xylosteum*, *Corylus avellana*, *Crataegus* spp.); sometimes it is luxuriantly developed at the expense of herb species richness and cover. The herb layer is usually dominated by mesophilous grasses (*Melica uniflora*, *Brachypodium sylvaticum*) or *Lithospermum purpurocaeruleum*, on heavy soils also by *Carex montana*. It is rich in dry-mesic forest species (*Lathyrus niger*, *Tanacetum corymbosum*, *Vincetoxicum hirundinaria*, *Viola hirta, Laser trilobum*) and species of eutrophic soils (*Campanula rapunculoides*, *Glechoma hirsuta*, *Geum urbanum*).

Xeric variant with *Carex michelii* grows on more open sites and is rich in heliophilous species (*Veronica teucrium*, *Laserpitium latifolium*, *Hylotelephium maximum*); it is close to dry oak forest on basic rocky substrates (*Pruno mahaleb-Quercetum pubescentis* Jakucs et Fekete 1957). The mesic variant with *Brachypodium sylvaticum* is enriched with forest mesophytes (*Asarum europaeum*, *Pulmonaria officinalis* agg.) and constitutes a transitional community to oak-hornbeam forests. The variant with *Carex montana* is

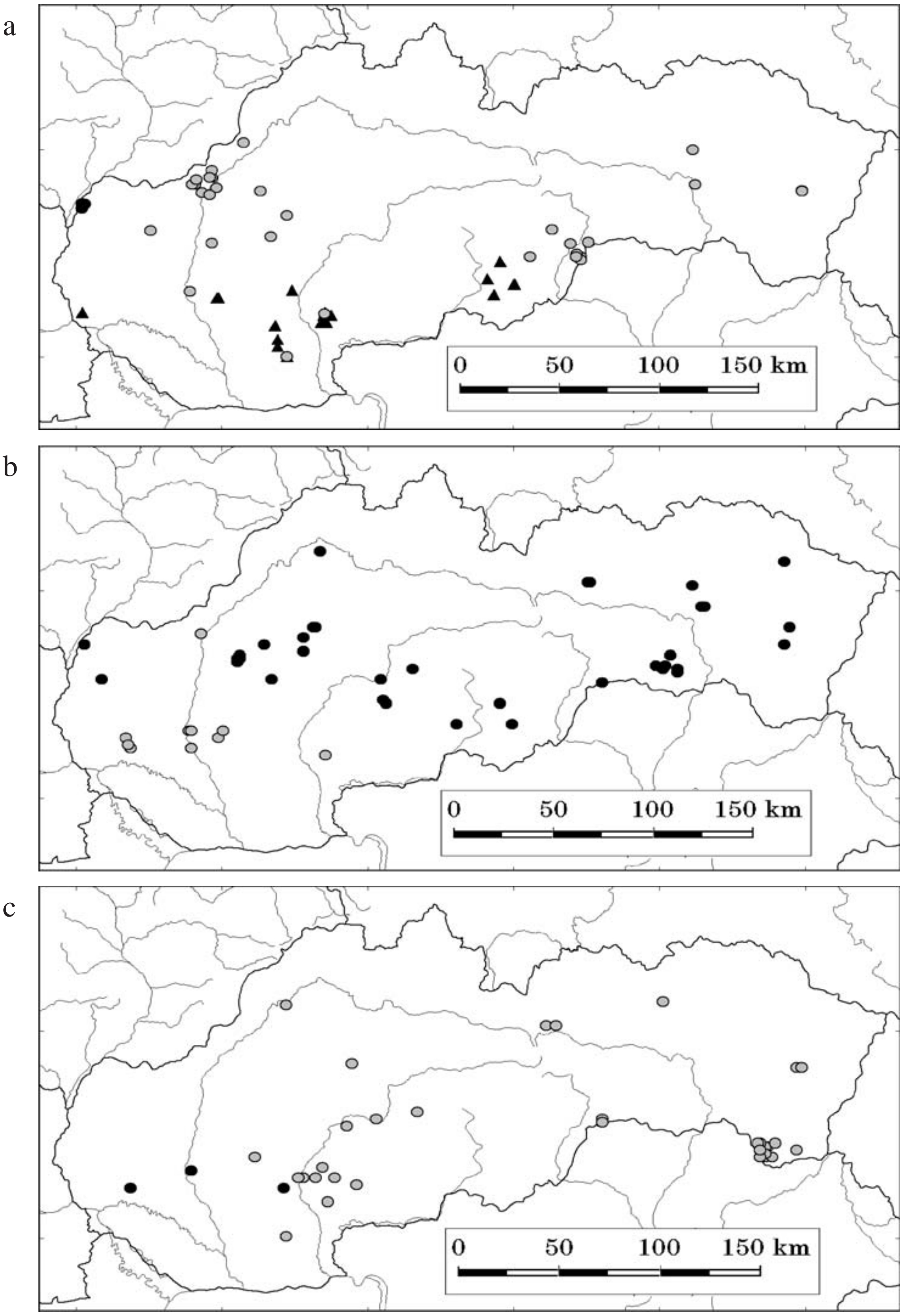

Fig. 2. – Distribution of vegetation types in Slovakia according to relevé data. (a) *Carici fritschii-Quercetum* (●), *Corno-Quercetum* (◎) and *Quercetum petraeae-cerris* (▲); (b) *Potentillo albae-Quercetum* (●) and *Convallario-Quercetum* (◎); (c) *Quercetum pubescenti-roboris* (●) and *Sorbo torminalis-Quercetum* (◎).

confined to the gentle slopes of hill tops or foothills and it is characterized by an abundant occurrence of species of heavy soils (*Carex montana*, *Betonica officinalis*, *Peucedanum cervaria*) and often by some mesophilous *Carpinion* species.

Corno-Quercetum typically grows on eutrophic deeper soils on gentle slopes, foothills and flat hill tops, often in contact with open dry forests of *Quercus pubescens*. It is widespread in the limestone and dolomite regions of the southern half of Slovakia, mainly in Slovenský kras karst, Považsky Inovec and Strážovské vrchy uplands and in the belt zone of the Biele Karpaty mountains. It is recorded also from the Malé Karpaty, Tribeč, Spišsko-šarišské mezihorie and Stredné Pohornádie regions and Vihorlatské vrchy uplands. Some transitional stands to *Convallario-Quercetum* type, which is floristically and ecologically very similar, occur in the Nitrianská and Hronská pahorkatina hills. Probably it is even more widespread, but has not been sampled by phytosociologists as often as dry *Quercus pubescens* forests.

Corno-Quercetum type includes most Slovak relevés formerly treated as *Corno-Quercetum* Máthé et Kovács 1962 and *Carici montanae-Quercetum pedunculiflorae* Šomšák et Háberová 1979, partly also *Waldsteinio-Carpinetum* Jakucs et Jurko 1967 and *Lithospermo-Quercetum virgilianae* Klika 1957 (Table 2).

Outside Slovakia it occurs in all Central European countries except Poland, but it is often reported under different names.

Dry-mesic oak forest on acidic substrates: *Sorbo torminalis-Quercetum* type (Fig. 2c)

Open oak forest on moderately acidic substrates with *Quercus petraea* agg. dominant in the tree layer, rarely also with *Q. cerris* or *Q. robur*. The shrub layer is usually poorly developed, with saplings of *Quercus petraea* agg., *Carpinus betulus* and the shrubs *Ligustrum vulgare*, *Crataegus* spp. and *Rosa canina* agg. being the most common. The herb layer is in most cases dominated by *Poa nemoralis*, seldom also by *Melica uniflora* or *Festuca heterophylla*. The typical components of herb layer are dry-mesic forest species (*Digitalis grandiflora*, *Clinopodium vulgare*, *Tanacetum corymbosum*, *Lathyrus niger*, *Vincetoxicum hirundinaria*, *Hylotelephium maximum* agg.), acidophytes (*Veronica officinalis*, *Genista tinctoria*, *Hieracium sabaudum*, *Lychnis viscaria*, *Luzula luzuloides*) and often also the mesophilous forest species (*Galium schultesii*, *Cruciata glabra*, *Dactylis polygama*, *Stellaria holostea*, *Lathyrus vernus*). The latter mainly occur in the variant with *Festuca heterophylla*, which constitutes a transition to mixed forests of the *Carpinion* alliance; this variant is treated as a separate association *Festuco heterophyllae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1964 within the *Carpinion* alliance by some authors (Neuhäusl & Neuhäuslová-Novotná 1964, 1967). The variant with *Campanula trachelium* is richer in basiphilous and eutrophic species and represents a transition to *Corno-Quercetum*. The distinctive variant with *Betonica officinalis* includes species of heavy soils (*Serratula tinctoria*, *Pulmonaria mollis* agg., *Potentilla alba*, *Frangula alnus*) and constitutes a transition to *Potentillo albae-Quercetum*.

