Oak-hornbeam forests of the Czech Republic: geographical and ecological approaches to vegetation classification

Dubohabřiny České republiky: geografický a ekologický přístup ke klasifikaci vegetace

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Vegetation classification should reflect the major environmental and phytogeographical gradients that influence species composition. However, the importance of different gradients depends on the geographical scale of particular studies. Locally defined vegetation units usually reflect local gradients, such as disturbance and soil properties, while regionally defined units reflect macroclimatic patterns and different evolutionary and migration histories of large regions. The classification of Central European oak-hornbeam forests (*Carpinion* alliance) is an example of a widely accepted, broad-scale classification with geographically delimited associations. However, in some cases it fails to describe adequately local vegetation patterns. In the Czech Republic, six associations, based on a broad-scale regional classification, were traditionally distinguished: (1) *Melampyro nemorosi-Carpinetum* – Hercynian association; (2) *Primulo veris-Carpinetum* – Pannonian association; (3) *Carici pilosae-Carpinetum* – Carpathian association; (4) *Tilio-Carpinetum* – Polonian association; (5) *Stellario-Tilietum* – local association of southern Bohemia; (6) *Tilio-Betuletum* – ecologically delimited and local association. The goal of this study was to evaluate, using a cluster analysis of a set of 601 geographically stratified relevés, whether the variation in species composition of oak-hornbeam forests in the Czech Republic reflects the traditional geographically based classification. Hercynian, Pannonian and Carpathian types of oak-hornbeam forests were reproduced by cluster analysis. No support was found for the Polonian type and the two local associations, *Stellario-Tilietum* and *Tilio-Betuletum*. Instead, a distinct group confined to wet soils emerged. On the basis of this analysis, we suggest a classification that combines ecological and geographical principles and distinguishes four associations: (1) Hercynian (*Melampyro nemorosi-Carpinetum* or *Galio sylvatici-Carpinetum*); (2) Pannonian (*Primulo veris-Carpinetum*); (3) Carpathian (*Tilio cordatae-Carpinetum* or *Carici pilosae-Carpinetum*); (4) *Stellario holosteae-Carpinetum*, which is a geographically delimited association of atlantic northwestern central Europe, defined ecologically by its occurrence on wet soils within the Czech Republic.

K e y w o r d s : broad-leaved deciduous woodland, *Carpinion*, *Carpinus,* classification, local and regional scale, phytosociology, plant communities, *Quercus*

Introduction

Vegetation classification reflects environmental and phytogeographical gradients, which operate on various scales. On a local scale, the most important gradients are usually those associated with small-scale heterogeneity in disturbance, light availability and soil properties such as moisture, nutrient status and pH. When a study is scaled up to a regional level, macroclimatic gradients and differences in the evolutionary and migration histories of local floras become increasingly important (Diekmann 1997). In most phytosociological studies, vegetation units are delimited locally and their boundaries mainly reflect local environmental gradients. In some studies, delimitation of vegetation units is based on data from large areas, and such units are often differentiated by geographically vicarious species with similar habitat requirements (Chytrý et al. 2002a). We call these two types of vegetation units ecologically delimited and geographically delimited, respectively. Due to differences in the geographical extent of studies, many local classifications of ecologically delimited units are not applicable on a regional scale, and the geographically delimited vegetation units of broad-scale classifications are often difficult to recognize locally (Kuželová & Chytrý 2004).

Associations of Central European oak-hornbeam forests of the alliance *Carpinion* are an example of a widely accepted broad-scale geographically based classification (Neuhäusl 1977). These mesic broad-leaved forests, dominated by *Carpinus betulus, Quercus petraea* or *Q. robur*, are widespread in low-altitude areas of Central Europe, that have a subcontinental climate. Some stands are natural but others have developed from natural beech forests due to coppicing and other human activities (Ellenberg 1996). In the Czech Republic, the broad-scale geographically based classification was applied and elaborated by R. Neuhäusl and Z. Neuhäuslová (Neuhäusl in Moravec et al. 1982, Neuhäuslová in Neuhäuslová et al. 1998, Neuhäuslová in Moravec et al. 2000). In this classification, they distinguished five associations with distinct geographical ranges (Fig. 1): (1) *Melampyro nemorosi-Carpinetum* Passarge 1962, Hercynian oak-hornbeam forests, widespread in the area of the Bohemian Massif, mainly in northern, central and eastern Bohemia as well as in western Moravia; (2) *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová ex Neuhäuslová-Novotná 1964, Pannonian oak-hornbeam forests, occupying southern Moravia; (3) *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964, Carpathian oak-hornbeam forests, distributed in the Carpathian part of the Czech Republic; (4) *Tilio-Carpinetum* Traczyk 1962, Polonian oak-hornbeam forests, distributed in northern Moravia and Silesia; (5) *Stellario-Tilietum* Moravec 1964, a local association of lime-oak forests in southern Bohemia where *Carpinus betulus* is absent due to constraints on its migration. Somewhat inconsistently, this geographically based classification also includes one ecologically delimited association, the *Tilio-Betuletum* Passarge 1957, which occurs on nutrient-poor soils in central and eastern Bohemia, within the distribution range of the *Melampyro nemorosi-Carpinetum*.

The classification of oak-hornbeam forests with geographically delimited associations is useful for describing broad-scale biogeographical patterns on the scale of Central Europe. This was used in systems of habitat classification such as CORINE (Commission of European Communities 1991) and subsequently in the EU Habitats Directive, which defines habitats recognized in the NATURA 2000 project (European Commission 1999, Chytrý et al. 2001). However, during the Czech national project of NATURA 2000 habitat mapping, the geographically delimited associations of oak-hornbeam forests turned out to be rather difficult to recognize on a local scale, especially in Moravia where the transitional zones between these associations were traditionally delineated (Neuhäuslová et al. 1998). On the local scale used for habitat mapping (maps of 1 : 10 000 scale), strong vegetation differentiation due to variation in soil properties was observed in many places, but assignment of individual oak-hornbeam stands to one of the geographically delimited associations was difficult due to the joint occurrence of diagnostic species from different associations.

The goal of the present study is to evaluate whether the variation in species composition of oak-hornbeam forests in the Czech Republic follows a geographical pattern, recognized by traditional phytosociological studies, and if so, what is the location of the boundaries or transitional zones between the major types, which diagnostic species can be used for char-

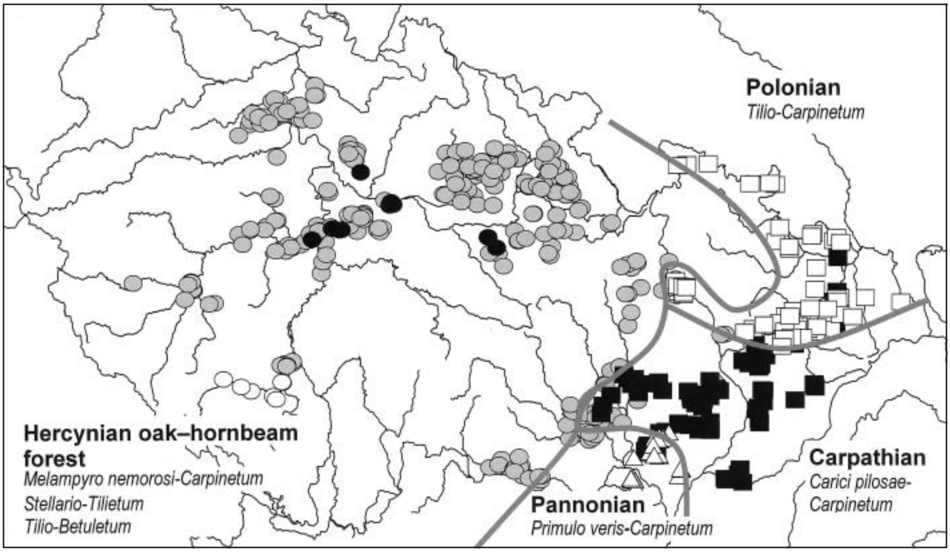


Fig. 1. – Distribution of the traditional oak-hornbeam forest associations in the Czech Republic according to Neuhäuslová (in Moravec et al. 2000), with the boundaries between four major geographical groups delineated. ◯ *Melampyro nemorosi-Carpinetum*, △ *Primulo veris-Carpinetum*, ■ *Carici pilosae-Carpinetum*, □ *Tilio-Carpinetum*, ○ *Stellario-Tilietum*, ● *Tilio-Betuletum*

acterization of these types and what is the relative role of habitat factors in producing floristic variation. We try to achieve these goals by applying numerical classification techniques to a nation-wide set of oak-hornbeam forest relevés. We also discuss the possible syntaxonomic interpretations of the detected patterns.

Materials and methods

Data set

The data set used for the present analysis consists of phytosociological relevés that were obtained from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). Only those relevés were selected that had been assigned to one of six associations of the *Carpinion* alliance by Neuhäuslová (in Moravec et al. 2000). Thus the data set corresponded to the traditional delimitation of the *Carpinion* alliance. 44 relevés with deviating floristic compositions were excluded from the data set by the outlier analysis in the PC-ORD 4 program (McCune & Mefford 1999). Relative Euclidean (chord) distance was used as the measure of dissimilarity among relevés and the relevés remoted by more than two units of standard deviation from the mean distance between pairs of relevés were considered as outliers. Most of the outliers were either extremely species-poor or extremely species-rich relevés, the latter being often closely related to thermophilous oak forests. To reduce patchiness in the geographical distribution of the relevés and oversampling of some areas, the data set was geographically stratified in such a way that only one relevé of each subassociation was selected for each cell of a geographical grid dividing the Czech Republic into quadrangles of 2.5 longitudinal × 1.5 latitudinal minutes (ca. 3 × 3 km). If a quadrangle contained more than one relevé of the same subassociation (according to Neuhäuslová in Moravec et al. 2000), one of them was selected at random. The resulting data set contained 601 relevés, ranging in size from 25 to 750 m^2. We deleted all records of bryophytes, lichens and juvenile trees and shrubs, as these were not recorded in all relevés (note that terricolous cryptogams are usually not common in this vegetation type). Shrub-layer and herb-layer records for the low-grown woody species (e.g. *Daphne mezereum, Rubus* spp.) were merged. Nomenclature of taxa follows Kubát et al. (2002).

Data analysis

Using the cluster analysis in the PC-ORD 4 package (McCune & Mefford 1999), the data set was classified into six clusters, i.e. the same number as the number of associations in the traditional classification of oak-hornbeam forests (Neuhäuslová in Moravec et al. 2000). As the results of a cluster analysis are generally dependent on the data transformations, resemblance measures and clustering algorithms used, we performed several pilot analyses that combined different options, including species presence/absence with Sörensen distance and square-root transformation of species percentage cover with relative Euclidean (chord) distance. Then we applied the beta flexible clustering algorithm with several different β values. Except for the trials with high β values, which led to chaining of dendrograms, all of these analyses resulted in very similar relevé groups in the six clusters, which indicated the robustness of the results. Consequently, only the results of a single cluster analysis are presented in this paper, the one that included presence/absence data, Sörensen distance and $\beta = -0.20$.

Robustness of the classification was further evaluated using a reduced data set containing equal numbers of relevés from each traditional association, following the assignments to associations according to Neuhäuslová (in Moravec et al. 2000). This was done because of the varying number of relevés assigned to these associations in our data set (*Melampyro-Carpinetum* 356, *Primulo-Carpinetum* 26, *Carici-Carpinetum* 123, *Tilio-Carpinetum* 76, *Stellario-Tilietum* 8, *Tilio-Betuletum* 12). As one of our aims was the comparison of traditional and numerical classification, we suspected that the high proportion of the *Melampyro-Carpinetum* relevés might have resulted in an excessively detailed division of this association or in an increased tendency of assignment of some of those relevés to other associations. Therefore, we randomly selected 26 relevés from each of the former four associations. However, we deleted relevés of the *Stellario-Tilietum* and *Tilio-Betuletum* associations, as there were too few of them. Then we subjected the resulting reduced data set of 104 relevés to cluster analysis with the same options as the full data set.

Both the traditional associations and the results of the cluster analysis are summarized in synoptic tables. In these tables, the diagnostic species for each association or cluster were determined using the phi coefficient of association in the JUICE 6.1 program (Tichý 2002). The phi coefficient (Sokal & Rohlf 1995, Chytrý et al. 2002b) compares the occurrence of each species within and outside each vegetation unit. It ranges from –1 to 1. The value of $\Phi = 1$ indicates that the species occurs in all relevés of a particular vegetation unit but is absent in others. If $\Phi = 0$, the species occurs equally frequently within and outside the vegetation unit. Species with $\Phi = -1$ is absent from all relevés of a particular vegetation unit and present in all relevés not belonging to this vegetation unit. In this study, species with $\Phi > 0.19$ were considered as diagnostic. This value was selected subjectively, after a preliminary inspection of the synoptic table, as it yielded informative but not too extensive lists of diagnostic species for each vegetation unit.

Environmental affinities of the clusters were determined by calculating Ellenberg indicator values (Ellenberg et al. 1992) for relevés, using the JUICE 6.1 program (Tichý 2002). The Ellenberg indicator values of the clusters were compared by one-way ANOVA in STATISTICA 6 package (StatSoft Inc. 2001). The homogeneous groups were determined using the Tukey test.

Results

The traditional classification of Czech oak-hornbeam forests into six associations, with statistically determined diagnostic species, is presented in Table 1 (see also Fig. 1).

Cluster analysis to the level of six groups yielded very similar results when performed with the full data set (601 relevés) and the reduced data set (104 relevés) that contained equal numbers of relevés assigned to the four major traditional associations. This concordance suggested that the results obtained using the full data set were robust; thus only these results are presented (Table 2, Figs. 2 and 3). The first division separated relevés from dry and mesic habitats (Fig. 2, clusters I–IV), and wet habitats (Fig. 2, clusters V and VI). In the former group, further divisions followed the geographical differentiation between Hercynian (clusters I–II), Pannonian (cluster III) and Carpathian (cluster IV) oak-hornbeam forests. Clusters V and VI had distinct distribution centres in eastern Bohemia, northern Moravia and Silesia.

Clusters I and II largely included relevés of Hercynian oak-hornbeam forests, occurring in the Bohemian Massif (Fig. 3) and traditionally assigned to the *Melampyro nemorosi-Carpinetum* association (Table 3). Thermophilous and acidophilous species were diagnostic of cluster I, e.g. *Festuca ovina, Melampyrum pratense, Avenella flexuosa, Tanacetum corymbosum* and *Primula veris*. By contrast, cluster II was characterized by nutrient-demanding species such as *Cardamine impatiens, Dryopteris filix-mas* and the invasive alien species, *Impatiens parviflora.*

Cluster III included relevés of Pannonian oak-hornbeam forests, mainly from the area of Pannonian flora in southern Moravia (Fig. 3), except one relevé from the Berounka valley in central Bohemia and relevés from the Dyje valley in south-western Moravia. Most relevés assigned to the Pannonian association *Primulo veris-Carpinetum* by Neuhäuslová (in Moravec et al. 2000) are in this cluster (Table 3). At the same time, many relevés in this cluster are transitional to mesic variants of thermophilous oak forests, as indicated by the diagnostic species, which include several thermophilous shrubs such as *Euonymus verrucosa, Ligustrum vulgare* and *Cornus mas,* and thermophilous herbs such as *Viola mirabilis, Carex michelii, Melittis melissophyllum* and *Campanula rapunculoides*.