Sorbo torminalis-Quercetum occupies moderately acidic soils, usually on gentle to moderate slopes, but also in flat areas. On steep slopes and in warm and dry regions it is replaced by the *Genisto pilosae-Quercetum petraeae* Zólyomi et al. ex Soó 1963 association. *Sorbo torminalis-Quercetum* type occurs also on basic (but often leached) substrates, particularly at higher altitudes and in colder regions, where it is confined to rather steep south-facing slopes and often is locally the most xerophilous forest community. It is a widespread vegetation type, with a scattered distribution across Slovakia.

Many relevés of *Festuco heterophyllae-Quercetum* Neuhäusl et Neuhäuslová-Novotná fall within the definition of this type, together with *Poo nemoralis-Quercetum petraeae* Michalko 1980 and *Poo nemoralis-Quercetum dalechampii* Šomšák et Háberová 1979. Also some relevés assigned to *Quercetum petraeae-cerris* Soó 1963 by previous authors (e.g. Neuhäusl & Neuhäuslová-Novotná 1967) were classified within this type (Table 2).

Outside Slovakia it is common in the Czech Republic (Chytrý 1997), where it was formally described as an association (*Sorbo torminalis-Quercetum* Svoboda ex Blažková 1962). It also occurs in SW Poland (Kwiatkowski 2003) and Austria (Wallnöfer et al. 1993). In Germany analogous vegetation is treated as *Luzulo-Quercetum* Hilitzer 1932 within the *Quercetalia roboris* order (Pott 1995). In Hungary it is probably replaced by *Quercetum petraeae-cerris* (Borhidi 2003), but the relation between these two vegetation types in Central Europe requires further synthetic study – single differential criteria, like the dominance of *Quercus petraea* agg. or *Q. cerris*, are not sufficient for floristic classification.

Dry oak forest on loess: *Quercetum pubescenti-roboris* type (Fig. 2c)

Species-rich forest-steppe oak forest community dominated by *Quercus pubescens* agg., *Q. cerris*, *Q. robur* agg. and *Q. petraea* agg. in a distinctly open tree layer. *Acer campestre*, *Ulmus minor* and rare thermophilous trees *Sorbus domestica* and *Quercus frainetto* also occur locally. If not cut, the shrub layer develops very well, with *Ligustrum vulgare*, *Cornus mas*, *Rhamnus cathartica, Rosa canina*, *Crataegus* spp. or *Prunus spinosa*. Herb layer is dominated by light demanding species of dry grasslands and forest edges (*Brachypodium pinnatum*, *Poa angustifolia*, *Festuca rupicola*, *Dictamnus albus*, *Lithospermum purpurocaeruleum*, *Inula salicina*). It is remarkably rich in thermophilous herbs (*Teucrium chamaedrys, Pulmonaria mollis* agg., *Iris variegata*, *Adonis vernalis*, *Phlomis tuberosa*, *Euphorbia salicifolia*), some of which do not occur in similar dry oak forests on shallow rocky soils (*Pruno mahaleb-Quercetum pubescentis*).

Quercetum pubescenti-roboris is probably a mainly anthropogenic community, formerly occurring within openings in coppiced and grazed oak forests on loess. It could also occur naturally on the most extreme sites in loess oak forests, in a mosaic with low-grown thermophilous scrub (*Prunetum tenellae*), thermophilous herbaceous vegetation (*Geranio-Dictamnetum*) and dry-mesic mixed forest (*Convallario-Quercetum roboris*). Before modern landuse it was probably widespread on loess plateaus of Podunajská nížina lowland, Nitrianská pahorkatina and Hronská pahorkatina hills, locally perhaps also on the Východoslovenská nížina lowland. Nowadays, due to successional changes, the last small stands of this vegetation remain only along old forest roads in Martinský les forest near Senec (Ružičková 2003); in the 1960s it was also recorded in Dubník forest near Sereď and in the Hronská pahorkatina hills (Čifáre – Michalko & Džatko 1965).

The name of this vegetation type is derived from the ass. *Quercetum pubescenti-roboris* (Zólyomi 1957) Michalko et Džatko 1965, but the concept adopted here is stricter than that of J. Michalko and M. Džatko; only relevés with a dominance of drought-tolerant heliophilous species are included. Also the name *Aceri tatarici-Quercetum roboris* Zólyomi 1957 is sometimes used for this vegetation type (see Michalko in Mucina & Maglocký 1985 and Table 2).

Table 1. – Frequency table of dry-mesic oak forest types in Slovakia. The numbers given in the rows are percentage values of species frequency. Their upper indices express the indicator value of a species for a particular vegetation type. Indicator species (I.S., Dufręne-Legendre indicator value index greater than 30) are in bold on a grey background. Other indicator species are sorted according to the sum of frequencies. CfQ – *Carici fritschii-Quercetum roboris*, PQ – *Potentillo albae-Quercetum*, CorQ – *Corno-Quercetum*, SQ – *Sorbo torminalis-Quercetum*, Qpc – *Quercetum petraeae-cerris*, ConQ – *Convallario-Quercetum*, Qpr – *Quercetum pubescenti-roboris*.