Cluster IV also has a distinct geographical pattern (Fig. 3) as it includes relevés from lower altitudes of the flysch Western Carpathians in eastern Moravia and from the eastern fringes of the Bohemian Massif, mainly from the surroundings of the city of Brno. This cluster largely overlaps with the traditional association *Carici pilosae-Carpinetum* (Table 3). Its diagnostic species include those confined to the Carpathian part of the Czech Republic, e.g. *Carex pilosa, Hacquetia epipactis* and *Euphorbia amygdaloides*.

Table 1. – Synoptic table of the traditional oak-hornbeam forest associations in the Czech Republic, based on relevé assignments to particular associations by Neuhäuslová (in Moravec et al. 2000). On the left side of the table are the species percentage frequencies (constancies) and on the right side the fidelity values, represented by the phi coefficient (multiplied by 1000). Species are sorted according to the decreasing value of the phi coefficient. Diagnostic species for particular columns have a $\Phi > 0.19$ and are highlighted by bold figures on a shaded background. Species that occurred in less than two relevés were not considered as diagnostic even if they exceeded this threshold Φ value. Negative values of Φ are not shown. Of the non-diagnostic species, only those with a frequency greater than 50 % in at least one column are included in the table. MnC *Melampyro nemorosi-Carpinetum*, PvC *Primulo veris-Carpinetum*, CpC *Carici pilosae-Carpinetum*, TC *Tilio-Carpinetum*, TB *Tilio-Betuletum*, ST *Stellario-Tilietum.*

	Frequency (%)						Fidelity ($\Phi \times 1000$)					
Association	MnC	PvC	CpC	TC	TB	ST	MnC	PvC	CpC	TC	TB	ST
Number of relevés	356	26	123	76	12	8	356	26	123	76	12	8
E_3 – tree layer												
Carici pilosae-Carpinetum												
Fagus sylvatica	12	–	**33**	3	8	–	–	–	**276**	–	–	–
Tilio-Carpinetum												
Betula pubescens	1	–	2	**22**	–	–	–	–	–	**379**	–	–
Quercus robur	35	69	33	**76**	42	100	–	117	–	**264**	–	136
Alnus glutinosa	–	–	2	**11**	–	–	–	–	23	**247**	–	–
Sorbus aucuparia	1	–	2	**12**	–	25	–	–	–	**197**	–	150
Species diagnostic for two and more associations												
Tilia cordata	38	38	**72**	**95**	83	75	–	–	**186**	**316**	86	51
Other frequent species												
Carpinus betulus	78	88	93	79	8	12	–	49	170	–	–	–
Quercus petraea agg.	69	73	66	20	83	25	175	48	40	–	63	–
E_2 – shrub layer												
Primulo veris-Carpinetum												
Euonymus verrucosa	2	**46**	11	–	–	–	–	**394**	124	–	–	–
Ligustrum vulgare	5	**50**	12	4	8	–	–	**321**	71	–	–	–
Rhamnus cathartica	4	**31**	1	–	–	–	–	**307**	–	–	–	–
Crataegus monogyna	12	**54**	15	5	–	–	–	**251**	29	–	–	–
Cornus mas	3	**27**	4	–	–	–	–	**249**	–	–	–	–
Cornus sanguinea	24	**65**	21	13	17	–	17	**212**	–	–	–	–
Staphylea pinnata	–	**12**	3	–	–	–	–	**206**	99	–	–	–
Sambucus nigra	4	4	13	**36**	17	–	–	–	45	**315**	30	–
Rubus caesius	2	4	–	**11**	–	–	–	18	–	**196**	–	–
Ribes rubrum	–	–	2	3	**17**	–	–	–	32	63	**225**	–
Other frequent species												
Corylus avellana	37	58	30	34	–	–	51	102	–	–	–	–
Rubus fruticosus agg.	28	15	27	51	58	38	–	–	–	166	84	16
E_1 – herb layer												
Melampyro nemorosi-Carpinetum												
Hepatica nobilis	**60**	4	5	5	–	62	**539**	–	–	–	–	58
Stellaria holostea	**64**	–	34	42	42	100	**284**	–	–	–	–	110
Tanacetum corymbosum	**35**	42	11	–	17	50	**254**	78	–	–	–	63
Galium sylvaticum	**62**	85	54	3	8	50	**229**	136	11	–	–	–
Festuca ovina	**21**	–	2	1	58	25	**223**	–	–	–	179	35
Primula veris	**18**	23	2	–	–	–	**212**	73	–	–	–	–
Fragaria moschata	**32**	12	18	11	–	50	**192**	–	–	–	–	67
Primulo veris-Carpinetum												
Carex michelii	–	**27**	–	–	–	–	–	**511**	–	–	–	–
Viola mirabilis	12	**85**	5	–	–	–	–	**488**	–	–	–	–

Vicia pisiformis	2	**54**	7	–	–	25	–	**468**	50	–	–	104
Clematis vitalba	–	**12**	–	–	–	–	–	**333**	–	–	–	–
Melittis melissophyllum	15	**73**	27	–	–	–	–	**314**	128	–	–	–
Lithospermum purpurocaeruleum	1	**15**	–	–	–	–	–	**308**	–	–	–	–
Lapsana communis	6	**42**	11	1	–	25	–	**262**	41	–	–	70
Campanula rapunculoides	25	**77**	36	–	–	–	–	**251**	120	–	–	–
Hypericum montanum	4	**38**	15	1	17	–	–	**250**	138	–	50	–
Clinopodium vulgare	19	**62**	13	1	42	38	30	**240**	–	–	87	58
Carex muricata agg.	8	**42**	11	4	33	38	–	**218**	12	–	105	101
Chamaecytisus supinus	1	**8**	–	–	–	–	–	**217**	–	–	–	–
Dactylis glomerata agg.	37	**92**	56	30	58	12	–	**213**	137	–	45	–
Pimpinella major	5	**31**	9	3	–	–	–	**210**	51	–	–	–
Lathyrus niger	33	**73**	28	1	–	12	109	**208**	–	–	–	–
Carici pilosae-Carpinetum												
Carex pilosa	13	42	**88**	21	–	–	–	56	**635**	–	–	–
Euphorbia amygdaloides	2	–	**53**	16	–	–	–	–	**574**	22	–	–
Hacquetia epipactis	1	–	**23**	4	–	–	–	–	**394**	–	–	–
Symphytum tuberosum	7	–	**45**	21	–	12	–	–	**390**	49	–	–
Neottia nidus-avis	16	31	**52**	4	–	–	–	45	**368**	–	–	–
Carex digitata	31	50	**70**	12	–	38	–	57	**345**	–	–	–
Galium odoratum	31	65	**76**	53	–	12	–	93	**334**	68	–	–
Sanicula europaea	20	4	**54**	34	8	25	–	–	**293**	55	–	–
Ajuga reptans	28	4	**66**	59	8	25	–	–	**286**	162	–	–
Dentaria bulbifera	4	27	**24**	–	–	–	–	143	**280**	–	–	–
Platanthera bifolia	7	15	**25**	1	8	–	–	35	**248**	–	–	–
Orchis pallens	–	–	**9**	3	–	–	–	–	**236**	12	–	–
Maianthemum bifolium	47	–	**74**	66	8	38	–	–	**224**	106	–	–
Cephalanthera longifolia	1	–	**9**	–	–	–	–	–	**222**	–	–	–
Pulmonaria officinalis s.l.	62	73	**86**	57	8	75	–	33	**219**	–	–	23
Stachys alpina	–	–	**7**	1	–	–	–	–	**209**	–	–	–
Pyrola rotundifolia	1	–	**7**	–	–	–	–	–	**209**	–	–	–
Polygonatum multiflorum	43	77	**74**	70	42	25	–	97	**203**	120	–	–
Viola reichenbachiana	47	73	**76**	67	25	75	–	71	**196**	82	–	44
Fragaria vesca	42	96	**72**	54	67	50	–	186	**194**	12	41	–
Tilio-Carpinetum												
Primula elatior	9	–	22	**50**	–	–	–	–	83	**353**	–	–
Circaea lutetiana	4	–	24	**42**	–	–	–	–	174	**345**	–	–
Anthriscus nitidus	–	–	3	**18**	–	–	–	–	–	**344**	–	–
Senecio nemorensis agg.	15	–	23	**55**	8	12	–	–	20	**318**	–	–
Carex brizoides	7	–	7	**37**	8	62	–	–	–	**307**	–	188
Lysimachia vulgaris	3	–	1	**20**	–	–	–	–	–	**288**	–	–
Athyrium filix-femina	6	–	24	**39**	17	–	–	–	147	**286**	13	–
Impatiens noli-tangere	6	–	17	**37**	8	38	–	–	73	**284**	–	89
Deschampsia cespitosa	10	–	14	**39**	8	12	–	–	–	**280**	–	–
Urtica dioica	7	8	7	**33**	17	12	–	–	–	**274**	28	–
Festuca gigantea	5	8	7	**29**	25	12	–	–	–	**270**	81	15
Paris quadrifolia	5	–	15	**30**	–	–	–	–	79	**257**	–	–
Ficaria verna subsp. *bulbifera*	5	–	11	**26**	–	–	–	–	35	**239**	–	–
Oxalis acetosella	18	–	31	**50**	8	12	–	–	87	**236**	–	–
Angelica sylvestris	3	–	4	**18**	–	–	–	–	–	**228**	–	–
Aegopodium podagraria	29	23	45	**66**	8	62	–	–	82	**227**	–	62
Stachys sylvatica	9	–	6	**26**	–	–	–	–	–	**211**	–	–
Milium effusum	15	38	30	**46**	17	38	–	74	77	201	–	38
Tilio-Betuletum												
Holcus mollis	3	–	–	1	**50**	–	–	–	–	–	**420**	–
Agrostis capillaris	1	–	–	1	**42**	12	–	–	–	–	**405**	87
Carex pilulifera	1	–	1	–	**25**	–	–	–	–	–	**295**	–

Carex pallescens	6	4	2	3	**50**	–	27	–	–	–	**274**	–
Anthoxanthum odoratum	4	12	–	1	**42**	–	20	79	–	–	**268**	–
Avenella flexuosa	12	–	–	3	**58**	–	151	–	–	–	**249**	–
Moehringia trinervia	15	23	27	21	**83**	50	–	14	80	–	**222**	85
Campanula patula	1	4	–	3	**17**	–	–	53	–	52	**206**	–
Stellaria media	4	12	4	13	**42**	–	–	44	–	103	**204**	–
Stellario-Tilietum												
Festuca rubra agg.	2	–	–	–	–	**50**	12	–	–	–	–	**417**
Galeopsis bifida	3	–	–	4	–	**62**	–	–	–	17	–	**394**
Adoxa moschatellina	3	–	–	3	–	**50**	27	–	–	–	–	**320**
Chelidonium majus	1	–	–	3	–	**25**	–	–	–	75	–	**309**
Galium aparine s.l.	10	4	8	7	8	**62**	14	–	–	–	–	**210**
Torilis japonica	2	8	–	1	–	**25**	–	93	–	–	–	**201**
Species diagnostic for two and more associations												
Melica uniflora	6	**77**	**41**	13	–	–	–	**342**	**335**	–	–	–
Fallopia convolvulus	2	**27**	–	–	**33**	12	–	**299**	–	–	**254**	65
Galium schultesii	4	–	**28**	**50**	–	–	–	–	**197**	**392**	–	–
Cruciata glabra	1	–	**15**	**20**	–	–	–	–	**191**	**226**	–	–
Poa angustifolia	2	8	4	–	**42**	**38**	–	43	–	–	**282**	**204**
Other frequent species												
Poa nemoralis	84	100	91	78	92	100	–	87	80	–	25	48
Melica nutans	68	62	83	64	42	62	–	–	146	–	–	–
Lathyrus vernus	67	81	75	30	–	62	92	79	125	–	–	–
Hieracium murorum	64	65	66	32	83	75	81	19	50	–	65	33
Convallaria majalis	51	92	60	41	33	25	–	169	75	–	–	–
Veronica chamaedrys agg.	48	38	54	26	58	75	32	–	74	–	34	67
Campanula trachelium	42	54	51	43	25	88	–	39	66	–	–	100
Anemone nemorosa	51	–	28	43	58	62	180	–	–	–	43	45
Asarum europaeum	35	69	51	59	–	25	–	118	95	133	–	–
Scrophularia nodosa	34	69	55	43	83	12	–	118	137	11	120	–
Galeobdolon luteum s.l.	30	38	51	62	–	50	–	–	133	183	–	28
Hieracium sabaudum	35	65	53	20	50	25	–	118	150	–	34	–
Geum urbanum	28	54	48	58	33	38	–	74	114	164	–	–
Brachypodium sylvaticum	30	46	48	49	58	–	–	41	118	94	64	–
Campanula persicifolia	33	69	37	14	8	62	–	163	37	–	–	73
Viola riviniana	31	8	46	25	75	–	–	–	149	–	129	–
Luzula luzuloides	35	–	32	25	33	62	79	–	–	–	–	77
Festuca heterophylla	26	65	34	14	17	–	–	183	80	–	–	–
Carex montana	24	54	23	–	33	–	61	165	12	–	40	–

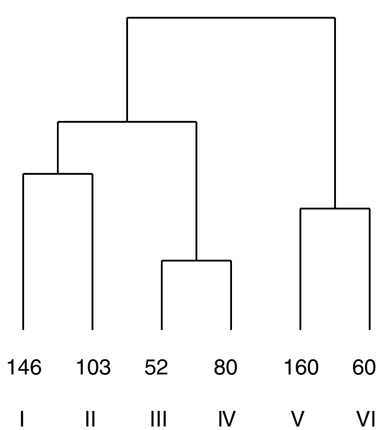


Fig. 2. – Dendrogram based on the cluster analysis of Czech oak-hornbeam forests. Arabic numerals denote numbers of relevés assigned to each cluster and Roman numerals are cluster codes.