Group no. Vegetation type No. of relevés	1 CfQ 11	2 PQ 70	3 CorQ 56	4 SQ 80	5 Qpc 43	6 ConQ 42	7 Qpr 7
I.S. *Carici fritschii-Quercetum*							
Festuca rubra	**91**$^{82.1}$	21$^{14.6}$	2^{-}	1^{-}	26$^{18.1}$	2^{-}	.
Iris variegata	**73**$^{72.4}$	.	.	.	.	.	14$^{12.1}$
Arrhenatherum elatius	**73**$^{70.8}$	4$^{2.1}$	.	.	7$^{4.4}$	.	.
Polygonatum odoratum	**82**$^{69.8}$	4^{-}	12$^{5.2}$	29$^{20.2}$	5^{-}	17$^{8.4}$	.
Carex fritschii	**64**$^{63.0}$	3$^{1.4}$	.	.	.	.	.
Festuca ovina agg.	**64**$^{61.1}$	4$^{2.0}$	.	6$^{3.7}$	.	.	.
Anthoxanthum odoratum	**55**$^{51.7}$	9$^{6.0}$	.	4$^{1.6}$	.	.	.
Pinus sylvestris	**55**$^{48.3}$	26$^{22.4}$	2^{-}	2^{-}	.	.	.
Cerastium arvense	**45**$^{45.5}$	.	.	.	.	.	.
Viola canina	**45**$^{44.2}$	6$^{4.2}$	.	.	.	.	.
Carex caryophyllea	**45**$^{42.3}$	4$^{2.0}$	.	2^{-}	12$^{8.8}$	.	.
Luzula campestris agg.	**45**$^{40.1}$	6$^{2.4}$	2^{-}	10$^{6.0}$	9$^{5.3}$	.	14$^{9.5}$
Mycelis muralis	**55**$^{39.0}$	31$^{19.0}$	16$^{6.4}$	29$^{16.6}$	14$^{5.1}$	12$^{3.9}$	.
Hieracium umbellatum	**45**$^{38.9}$	20$^{15.5}$	7$^{3.1}$	6$^{2.4}$	.	.	.
Pulmonaria angustifolia	**36**$^{36.4}$	.	.	.	.	.	.
Molinia caerulea s.l.	**36**$^{34.2}$	10$^{8.6}$	.	.	.	.	.
Galium verum	**45**$^{33.2}$	29$^{18.9}$	9$^{2.8}$	12$^{4.9}$	28$^{17.7}$	2^{-}	29$^{17.7}$
Scrophularia nodosa	**45**$^{32.8}$	39$^{29.1}$	.	14$^{5.6}$	2^{-}	31$^{20.2}$	.
Convallaria majalis	**45**$^{32.7}$	19$^{9.2}$	7$^{1.8}$	21$^{11.5}$	2^{-}	38$^{27.0}$	29$^{17.3}$
I.S. *Potentillo albae-Quercetum*							
Carex montana	9$^{2.1}$	**77**$^{64.2}$	36$^{20.0}$	11$^{2.7}$	7$^{1.2}$	10$^{2.2}$	.
Viola riviniana/reichenbachiana	.	**81**$^{60.6}$	16$^{4.2}$	31$^{13.1}$	42$^{21.4}$	36$^{16.7}$	.
Carpinus betulus	.	**77**$^{52.6}$	46$^{23.6}$	42$^{20.3}$	33$^{13.3}$	29$^{10.7}$	.
Corylus avellana	.	**53**$^{41.4}$	38$^{24.4}$	11$^{3.3}$	5^{-}	5^{-}	14$^{5.4}$
Carex pallescens	36$^{27.3}$	**43**$^{39.0}$	2^{-}	.	12$^{5.5}$	.	.
Ajuga reptans	36$^{20.8}$	**53**$^{38.3}$	16$^{5.6}$	34$^{19.3}$	12$^{3.2}$	5^{-}	14$^{4.8}$
Hieracium sabaudum	27$^{10.9}$	**60**$^{37.8}$	30$^{12.5}$	50$^{28.6}$	51$^{29.0}$	5^{-}	.
Symphytum tuberosum	.	**57**$^{37.6}$	43$^{23.8}$	48$^{28.4}$	12$^{2.6}$	10$^{1.8}$	.
Luzula luzuloides	.	**47**$^{36.7}$	4^{-}	38$^{26.6}$	.	.	.
Melampyrum pratense	36$^{25.4}$	**43**$^{35.6}$	5$^{1.2}$	18$^{9.1}$	.	.	.
Potentilla erecta	.	**31**$^{31.4}$	.	.	.	.	.
Selinum carvifolia	.	**30**$^{30.0}$	.	.	.	.	.
I.S. *Corno-Quercetum*							
Sorbus torminalis	.	7$^{1.4}$	**73**$^{61.6}$	30$^{17.1}$	5^{-}	10$^{2.5}$	.
Campanula rapunculoides	.	14$^{5.2}$	**55**$^{43.3}$	31$^{19.2}$	.	10$^{2.6}$	.
Glechoma hederacea agg.	9$^{3.2}$	3^{-}	**45**$^{36.6}$	6$^{1.5}$	16$^{8.2}$	19$^{10.4}$	29$^{18.4}$
I.S. *Sorbo-Quercetum*							
Galium schultesii	.	29$^{12.6}$	30$^{14.0}$	**74**$^{57.4}$	23$^{9.1}$	2^{-}	.
Genista tinctoria	9$^{2.0}$	39$^{21.5}$	14$^{4.0}$	**59**$^{42.1}$	33$^{16.3}$	5^{-}	14$^{4.3}$
Stellaria holostea	.	17$^{8.0}$	11$^{3.6}$	**49**$^{41.3}$	5^{-}	.	.
Campanula persicifolia	9$^{1.7}$	33$^{15.0}$	27$^{10.7}$	**61**$^{41.3}$	44$^{24.1}$	17$^{4.8}$	43$^{22.8}$
Hylotelephium maximum	45$^{26.7}$	6^{-}	39$^{22.0}$	**58**$^{40.8}$	37$^{20.1}$	10$^{2.0}$	43$^{24.5}$
Lathyrus vernus	.	10$^{2.8}$	32$^{19.6}$	**50**$^{39.6}$	5^{-}	7$^{1.6}$	.