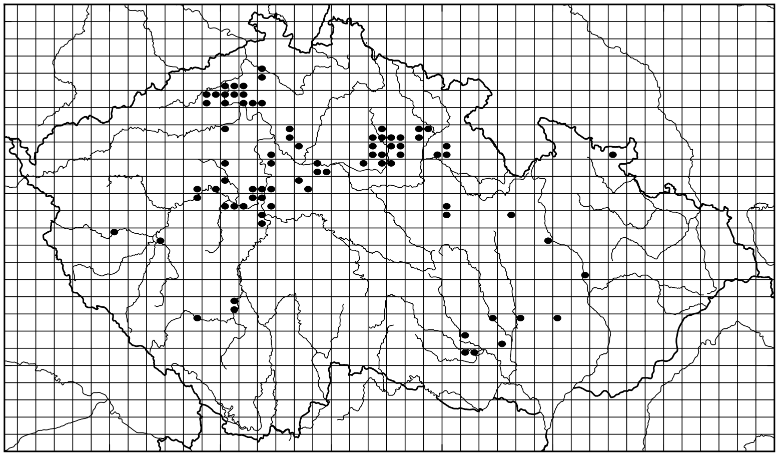
Table 2. – Synoptic table of clusters identified by cluster analysis. On the left side of the table are the species percentage frequencies (constancies) and on the right side the fidelity values, represented by the phi coefficient (multiplied by 1000). Species are sorted according to the decreasing value of the phi coefficient. Diagnostic species for particular columns have a $\Phi > 0.19$ and are highlighted by bold figures on a shaded background. Negative values of Φ are not shown. Of the non-diagnostic species, only those with a frequency greater than 50% in at least one column are included in the table.

	Frequency (%)						Fidelity ($\Phi \times 1000$)					
Cluster number	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Cluster hierarchy	000	001	010	011	10	11	000	001	010	011	10	11
Number of relevés	146	103	52	80	160	60	146	103	52	80	160	60
E_3 – tree layer												
Robinia pseudacacia	–	–	**10**	2	–	–	–	–	**242**	49	–	–
Fagus sylvatica	12	21	4	**38**	9	–	–	92	–	**260**	–	–
Betula pendula	14	19	6	**49**	21	45	–	–	–	**228**	–	164
Fraxinus excelsior	1	1	6	2	**21**	10	–	–	–	–	**295**	25
Acer pseudoplatanus	2	11	2	5	**22**	15	–	–	–	–	**231**	47
Abies alba	3	12	–	1	**18**	–	–	65	–	–	**231**	–
Picea abies	5	11	–	1	**19**	5	–	30	–	–	**224**	–
Tilia platyphyllos	1	4	2	1	**11**	–	–	–	–	–	**214**	–
Acer campestre	12	2	15	6	**24**	7	–	–	27	–	**205**	–
Betula pubescens	–	1	–	–	2	**30**	–	–	–	–	–	**467**
Tilia cordata	34	28	44	75	64	**95**	–	–	–	171	127	**279**
Quercus robur	32	23	38	26	58	**83**	–	–	–	–	188	**278**
Quercus petraea agg.	**86**	74	77	**88**	30	22	**283**	110	94	**205**	–	–
Carpinus betulus	60	83	94	94	81	78	–	50	115	142	33	–
E_2 – shrub layer												
Euonymus verrucosa	1	2	**46**	4	–	–	–	–	**570**	–	–	–
Ligustrum vulgare	8	3	**37**	8	7	–	–	–	**314**	–	–	–
Cornus mas	6	1	**21**	2	1	–	63	–	**270**	–	–	–
Rhamnus cathartica	5	3	**19**	–	1	2	34	–	**255**	–	–	–
Crataegus monogyna	15	6	**37**	20	9	7	26	–	**208**	75	–	–
Viburnum opulus	3	5	–	–	**27**	2	–	–	–	–	**384**	–
Sambucus nigra	1	8	4	1	**28**	8	–	–	–	–	**340**	–
Daphne mezereum	13	22	–	26	**51**	25	–	–	–	–	**336**	–
Crataegus laevigata	21	6	35	16	**35**	5	–	–	103	–	**208**	–
Lonicera xylosteum	12	13	8	4	**23**	–	–	–	–	–	**198**	–
Corylus avellana	42	22	62	15	44	18	83	–	173	–	114	–
E_1 – herb layer												
Hercynian group (nutrient-poor)												
Tanacetum corymbosum	**62**	16	52	19	4	3	**458**	–	181	–	–	–
Festuca ovina	**38**	14	–	11	2	7	**389**	–	–	–	–	–
Melampyrum pratense	**53**	23	19	30	1	25	**364**	–	–	41	–	–
Viola hirta	**22**	1	17	–	2	–	**304**	–	112	–	–	–
Avenella flexuosa	**24**	15	–	1	1	–	**303**	92	–	–	–	–
Hieracium murorum	**86**	54	63	78	52	12	**293**	–	15	132	–	–
Primula veris	**28**	6	17	1	7	7	**281**	–	50	–	–	–
Anemone nemorosa	**66**	40	4	26	48	40	**263**	–	–	–	49	–
Achillea millefolium agg.	**10**	–	2	–	–	–	**258**	–	–	–	–	–
Trifolium alpestre	**14**	2	12	–	–	–	**253**	–	96	–	–	–
Anthoxanthum odoratum	**13**	1	6	–	1	2	**251**	–	25	–	–	–
Betonica officinalis	**13**	–	4	–	1	5	**242**	–	–	–	–	11
Campanula rotundifolia	**8**	1	–	–	–	–	**224**	–	–	–	–	–
Carex pallescens	**14**	1	2	2	3	7	**214**	–	–	–	–	15