I.S. *Quercetum petraeae-cerris*							
Vicia cassubica	.	$13^{5.4}$	4^{-}	$10^{3.4}$	**$67^{59.8}$**	$5^{1.0}$	$29^{18.1}$
Torilis japonica	$27^{15.5}$	1^{-}	$9^{2.4}$	$24^{12.9}$	**$60^{48.7}$**	$24^{12.8}$	$14^{5.8}$
Hypericum hirsutum	.	$13^{5.1}$	$5^{1.1}$	$14^{5.7}$	**$49^{38.7}$**	$21^{11.9}$	$29^{17.7}$
Pyrus communis agg.	$9^{2.3}$	$16^{5.6}$	$38^{23.3}$	$20^{8.4}$	**$51^{36.1}$**	$14^{4.9}$	$29^{15.1}$
Filipendula vulgaris	$9^{4.4}$	1^{-}	$9^{4.2}$	2^{-}	**$40^{35.2}$**	$5^{1.5}$	$29^{21.6}$
Rubus fruticosus agg.	$45^{27.2}$	$36^{19.5}$	$9^{1.8}$	$41^{24.7}$	**$51^{33.1}$**	$12^{3.1}$	$14^{4.5}$
Festuca valesiaca/pseudodalmatica	.	3^{-}	4^{-}	$11^{6.3}$	**$37^{32.9}$**	.	.
Fragaria viridis	.	1^{-}	2^{-}	$9^{4.1}$	**$37^{32.6}$**	$12^{6.7}$	.
Lychnis coronaria	.	.	.	1^{-}	**$33^{31.8}$**	2^{-}	.
Rosa gallica	.	$6^{2.0}$	$5^{1.8}$	4^{-}	**$35^{30.0}$**	$7^{3.0}$	$29^{21.6}$
I.S. *Convallario-Quercetum*							
Sambucus nigra	.	3^{-}	2^{-}	1^{-}	.	**$45^{43.8}$**	.
Viola odorata	.	$16^{10.1}$	.	2^{-}	2^{-}	**$38^{32.9}$**	$29^{21.2}$
Viola mirabilis	.	$13^{7.4}$	$9^{4.1}$	2^{-}	.	**$38^{32.9}$**	.
Urtica dioica	.	3^{-}	.	1^{-}	.	**$33^{32.2}$**	.
I.S. *Quercetum pubescenti-roboris*							
Brachypodium pinnatum	$36^{24.6}$	$24^{14.5}$	$29^{18.4}$	5^{-}	5^{-}	$14^{6.2}$	**$100^{86.0}$**
Carex michelii	$18^{7.9}$	$19^{8.0}$	$36^{22.7}$	$15^{5.5}$	$23^{11.6}$	$19^{8.4}$	**$100^{82.3}$**
Cruciata laevipes	.	.	$5^{1.7}$	4^{-}	$19^{12.4}$	$31^{24.9}$	**$86^{77.6}$**
Vicia tenuifolia	.	$6^{2.5}$	$5^{2.2}$	$5^{1.9}$	$14^{9.8}$	.	**$71^{66.2}$**
Pulmonaria mollis	$9^{1.9}$	$40^{22.5}$	$25^{10.5}$	$30^{14.0}$	$26^{10.9}$	$43^{24.7}$	**$86^{62.5}$**
Inula salicina	.	.	.	.	.	$7^{5.9}$	**$57^{56.2}$**
Festuca heterophylla	.	$44^{29.0}$	$14^{4.5}$	$30^{15.6}$	$23^{10.4}$	$21^{9.1}$	**$71^{51.8}$**
Ranunculus polyanthemos	.	$29^{23.7}$	4^{-}	2^{-}	2^{-}	$12^{6.2}$	**$57^{48.7}$**
Taraxacum sect. *Ruderalia*	$9^{3.7}$	$19^{11.4}$	$20^{12.2}$	$6^{1.8}$	$7^{2.3}$	$10^{3.9}$	**$57^{47.1}$**
Teucrium chamaedrys	$36^{26.2}$	.	$38^{29.7}$	$12^{5.5}$	$16^{8.6}$	.	**$57^{46.0}$**
Securigera varia	$9^{3.2}$	4^{-}	$27^{17.7}$	$24^{15.1}$	$19^{10.1}$	.	**$57^{45.1}$**
Phlomis tuberosa	.	.	.	.	.	$2^{1.6}$	**$43^{42.5}$**
Adonis vernalis	.	.	$4^{2.7}$	.	.	.	**$43^{42.2}$**
Stellaria graminea	$18^{16.6}$	1^{-}	.	.	.	$2^{1.2}$	**$43^{41.6}$**
Veronica teucrium	.	.	$9^{7.6}$	1^{-}	.	.	**$43^{41.0}$**
Potentilla heptaphylla	.	.	$7^{5.4}$	$2^{1.0}$	2^{-}	.	**$43^{40.7}$**
Inula conyza	.	1^{-}	$4^{1.6}$	2^{-}	$9^{6.8}$	2^{-}	**$43^{39.8}$**
Allium scorodoprasum	.	.	2^{-}	.	$12^{8.4}$	$19^{16.2}$	**$43^{38.7}$**
Polygonatum latifolium	.	.	2^{-}	.	2^{-}	$31^{29.2}$	**$43^{38.4}$**
Vicia pisiformis	.	1^{-}	$4^{1.3}$	$4^{1.4}$	$14^{10.5}$	$7^{4.0}$	**$43^{38.4}$**
Robinia pseudacacia	.	$4^{1.6}$	2^{-}	2^{-}	$7^{3.6}$	$19^{15.4}$	**$43^{37.9}$**
Origanum vulgare	$9^{5.2}$	$4^{1.6}$	$5^{2.3}$	$10^{6.4}$	$5^{1.8}$	2^{-}	**$43^{37.6}$**
Lactuca quercina	.	.	$4^{1.1}$	$9^{5.0}$	$9^{5.4}$	$14^{10.1}$	**$43^{37.4}$**
Ajuga genevensis	.	1^{-}	$11^{5.8}$	$20^{15.6}$	$7^{2.9}$	.	**$43^{35.7}$**
Platanthera sp.	$27^{19.7}$	$21^{15.6}$	4^{-}	$10^{4.7}$	$5^{1.3}$	2^{-}	**$43^{34.6}$**
Agrimonia eupatoria	.	$9^{3.2}$	$16^{9.0}$	4^{-}	$37^{29.7}$	$10^{3.9}$	**$43^{33.1}$**
Galium aparine	.	$7^{1.9}$	$25^{15.5}$	$11^{4.2}$	$14^{6.2}$	$38^{27.9}$	**$43^{30.9}$**
Indicator species common for two vegetation types							
Frangula alnus	**$64^{51.0}$**	**$66^{62.5}$**	.	1^{-}	.	.	.
Potentilla alba	**$45^{33.4}$**	$41^{33.1}$	2^{-}	$8^{2.0}$	$28^{17.8}$	2^{-}	.
Hieracium murorum	**$55^{35.4}$**	$44^{27.8}$	$16^{5.2}$	**$48^{31.4}$**	$21^{8.3}$	2^{-}	.
Agrostis capillaris	**$64^{49.7}$**	$24^{14.0}$	.	$19^{9.2}$	**$44^{32.8}$**	5^{-}	.
Calamagrostis epigeios	**$55^{47.5}$**	$4^{1.2}$	2^{-}	1^{-}	**$37^{32.6}$**	2^{-}	$29^{21.6}$
Dactylis glomerata agg.	**$64^{35.7}$**	$41^{18.2}$	$55^{29.4}$	$52^{27.1}$	$44^{20.5}$	$50^{25.0}$	**$86^{54.4}$**
Achillea millefolium agg.	**$45^{37.2}$**	$4^{1.0}$	$12^{6.6}$	$11^{5.6}$	$16^{9.9}$	.	**$57^{48.4}$**
Geranium sanguineum	**$36^{33.9}$**	.	$9^{6.8}$	.	.	.	**$43^{40.1}$**
Peucedanum oreoselinum	**$73^{70.1}$**	1^{-}	$4^{1.4}$	1^{-}	2^{-}	.	**$43^{38.9}$**
Cruciata glabra	.	**$71^{46.8}$**	$25^{8.4}$	**$64^{39.6}$**	$47^{23.6}$	$12^{2.3}$	.