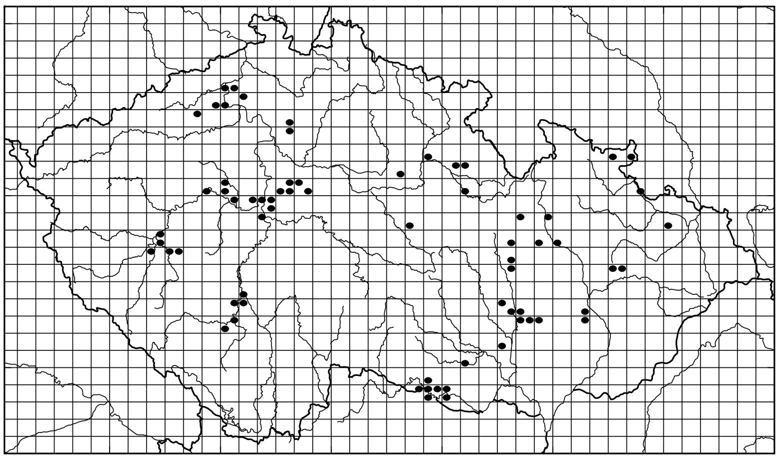
Galium pumilum s.l.	**6**	1	–	–	–	–	**199**	–	–	–	–	–
Carex montana	**36**	7	44	35	7	15	**199**	–	167	125	–	–
Euphorbia cyparissias	**10**	1	6	–	2	–	**190**	–	31	–	–	–
Hercynian group (nutrient-rich)												
Impatiens parviflora	8	**26**	2	2	6	27	–	**218**	–	–	–	164
Cardamine impatiens	2	**11**	4	1	–	–	–	**215**	19	–	–	–
Myosotis sylvatica	12	**25**	6	1	12	–	–	**204**	–	–	26	–
Dryopteris filix-mas	2	**25**	2	10	18	5	–	**193**	–	–	122	–
Pannonian group												
Vicia pisiformis	4	1	**37**	6	–	–	–	–	**437**	19	–	–
Viola mirabilis	8	2	**54**	6	11	8	–	–	**409**	–	–	–
Lapsana communis	5	5	**44**	9	4	2	–	–	**400**	–	–	–
Melittis melissophyllum	14	8	**62**	35	9	2	–	–	**360**	183	–	–
Carex michelii	–	–	**13**	–	–	–	–	–	**353**	–	–	–
Hypericum montanum	10	3	**37**	10	–	2	45	–	**340**	37	–	–
Clinopodium vulgare	25	14	**60**	12	8	7	106	–	**331**	–	–	–
Pimpinella major	1	1	**31**	4	7	10	–	–	**303**	–	–	47
Hylotelephium maximum	2	2	**17**	–	1	–	–	–	**292**	–	–	–
Lithospermum purpurocaeruleum	1	–	**10**	–	–	–	–	–	**267**	–	–	–
Pulmonaria mollis	–	–	**8**	–	–	–	–	–	**266**	–	–	–
Dactylis glomerata s.l.	34	30	**85**	64	24	70	–	–	**260**	166	–	183
Astragalus glycyphyllos	23	6	**42**	12	6	2	148	–	**257**	–	–	–
Campanula persicifolia	46	36	**71**	45	9	13	154	27	**249**	99	–	–
Lathyrus niger	42	17	**65**	44	9	18	171	–	**249**	130	–	–
Carex muricata agg.	14	5	**35**	15	2	8	56	–	**239**	55	–	–
Fragaria vesca	46	39	**90**	75	49	37	–	–	**234**	177	–	–
Asplenium trichomanes	–	–	**6**	–	–	–	–	–	**230**	–	–	–
Clematis vitalba	–	–	**6**	–	–	–	–	–	**230**	–	–	–
Cyclamen purpurascens	1	4	**13**	2	–	–	–	47	**227**	–	–	–
Fallopia convolvulus	4	2	**15**	2	–	–	37	–	**224**	–	–	–
Silene nutans	10	8	**23**	4	1	2	82	20	**203**	–	–	–
Verbascum austriacum	1	–	**6**	–	–	–	–	–	**193**	–	–	–
Carpathian group												
Neottia nidus-avis	7	17	23	**74**	16	13	–	–	–	**490**	–	–
Symphytum tuberosum	4	9	15	**60**	14	7	–	–	–	**463**	–	–
Carex digitata	25	33	63	**85**	32	2	–	–	168	**389**	–	–
Hieracium sabaudum	51	25	62	**82**	11	27	143	–	146	**355**	–	–
Euphorbia amygdaloides	1	8	12	**42**	18	7	–	–	–	**326**	75	–
Hacquetia epipactis	1	–	–	**24**	6	5	–	–	–	**322**	–	–
Veronica officinalis	20	4	35	**39**	2	3	84	–	174	**267**	–	–
Viola riviniana	41	25	21	**64**	12	47	103	–	–	**260**	–	100
Dentaria bulbifera	3	10	25	**26**	1	–	–	23	186	**254**	–	–
Hieracium lachenalii	32	22	44	**52**	6	8	97	–	139	**251**	–	–
Galium odoratum	12	39	62	**75**	52	52	–	–	110	**247**	99	53
Lathyrus vernus	62	48	63	**92**	63	50	–	–	–	**240**	–	–
Pyrola rotundifolia	1	1	–	**9**	–	–	–	–	–	**234**	–	–
Cephalanthera longifolia	1	4	–	**11**	–	–	–	47	–	**232**	–	–
Galium sylvaticum	60	46	73	**81**	36	35	80	–	126	**225**	–	–
Platanthera bifolia	12	3	23	**26**	4	3	37	–	129	**205**	–	–
Cruciata glabra	2	5	–	**18**	4	10	–	–	–	**195**	–	59
Genista tinctoria	5	2	4	**14**	1	–	43	–	–	**195**	–	–
Orthilia secunda	1	1	–	**8**	–	–	–	–	–	**194**	–	–
Scrophularia nodosa	32	35	54	**66**	36	52	–	–	74	**193**	–	66
Wet group (nutrient-rich)												
Primula elatior	–	6	–	4	**49**	15	–	–	–	–	**539**	–
Carex sylvatica	3	–	4	20	**49**	13	–	–	–	17	**484**	–
Asarum europaeum	17	18	62	31	**80**	38	–	–	122	–	**465**	–

Circaea lutetiana	–	4	–	4	**38**	12	–	–	–	–	**462**	–
Galeobdolon luteum s.l.	10	36	31	25	**74**	42	–	–	–	–	**445**	22
Stachys sylvatica	1	5	–	4	**31**	–	–	–	–	–	**434**	–
Paris quadrifolia	–	6	–	8	**28**	5	–	–	–	–	**365**	–
Campanula trachelium	32	22	40	50	**74**	33	–	–	–	41	**359**	–
Impatiens noli-tangere	1	10	2	2	**32**	15	–	–	–	–	**359**	27
Senecio nemorensis agg.	8	30	–	5	**45**	15	–	100	–	–	**352**	–
Euphorbia dulcis	5	14	2	8	**44**	42	–	–	–	–	**350**	171
Brachypodium sylvaticum	23	21	37	31	**64**	32	–	–	–	–	**337**	–
Ranunculus lanuginosus	–	14	–	4	**29**	7	–	35	–	–	**337**	–
Oxalis acetosella	8	32	–	9	**46**	28	–	90	–	–	**321**	37
Astrantia major	–	–	–	–	**17**	7	–	–	–	–	**319**	23
Pulmonaria officinalis s.l.	40	46	81	85	**89**	60	–	–	98	159	**300**	–
Heracleum sphondylium	10	6	13	9	**34**	15	–	–	–	–	**295**	–
Mercurialis perennis	17	26	23	10	**46**	5	–	17	–	–	**294**	–
Geum urbanum	19	24	62	34	**61**	23	–	–	156	–	**293**	–
Anthriscus nitidus	–	–	–	–	**11**	–	–	–	–	–	**292**	–
Hedera helix	3	3	4	10	**25**	7	–	–	–	–	**291**	–
Ajuga reptans	25	20	–	61	**62**	42	–	–	–	184	**290**	22
Sanicula europaea	14	25	6	40	**48**	13	–	–	–	107	**273**	–
Festuca gigantea	1	6	4	1	**21**	15	–	–	–	–	**264**	73
Geranium robertianum	10	26	25	8	**37**	2	–	69	37	–	**251**	–
Actaea spicata	2	17	–	5	**23**	2	–	104	–	–	**249**	–
Colchicum autumnale	–	–	–	–	**10**	3	–	–	–	–	**248**	–
Orchis pallens	–	–	–	–	**8**	–	–	–	–	–	**247**	–
Urtica dioica	1	13	6	1	**23**	15	–	29	–	–	**244**	47
Ficaria verna subsp. *bulbifera*	3	3	–	5	**19**	15	–	–	–	–	**230**	75
Chaerophyllum aromaticum	–	–	–	–	**7**	–	–	–	–	–	**227**	–
Viola reichenbachiana	33	50	60	74	**75**	48	–	–	20	137	**226**	–
Equisetum arvense	–	–	–	–	**6**	–	–	–	–	–	**216**	–
Isopyrum thalictroides	1	1	12	4	**13**	3	–	–	78	–	**195**	–
Aquilegia vulgaris	1	1	–	–	**8**	–	–	–	–	–	**193**	–
Arum maculatum	–	–	–	–	**5**	–	–	–	–	–	**193**	–
Listera ovata	1	1	–	–	**8**	2	–	–	–	–	**192**	–
Wet group (nutrient-poor)												
Carex brizoides	5	5	–	4	12	**53**	–	–	–	–	23	**442**
Deschampsia cespitosa	5	2	–	12	20	**53**	–	–	–	–	105	**378**
Lysimachia vulgaris	4	–	–	–	4	**23**	–	–	–	–	–	**311**
Molinia caerulea s.l.	8	2	–	–	–	**20**	96	–	–	–	–	**264**
Milium effusum	8	14	25	32	28	**55**	–	–	10	82	55	**246**
Stellaria holostea	62	56	25	38	46	**83**	111	34	–	–	–	**205**
Convallaria majalis	51	39	77	75	32	**83**	–	–	149	175	–	**204**
Species diagnostic for two and more clusters												
Festuca heterophylla	**42**	12	50	**55**	2	25	**196**	–	158	**246**	–	–
Luzula luzuloides	39	**51**	10	**56**	7	33	88	**192**	–	**206**	–	11
Campanula rapunculoides	25	14	**81**	**51**	7	15	–	–	**391**	**232**	–	–
Melica uniflora	3	8	**65**	**46**	9	5	–	–	**400**	**309**	–	–
Polygonatum multiflorum	34	24	62	**80**	**71**	67	–	–	46	**204**	**208**	84
Carex pilosa	3	16	52	**89**	18	**60**	–	–	145	**499**	–	**215**
Maianthemum bifolium	36	33	15	**79**	66	**82**	–	–	–	**210**	165	**198**
Aegopodium podagraria	11	13	13	22	**79**	**68**	–	–	–	–	**530**	**217**
Galium schultesii	1	3	–	19	**26**	**42**	–	–	–	52	**198**	**263**
Other frequent species												
Poa nemoralis	85	89	88	100	83	65	–	49	26	161	–	–
Melica nutans	67	51	71	79	79	70	–	–	10	77	118	–
Veronica chamaedrys agg.	58	47	48	66	30	35	126	–	10	156	–	–
Hepatica nobilis	53	43	17	18	42	28	171	43	–	–	55	–