Prunus avium	$18^{5.2}$	**$64^{40.0}$**	$32^{13.0}$	$45^{22.6}$	**$70^{44.1}$**	$14^{3.2}$	$14^{3.4}$
Betonica officinalis	$45^{24.6}$	**$56^{34.6}$**	$39^{19.8}$	$30^{12.5}$	$42^{21.8}$	$17^{4.7}$	**$71^{46.6}$**
Melittis melissophyllum	.	$31^{13.1}$	**$54^{31.2}$**	$58^{35.6}$	$28^{10.9}$	$38^{18.2}$	$14^{3.6}$
Melica uniflora	.	7^{-}	**$64^{41.2}$**	$48^{26.1}$	$16^{4.3}$	**$93^{68.5}$**	$29^{11.7}$
Quercus pubescens agg.	.	.	**$43^{35.9}$**	2^{-}	2^{-}	$33^{24.7}$	**$57^{46.2}$**
Veronica officinalis	$27^{11.6}$	$49^{29.1}$	2^{-}	**$62^{43.6}$**	$51^{30.8}$	2^{-}	$14^{4.0}$
Verbascum austriacum	.	1^{-}	$25^{14.2}$	$25^{14.4}$	**$47^{34.7}$**	2^{-}	**$86^{70.5}$**
Festuca rupicola	$18^{8.5}$	$7^{1.6}$	$23^{12.4}$	$16^{6.9}$	**$51^{39.1}$**	$7^{1.7}$	**$86^{70.0}$**
Carex muricata agg.	$27^{11.8}$	$21^{7.6}$	$27^{11.2}$	$35^{17.4}$	**$70^{48.9}$**	$29^{12.6}$	**$86^{61.3}$**
Fragaria moschata	$9^{1.8}$	**$49^{29.7}$**	$34^{16.7}$	$19^{5.9}$	**$53^{33.5}$**	$26^{11.0}$	**$71^{48.3}$**
Ulmus minor	.	1^{-}	$11^{4.0}$	1^{-}	$14^{6.3}$	**$71^{64.3}$**	$100^{87.3}$
Dictamnus albus	.	.	$5^{1.6}$	1^{-}	.	**$62^{58.4}$**	**$86^{76.8}$**
Alliaria petiolata	.	$6^{1.2}$	$20^{10.2}$	$16^{7.4}$	5^{-}	**$55^{44.4}$**	$57^{43.7}$
Euonymus europaeus	$9^{2.8}$	$20^{10.0}$	$5^{1.0}$	$14^{5.2}$	$12^{4.1}$	**$52^{40.7}$**	$86^{70.5}$
Arum maculatum agg.	.	.	2^{-}	.	.	**$40^{38.7}$**	**$57^{51.7}$**
Rhamnus cathartica	$27^{17.1}$	4^{-}	$9^{2.9}$	$10^{3.5}$	$21^{11.9}$	**$45^{35.8}$**	$57^{44.9}$
Fallopia sp.	$36^{20.0}$	3^{-}	$20^{7.4}$	$42^{26.5}$	$37^{20.9}$	**$48^{30.3}$**	$86^{64.2}$
Other abundant species							
Crataegus sp.	$55^{22.1}$	$77^{37.9}$	$89^{47.9}$	$68^{30.2}$	$86^{45.1}$	$88^{46.8}$	$100^{55.9}$
Ligustrum vulgare	$27^{7.1}$	$56^{22.5}$	$89^{49.1}$	$74^{36.1}$	$86^{46.1}$	$95^{53.9}$	$100^{57.0}$
Clinopodium vulgare	$82^{44.9}$	$51^{21.4}$	$61^{28.4}$	$84^{48.1}$	$88^{51.2}$	$43^{16.1}$	$100^{59.9}$
Veronica chamaedrys agg.	$73^{36.4}$	$91^{52.8}$	$55^{23.3}$	$89^{50.6}$	$81^{43.5}$	$21^{4.5}$	$86^{46.5}$
Rosa canina s.l.	$36^{12.1}$	$60^{26.7}$	$80^{43.1}$	$75^{38.7}$	$91^{51.7}$	$60^{26.7}$	$86^{46.8}$
Poa nemoralis	$27^{7.4}$	$79^{41.6}$	$39^{13.0}$	$98^{59.3}$	$81^{43.7}$	$55^{23.2}$	$86^{46.7}$
Quercus petraea agg.	$18^{3.4}$	$71^{34.0}$	$84^{44.2}$	$96^{55.6}$	$72^{34.7}$	$67^{30.6}$	$43^{15.2}$
Acer campestre	$9^{1.2}$	$23^{5.7}$	$96^{63.4}$	$44^{17.8}$	$65^{34.6}$	$98^{63.5}$	$86^{51.1}$
Geum urbanum	$27^{9.2}$	$37^{14.6}$	$57^{30.0}$	$31^{10.7}$	$74^{44.8}$	$90^{59.6}$	$100^{65.9}$
Prunus spinosa	$18^{4.4}$	$64^{35.1}$	$48^{21.9}$	$32^{10.9}$	$86^{54.0}$	$74^{42.9}$	$71^{40.2}$
Poa pratensis agg.	$73^{44.6}$	$54^{29.8}$	$36^{15.0}$	$34^{13.4}$	$93^{65.3}$	$14^{3.1}$	$86^{55.8}$
Vincetoxicum hirundinaria	$55^{28.9}$	$21^{5.9}$	$70^{42.7}$	$59^{33.3}$	$58^{32.2}$	$29^{10.2}$	$86^{55.1}$
Euphorbia cyparissias	$73^{46.1}$	$26^{9.0}$	$39^{18.6}$	$45^{23.2}$	$79^{53.8}$	$21^{6.8}$	$86^{57.5}$
Lathyrus niger	.	$44^{18.7}$	$71^{40.8}$	$70^{40.0}$	$47^{20.6}$	$62^{32.5}$	$43^{18.3}$
Quercus robur	$100^{76.2}$	$61^{43.4}$	$11^{2.3}$	$14^{3.5}$	$14^{3.8}$	$50^{30.8}$	$86^{62.2}$
Viola hirta	.	$20^{6.0}$	$34^{15.1}$	$39^{18.7}$	$77^{52.7}$	$52^{30.0}$	$100^{71.7}$
Brachypodium sylvaticum	$64^{37.9}$	$41^{19.9}$	$59^{34.9}$	$19^{4.9}$	$60^{35.9}$	$60^{35.0}$	$14^{3.5}$
Quercus cerris	.	$14^{3.3}$	$18^{5.1}$	$29^{11.4}$	$98^{74.5}$	$79^{55.0}$	$71^{46.2}$
Astragalus glycyphyllos	.	$20^{5.5}$	$57^{32.7}$	$65^{40.8}$	$60^{35.4}$	$26^{9.2}$	$71^{43.9}$
Fragaria vesca	$73^{44.8}$	$63^{37.9}$	$48^{24.7}$	$55^{30.8}$	$40^{18.0}$	7^{-}	.
Hypericum perforatum	$18^{6.2}$	$30^{13.7}$	$16^{4.7}$	$50^{31.7}$	$58^{38.2}$	$7^{1.1}$	$86^{61.8}$
Tanacetum corymbosum	.	$16^{3.9}$	$79^{55.6}$	$60^{38.3}$	$35^{15.9}$	$10^{1.6}$	$57^{33.5}$
Cornus mas	.	$9^{1.5}$	$84^{65.7}$	$16^{4.6}$	$12^{2.7}$	$74^{53.5}$	$57^{35.9}$
Silene nutans s.l.	$55^{39.1}$	$10^{2.8}$	$18^{7.7}$	$21^{10.2}$	$56^{42.6}$	5^{-}	$57^{41.3}$
Lithospermum purpurocaeruleum	.	.	$59^{47.5}$	.	.	$71^{59.3}$	$86^{68.9}$
Cornus sanguinea	.	$46^{28.2}$	$41^{23.6}$	$25^{10.4}$	$14^{3.9}$	$40^{22.9}$	$29^{13.4}$
Trifolium alpestre	$27^{16.1}$	$17^{8.0}$	$23^{13.0}$	$24^{13.7}$	$19^{9.2}$	2^{-}	$43^{29.9}$
Lapsana communis	$9^{3.0}$	4^{-}	$27^{16.5}$	$16^{7.4}$	$21^{11.2}$	$33^{22.5}$	$29^{17.4}$
Melica nutans	$27^{15.8}$	$40^{29.5}$	$27^{15.8}$	$8^{1.8}$	2^{-}	$19^{9.2}$	$14^{5.9}$
Galium album s.l.	$9^{2.7}$	$24^{13.3}$	$32^{20.4}$	$25^{14.0}$	$12^{4.0}$	5^{-}	$29^{16.5}$
Serratula tinctoria	$18^{9.5}$	$21^{12.4}$	$18^{9.3}$	$12^{5.1}$	$23^{13.9}$	$7^{2.0}$	$29^{18.1}$
Geranium robertianum	$9^{3.1}$	1^{-}	$16^{7.6}$	$29^{19.5}$	$14^{6.1}$	$33^{23.0}$	.
Cytisus nigricans	$18^{9.3}$	$27^{17.6}$	$14^{6.3}$	$26^{16.9}$	$9^{3.1}$	.	.
Primula veris	$9^{3.8}$	$6^{1.6}$	$14^{7.8}$	$9^{3.4}$	$9^{3.9}$	$31^{23.8}$	$14^{7.7}$
Pimpinella saxifraga agg.	$36^{29.8}$	$9^{4.1}$	$16^{11.0}$	$5^{1.6}$	$7^{3.0}$	2^{-}	$14^{8.8}$
Viburnum lantana	.	3^{-}	$29^{23.1}$	2^{-}	$7^{2.7}$	$19^{12.8}$	$29^{21.0}$
Steris viscaria	$27^{18.4}$	$6^{1.5}$	.	$34^{28.3}$	$19^{11.0}$	.	.
Hieracium lachenalii	.	$34^{24.7}$	$14^{6.1}$	$22^{12.9}$	$14^{5.9}$	.	.
Peucedanum cervaria	$9^{4.2}$	$4^{1.1}$	$27^{21.2}$	1^{-}	$23^{17.0}$	$5^{1.4}$	$14^{8.2}$

Trifolium medium	.	$16^{7.2}$	$25^{15.2}$	$32^{23.4}$	$9^{3.0}$	.	.
Digitalis grandiflora	$18^{10.2}$	$20^{12.3}$	2^{-}	$28^{20.4}$	$12^{5.1}$	.	.
Fraxinus excelsior	$9^{3.8}$	$20^{13.1}$	$12^{6.2}$	4^{-}	$14^{7.4}$	$19^{11.8}$	.
Bromus benekenii	.	$6^{1.7}$	$18^{11.3}$	$11^{5.5}$	.	$29^{21.7}$	$14^{7.9}$
Anthericum ramosum	$27^{19.9}$	$6^{1.8}$	$16^{10.1}$	$18^{11.9}$	$7^{2.7}$	.	.
Lonicera xylosteum	.	$9^{4.0}$	$12^{7.4}$	$10^{5.2}$	.	$14^{8.9}$	$29^{21.8}$
Euonymus verrucosus	.	1^{-}	$18^{12.0}$	$9^{3.9}$	$7^{2.7}$	$24^{17.7}$	$14^{8.3}$
Lysimachia nummularia	.	$36^{29.5}$	2^{-}	$6^{1.7}$	$16^{8.9}$	$12^{5.4}$	.
Acer tataricum	.	$6^{1.7}$	$18^{11.2}$	$9^{3.5}$	$35^{28.2}$	2^{-}	.