Cluster I



Cluster II



Cluster III

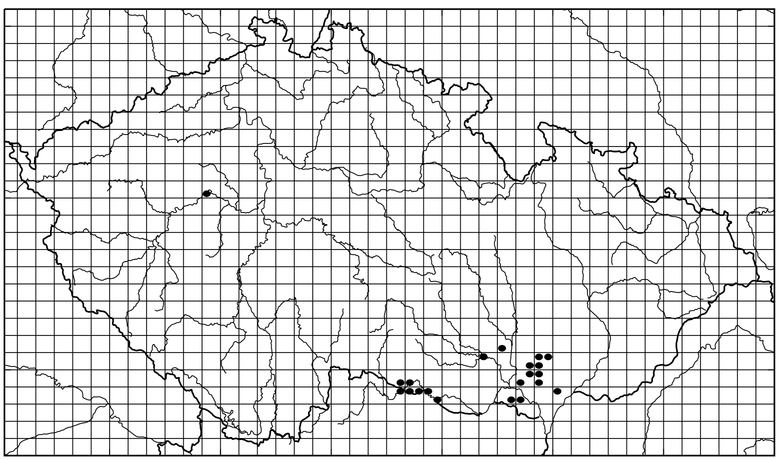
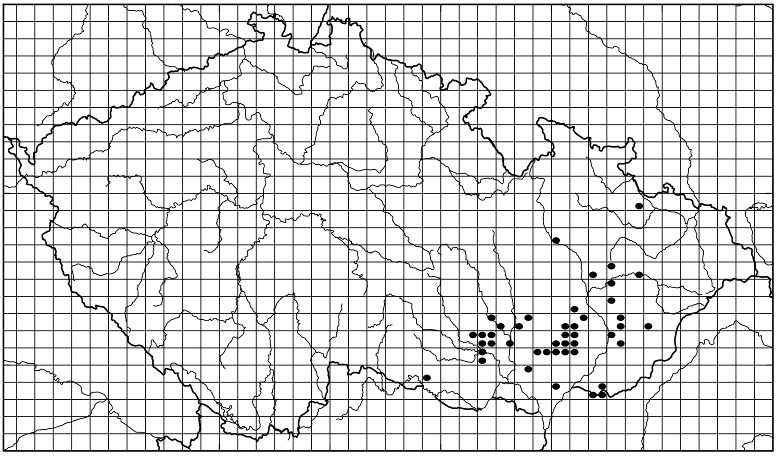
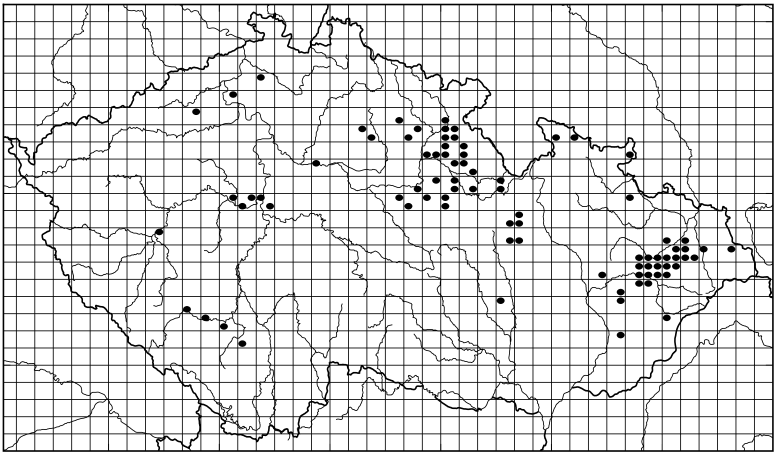


Fig. 3. – Geographical distribution of the relevés assigned to clusters I to VI.