Last fragments of open-canopy oak forests on loess occur also in the Pannonian part of the Czech Republic (Horák 1980, 1983, Chytrý & Horák 1997), Austria (Wallnöfer et al. 1993, Starlinger 1997) and Hungary (Borhidi 2003). Analogous vegetation, with *Quercus robur* as the only oak species, constitutes a component of E European zonal forest-steppe mosaic (Zólyomi 1957, Bohn et al. 2003).

Dry-mesic and mesic oak forest on loess: *Convallario-Quercetum roboris* type (Fig. 2b)

Mixed oak forest on loess dominated by *Quercus robur* agg., *Q. cerris*, *Q. petraea* agg., *Acer campestre* or *Ulmus minor*, with admixture of *Quercus pubescens* agg., *Sorbus domestica* and occasionally some mesophilous tree species (*Fraxinus excelsior*, *Carpinus betulus*). Thermophilous shrubs (*Ligustrum vulgare*, *Cornus mas*, *Rosa canina* agg., *Crataegus* spp., *Prunus spinosa*, *Acer tataricum*, *Staphyllea pinnata*) and also some more mesophilous species (*Euonymus europaeus*, *Lonicera xylosteum*, in the eutrophic sites *Sambucus nigra*) occur in the shrub layer. Often shrubby specimen of *Acer campestre* and *Ulmus minor* dominate there. The composition of the herb layer varies considerably depending on soil humidity, nutrient availability and openness of the canopy. Common dominants are *Melica uniflora*, *Dactylis polygama*, *Brachypodium sylvaticum*, *Lithospermum purpurocaeruleum* and *Poa nemoralis*. A more xeric variant with *Dictamnus albus* includes heliophilous forest-edge species (*Carex michelii*, *Pulmonaria mollis* agg., *Euphorbia cyparissias*), and forest mesophytes are also common (*Bromus benekenii*, *Viola mirabilis*, *Arum maculatum* agg., *Convallaria majalis* or *Geum urbanum*). It is close to *Quercetum pubescenti-roboris* and is its climax stage. A variant with *Galium odoratum* forms a closed oak forest, growing on more shady and humid sites, often with an admixture of mesophilous trees such as *Fraxinus excelsior* or *Carpinus betulus*. Besides forest mesophytes it is primarily rich and secondarily often enriched in nitrophytes, e.g. *Viola odorata, V. suavis*, *Lactuca quercina*, *Allium scorodoprasum*, *Geranium robertianum*, *Alliaria petiolata, Fagopyrum convolvulus*. *Lithospermum purpurocaeruleum* and *Polygonatum latifolium*, which are often the only dry-mesic forest species in this vegetation, which constitutes a transition to mesophilous vegetation of the *Carpinion* and *Ulmenion* (sub)alliances.

The distribution of *Convallario-Quercetum roboris* type in Slovakia overlaps the distribution of *Quercetum pubescenti-roboris*, with the centre situated in the loess-covered landscapes of Podunajská nížina lowland, Nitrianská pahorkatina and Hronská pahorkatina hills. One relevé that originated from the calcareous belt zone of the Biele Karpaty mountains was assigned to this group too, because of the abundant occurrence of

Table 2. – Cross-tabulation of the traditional associations with vegetation types used in this paper. Numbers indicate the number of relevés of a traditional association (as indicated in the relevé source, i.e. database or literature) assigned to a particular vegetation type. Column without any value relates to a vegetation type (CfQ) represented solely by relevés that were not assigned to an association by their authors. CfQ – *Carici fritschii-Quercetum roboris*, PQ – *Potentillo albae-Quercetum*, CorQ – *Corno-Quercetum*, SQ – *Sorbo torminalis-Quercetum*, Qpc – *Quercetum petraeae-cerris*, ConQ – *Convallario-Quercetum*, Qpr – *Quercetum pubescenti-roboris*.

	CfQ	PQ	CorQ	SQ	Qpc	ConQ	Qpr
Aceri tatarici-Quercetum Zólyomi 1957			1	1	1	3	7
Carici montanae-Quercetum pedunculiflorae Šomšák et Háberová 1979	4	7					
Corno-Quercetum Jakucs et Zólyomi in Zólyomi et Jakucs 1957			1				
Corno-Quercetum Máthé et Kovács 1963			11				
Festuco heterophyllae-Quercetum Neuhäusl et Neuhäuslová 1964		1	1	19			
Frangulo alni-Quercetum J. Michalko 1986		22					
Lithospermo-Quercetum virgilianae (Klika 1951) Miadok 1980			3				
Luzulo albidae-Quercetum (Hilitzer 1932) Passarge 1953				4			
Polygonato latifolii-Carpinetum J. Michalko et Džatko 1965						6	
Poo nemoralis-Quercetum dalechampii Šomšák et Háberová 1979				3			
Poo nemoralis-Quercetum petraeae J. Michalko 1980				3			
Poo scabrae-Quercetum (Magyar 1933) Neuhäusl et Neuhäuslová 1964			1				
Potentillo albae-Quercetum Libbert 1933		4					
Primulo veris-Carpinetum Neuhäusl et Neuhäuslová 1964						1	
Quercetum petraeae-cerris Soó 1957			2	6	24		
Quercetum virgilianae Šomšák et Háberová 1979			1				
Querco petraeae-Carpinetum Soó et Pócs (1931) 1957			1	7			

nitrophytes. This indicates an ecological and floristic similarity of the *Corno-Quercetum* and *Convallario-Quercetum* types, which differ more in physiognomy and distribution than in overall species-composition; the former is bound to rugged topography on hard base-rich rocks and the latter to flat loess regions.

Nowadays a well developed vegetation of this type occurs in the Dubník forest near Sereď and in Martinský les and Šenkvický háj forests near Senec (Ružičková 2003). Most stands are species-poor, with closed canopy, herb layer dominated by *Melica uniflora* and include many nitrophytes and few forest species. This is presumably partly due to human-induced eutrophication, partly due to eradication of mesophilous forest species in the past when traditional forest management included coppicing and woodland grazing.

This type has been syntaxonomically treated partly within ass. *Aceri tatrici-Quercetum* Zólyomi 1957 [syn. *Quercetum pubescenti-roboris* (Zólyomi 1957) Michalko et Džatko 1965] and partly within *Polygonato latifolii-Carpinetum* Michalko et Džatko 1965 (Table 2).

Closely related but more mesophilous oak forests are well preserved on the Východoslovenská nížina lowland, with subcontinental species *Acer tataricum* already common (Berta 1970); this community is traditionally classified as *Querco robori-Carpinetum* Soó et Pócs 1957 and assigned to the *Carpinion* alliance (Berta 1970).

Related association *Convallario-Quercetum roboris* Soó (1939) 1957 was formally described from Hungary (Soó 1963, Borhidi 2003). Analogous vegetation occurs in Austria (Starlinger 1997) and the Czech Republic – mainly S Moravia (Horák 1980, 1983, Chytrý & Horák 1997), more distant analogies also in Bohemia (J. Sádlo and J. Novák, personal communications).

Dry-mesic forest of Turkey oak: *Quercetum petraeae-cerris* type (Fig. 2a)

Oak forest dominated by *Quercus cerris*, less often by *Q. petraea* agg. The shrub layer is composed of thermophilous shrubs, mainly *Ligustrum vulgare*, *Prunus spinosa*, *Crataegus* spp., *Rosa canina* agg., *Pyrus pyraster*, and juveniles of *Quercus cerris*, the only Central European oak species that rejuvenates well under a rather closed canopy (Úradníček & Maděra 2001). The herb layer is typically dominated by *Poa angustifolia*, *P. nemoralis*, *Festuca rupicola* or *Vicia cassubica*, with an abundant admixture of species of dry oak forests (*Clinopodium vulgare*, *Euphorbia cyparissias*, *Viola hirta*, *Vincetoxicum hirundinaria*, *Lathyrus niger*, *Hypericum hirsutum*, *Verbascum austriacum*) and some acidophilous species (*Silene nutans*, *Hieracium sabaudum*, *Veronica officinalis*). The xeric variant with *Festuca rupicola* is rich in thermophilous species (*Fragaria viridis*, *Filipendula vulgaris*, *Rosa gallica*, *Lychnis coronaria*, *Festuca pseudodalmatica*) and typically occupies andesites, where it often borders open dry oak forest of the *Poo scabrae-Quercetum* (Magyar 1933) Neuhäusl et Neuhäuslová-Novotná 1964 association. The variant with *Poa nemoralis* contains more mesophilous species (*Galium schultesii*, *Astragalus glycyphyllos*, *Fragaria moschata*, *Cruciata glabra*) and is similar to *Sorbo tominalis-Quercetum*. On deeper heavy soils, species adapted to intermittently wet conditions (*Potentilla alba*, *Serratula tinctoria*, *Betonica officinalis*) occur. *Quercetum petraeae-cerris* grows also on decalcified loess and loess loam where it borders *Quercetum pubescenti-roboris* and *Convallario-Quercetum* communities; it differs from them in the increased occurrence of acidophytes (*Veronica officinalis*, *Agrostis capillaris*, *Carex pallescens*, *Hieracium* spp., and in places also in species of intermittently wet soils. The variant with *Festuca rubra* almost lacks species of dry forests and most stands probably represent human-made plantations of *Quercus cerris* in a mesic oak forest habitat.

Quercetum petraeae-cerris generally occurs on moderately acidic deep illimerized soils of flat terrains on Neogene sediments, decalcified loess, loess loams and andesite. It is confined to dry and warm regions of S Slovakia, mainly to the Hronská pahorkatina hills, Štiavnické vrchy uplands, Nitrianská pahorkatina hills (Neuhäusl & Neuhäuslová-Novotná 1964, Neuhäuslová-Novotná & Neuhäusl 1965), Juhoslovenská kotlina basin and Cerová vrchovina uplands; marginally it occurs in the southern foot-hills of the Malé Karpaty mountains. Locally it colonizes also steeper south-facing slopes, mainly on Neogene volcanic formations, where it is a vicarious community with *Sorbo torminalis-Quercetum*.

Quercetum petraeae-cerris type, though quite well floristically defined, is a problematic one syntaxonomically. It cannot be simply classified with ass. *Quercetum petraeae-cerris* Soó 1963 as previously (Neuhäusl & Neuhäuslová-Novotná 1964, 1967, Neuhäuslová-Novotná & Neuhäusl 1965) as a relation with the association *Sorbo torminalis-Quercetum* Svoboda ex Blažková 1962 is likely. The presence/absence of *Quercus cerris* is not a sufficient argument for making syntaxonomic decisions in this case.

Outside Slovakia, *Quercetum petraea-cerris* is common in the andesite uplands of N Hungary, mainly in the Börzsöny and Mátra (Borhidi 2003). It is reported from Romania (Pop & Cristea 2000) and Austria (Wallnöfer et al. 1993).

TWINSPAN classification

The dendrogram (Fig. 1) shows the relation between the numerical classification produced by TWINSPAN and the subsequent subjective delimitation of the final vegetation types. The most problematic and arbitrary seems to be the boundaries between *Sorbo-Quercetum* and *Corno-Quercetum* types, and *Convallario-Quercetum* and *Quercetum pubescenti-roboris* types. There is a continuous transition within these pairs of vegetation types and thus I have based their delimitation on ecological criteria.

Sorbo-Quercetum type differs from *Corno-Quercetum* mainly in the more frequent occurrence of (sub)acidophytes (*Campanula persicifolia*, *Hieracium murorum*, *Genista tinctoria*, *Veronica officinalis*) and less nutrient-demanding mesophilous species (*Poa nemoralis*, *Stellaria holostea*, *Galium schultesii*, *Cruciata glabra*). On the other hand, *Corno-Quercetum* type is richer in eutrophic forest species (*Campanula rapunculoides*, *Glechoma hirsuta*, *Brachypodium sylvaticum*, *Acer campestre*) and basiphilous thermophilous species (*Lithospermum purpurocaeruleum*, *Quercus pubescens*, *Cornus mas*, *Viburnum lantana*).

Quercetum pubescenti-roboris type differs from *Convallario-Quercetum* in the dominance of xerothermic species in the herb layer (*Brachypodium pinnatum*, *Festuca rupicola*, *Poa angustifolia*) and in the more frequent occurrence of thermophilous and heliophilous species (*Carex michelii*, *Vicia tenuifolia*, *Inula salicina*, *Teucrium chamaedrys*, *Phlomis tuberosa*, *Betonica officinalis*, *Geranium sanguineum*). On the other hand, herb layer of *Convallario-Quercetum* type is usually dominated by a mesophilous species *Melica uniflora* and eutrophic forest species and nitrophytes (*Sambucus nigra*, *Viola odorata*, *V. mirabilis*, *Geranium robertianum*) are more common.

Groups of relevés separated by TWINSPAN but sharing the above mentioned characters were merged within one final vegetation type.

Ordination

Detrended correspondence analysis was performed to determine the relation between the identified vegetation types and the main gradients in species composition. DCA revealed that only four of the seven oak forest types can be differentiated along the first two ordination axes (Fig. 3). The right half of the scatter-plot is occupied by relevés of *Carici fritschii-Quercetum* and *Potentillo-Quercetum* types, which are closely related, moderately acidophilous communities of deep, spring-wet and summer-dry soils, with *Potentilla alba*, *Betonica officinalis*, *Serratula tinctoria* and *Frangula alnus*. Syntaxonomically they are sometimes treated within a separate alliance; *Potentillo albae-Quercion petraeae* Jakucs 1967 (Michalko 1991, Matuszkiewicz 2001b, Oberdorfer 2001). *Potentillo-Quercetum* shows an extensive, nevertheless continuous variability within the ordination space and two or three narrow vegetation types could be distinguished within this type if a more detailed classification was desirable. The central part of the scatter-plot is occupied by the relevés of *Corno-Quercetum*, *Sorbo-Quercetum* and *Quercetum petraeae-cerris* types, which have a similar relation to the first two axes and cannot be distinguished using this projection of the ordination space. *Convallario-Quercetum* type dominates the left half of the scatter-plot, being well differentiated from the *Quercetum pubescenti-roboris* type.

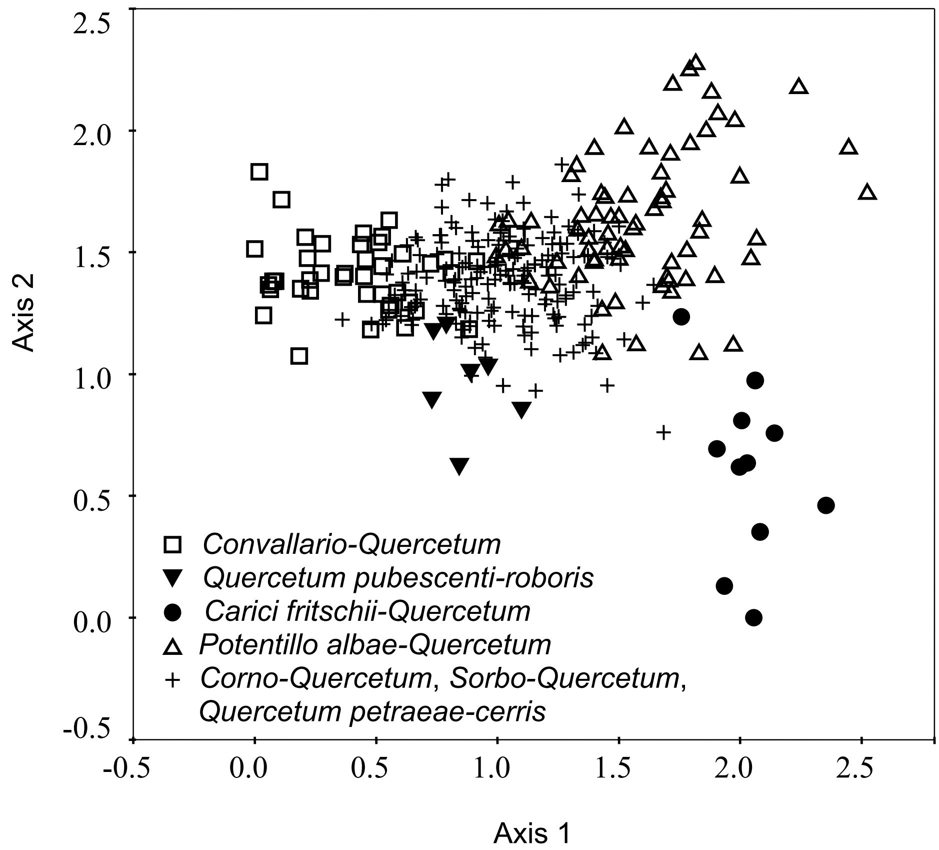

Fig. 3. – DCA of Slovak relevés of dry-mesic oak forest vegetation and the projected results of the TWINSPAN classification. Relevés classified within the same Twinspan group share the same symbols.

General comments on the dynamics of dry-mesic oak forests in Slovakia

The distinction between dry-mesic forests and thermophilous oak forests of shallow rocky soils, used in this paper, proved to be useful and yielded seven vegetation types with characteristic species composition, ecology and distribution in Slovakia. Nevertheless, the effect of man on oak forest vegetation is important in this context: while dry oak forests are usually confined to azonal habitats with shallow soils and their position in the vegetation mosaic is easy to understand, the dry-mesic oak forests regularly occupy zonal habitats within the vegetation matrix of shady mixed forests, which requires an extra explanation.

The striking absence or limited dominance of mesophilous tree competitors (*Carpinus betulus*, *Tilia cordata*, *Acer campestre*, *Fagus sylvatica*) in dry-mesic oak forests used to be attributed to local adverse factors like mesoclimate (Michalko et. al. 1986) and in particular by soil properties (Mráz 1958, Michalko et. al. 1986). Spring-wet and summer-dry pseudogleys were qualified as unfavourable for *Carpinus* and *Tilia*, thus *Potentillo albae-Quercetum* was considered to be a stable (climax) community on pseudogleyic soils. Ana-

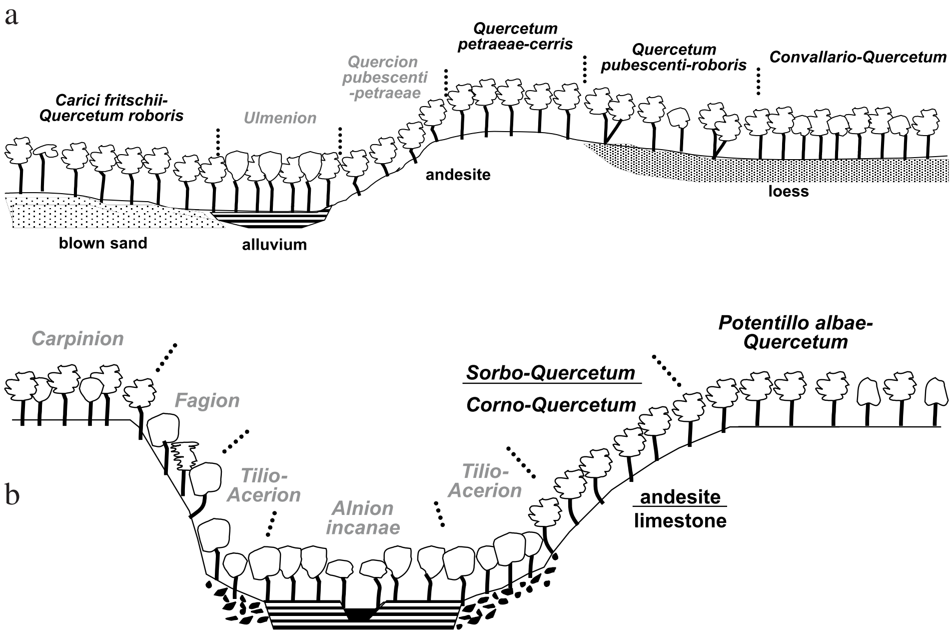

Fig. 4. – Landscape typical of Slovak dry-mesic oak forests in (a) warm and dry lowlands and hills, and (b) moderately warm hills and uplands. Names of vegetation units evaluated in the present paper are in black font.

logically, summer-dry chernozemic soils were qualified as too dry for *Acer campestre* and other shade-tolerating competitors, thus *Quercetum pubescenti-roboris* was considered to be a stable community (climax) on chernozemic soils. Recent succession, changing open oak forest communities into shady mixed forests across Central Europe (Jakubowska-Gabara 1996, Vera 2000), challenge this general opinion. The long-term human impact (especially coppicing and woodland pasture) was postulated to be the main factor restricting mesophilous tree competitors in the past. Nowadays only a limited number of dry-mesic oak forest stands persists in Slovakia, many of them are endangered by succession.

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Souhrn

Předkládaná fytocenologická syntéza subtermofilních doubrav Slovenské republiky vychází z analýzy 309 vegetačních snímků zapsaných metodikou curyšsko-montpellierské školy. Snímkový materiál byl analyzován pomocí klasifikačního algoritmu TWINSPAN, finální podoba klasifikace byla upravena subjektivně. Rozlišeno bylo sedm vegetačních typů, které jsou blízké sedmi v literatuře uváděným syntaxonům: *Carici fritschii-Quercetum roboris* – psamofilní střídavě vlhká doubrava s náročnými teplomilnými druhy, vyskytující se na slovenském Záhoří a blízká vegetaci Dúbravy u Hodonína, odkud je asociace popsána; *Potentillo albae-Quercetum* – boreálně laděná střídavě vlhká doubrava s mírně teplomilnými druhy, vyskytující se roztroušeně na těžkých půdách v nižších a středních polohách Slovenska; *Corno-Quercetum* – teplomilná doubrava živinami bohatých půd na bazických skalních substrátech, na Slovensku vázaná především na teplejší oblasti s podložím vápenců, dolomitů a bazických vyvřelin; *Sorbo torminalis-Quercetum* – mírně teplomilná doubrava kyselých a druhotně okyselených substrátů, vyskytující se roztroušeně v nižších a středních polohách Slovenska; *Quercetum pubescenti-roboris* – suchá doubrava hlubokých půd na spraši, s druhy teplomilných trávníků a lesních lemů, výskytem omezená na nejteplejší sprašovou oblast jihozápadního Slovenska; *Convallario-Quercetum roboris* – mezická až vysychavá doubrava hlubokých půd na spraši, s lesními druhy a druhy teplomilných lesních lemů, výskytem omezená na nejteplejší sprašovou oblast jihozápadního Slovenska; *Quercetum petraeae-cerris* – doubrava s dominancí *Quercus cerris*, s kombinací teplomilných a lesních druhů, výskytem omezená na teplé a suché oblasti Slovenska. Pro zobrazení podobnosti mezi rozlišenými vegetačními typy byla použita detrendovaná korespondenční analýza. Diskutována je otázka přirozenosti vegetace subtermofilních doubrav na Slovensku a je konstatován jejich sukcesní ústup ve prospěch mezofilních smíšených lesů.

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