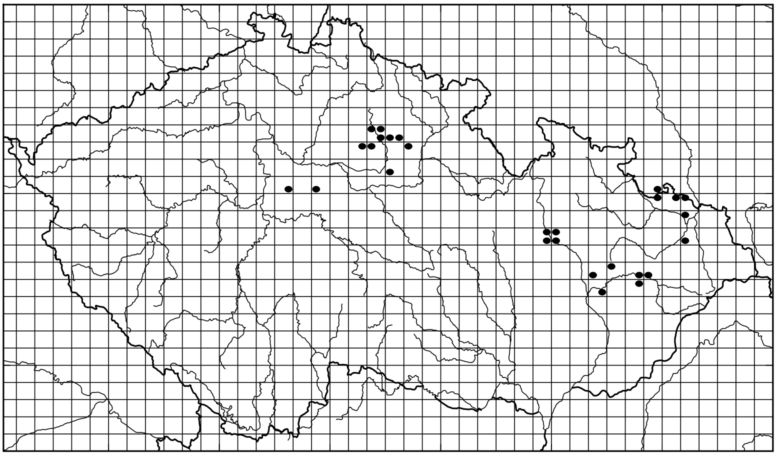
Cluster IV



Cluster V



Cluster VI



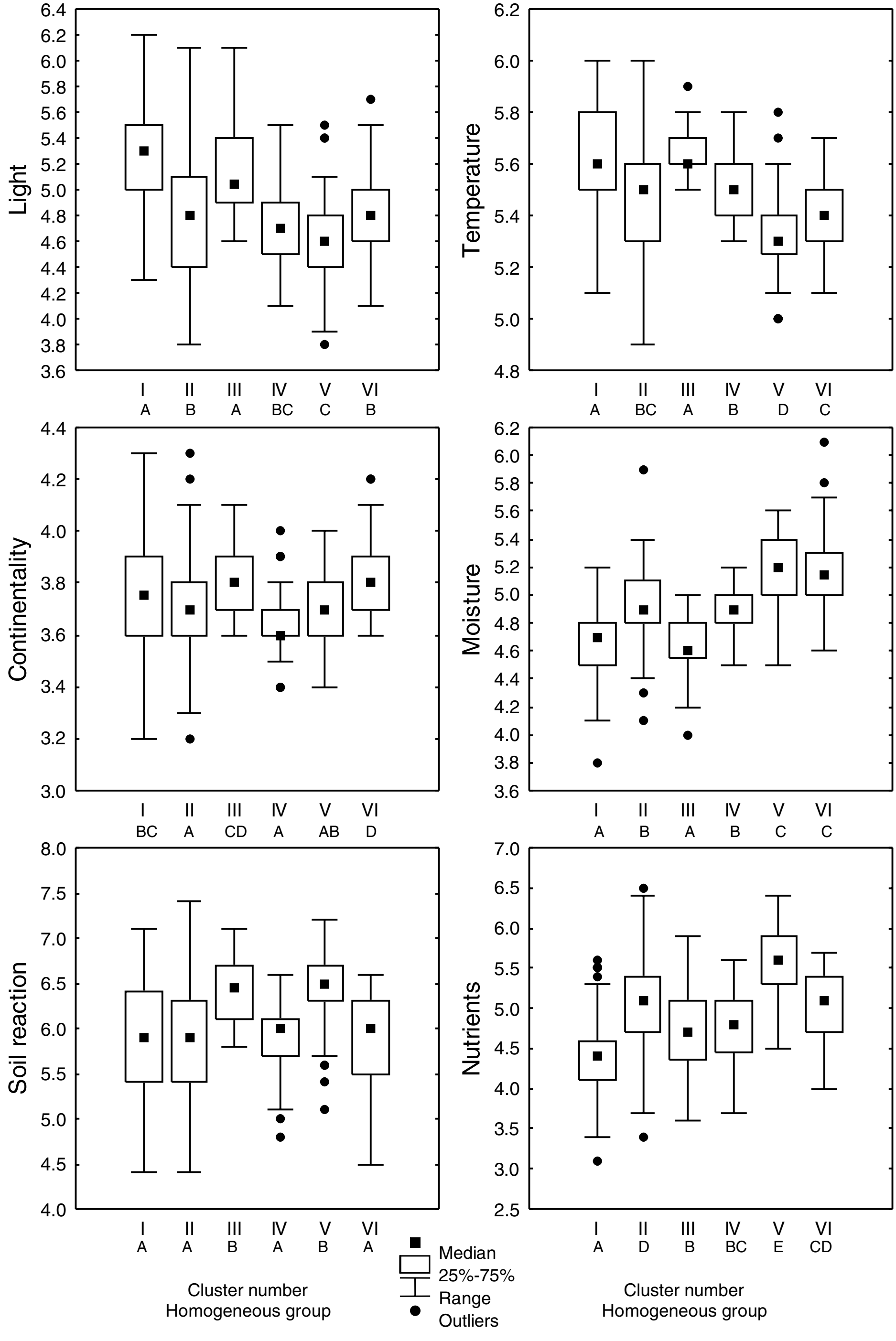


Fig. 4. – Box-and-whisker plots of the Ellenberg indicator values for clusters I–VI. Labels A–E indicate homogeneous groups according to *post-hoc* comparisons using ANOVA (Tukey test, P < 0.05).

Table 3. – Cross-tabulation of the traditional associations with clusters I–VI identified by the cluster analysis (numbers of relevés).

	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V	Cluster VI
Melampyro nemorosi-Carpinetum	134	83	14	18	77	30
Primulo veris-Carpinetum	0	0	24	2	0	0
Carici pilosae-Carpinetum	2	9	14	58	32	8
Tilio-Carpinetum	1	6	0	2	45	22
Tilio-Betuletum	7	3	0	0	2	0
Stellario-Tilietum	2	2	0	0	4	0

Clusters V and VI include relevés from wet habitats, which are mainly found in eastern Bohemia, northern Moravia and Silesia (Fig. 3). Cluster V includes oak-hornbeam forests on wet and nutrient-rich soils, which are often spatially connected with alluvial forests, as indicated by diagnostic species such as *Aegopodium podagraria, Stachys sylvatica* and *Circaea lutetiana*. Cluster VI consists of relevés from habitats with wet and nutrient-poor soils, with diagnostic species including *Molinia caerulea* s.l., *Carex brizoides* and *Deschampsia cespitosa*. These two clusters include most of the relevés assigned to the Polonian *Tilio-Carpinetum* association, but also many assigned to the Hercynian *Melampyro nemorosi-Carpinetum* association by Neuhäuslová (in Moravec et al. 2000) (Table 3).

ANOVA tests were significant for all Ellenberg indicator values ($P < 0.05$). Comparison of clusters (Fig. 4) shows that clusters I (Hercynian) and III (Pannonian) include the warmest types of oak-hornbeam forests. These communities are not separated along light, temperature and moisture gradients, but by soil pH and nutrient supply. Clusters V and VI both include communities with high moisture requirements, but differ in their soil pH and nutrient requirements.

Discussion

Cluster analysis generally confirmed the geographical differentiation of oak-hornbeam forests on the scale of the Czech Republic, and interestingly revealed an equally important ecological differentiation between wet and mesic-dry soils.

Hercynian, Pannonian and Carpathian oak-hornbeam forests: traditional associations confirmed

Hercynian oak-hornbeam forests make up a strong group, which is subdivided into a cluster with thermophilous, often calcifuge species (cluster I) and a cluster with nutrient demanding species (cluster II). Both clusters fit the concept of the *Melampyro nemorosi-Carpinetum* association with several subassociations on different soils, as defined by Neuhäuslová (in Moravec et al. 2000). However, the validity of the diagnostic species, *Hepatica nobilis* and *Melampyrum nemorosum*, reported by Neuhäuslová (in Moravec et al. 2000), was not confirmed (Table 2). The latter species was not confirmed as diagnostic even by the statistical analysis of diagnostic species done for the original classification of relevés as presented by Neuhäuslová (in Moravec et al. 2000) (Table 1). Our results further suggest that oak-hornbeam forests of the Hercynian group occur not only in Bohemia and western Moravia, as presumed by Neuhäuslová (in Neuhäuslová et al. 1998, in Moravec et al. 2000), but also on the eastern fringes of the Bohemian Massif in northern Moravia and Silesia (Fig. 3).

Although there is no doubt that the Hercynian oak-hornbeam forests form a distinct vegetation unit in the Czech Republic, it is unclear how this unit differs from similar forests in Germany and consequently, what is the correct association name for these forests. Oberdorfer (1957) described similar forests from southwestern Germany as the *Galio sylvatici-Carpinetum* association, and Passarge (1957, 1962) those from northeastern Germany as the *Melampyro nemorosi-Carpinetum* association. Czech authors (Neuhäusl 1977, Neuhäusl in Moravec et al. 1982, Neuhäuslová in Neuhäuslová et al. 1998, Neuhäuslová in Moravec et al. 2000) suggest that these two associations are different, geographically vicariant units, and include all such Czech forests in the latter. Most of the recent German authors (Pott 1995, Rennwald 2000, Schubert et al. 2001), however, assign all such German forests to a single association, which they call by the earlier valid name, i.e. *Galio sylvatici-Carpinetum*. The question of how reasonable is to split or lump these two types awaits a joint analysis of German and Czech *Carpinion* data.

The delimitation of Pannonian oak-hornbeam forests suggested by the cluster analysis (cluster III) is very close to the *Primulo veris-Carpinetum* association, as described by Neuhäuslová (in Moravec et al. 2000), both in terms of geographical distribution and diagnostic species. The only difference is the assignment of some of the oak-hornbeam forests growing on basic bedrocks in the Dyje valley in south-western Moravia to the Pannonian cluster. This valley is outside the Pannonian province according to phytogeographical and biogeographical land classifications, although it harbours several elements of Pannonian flora (Skalický 1988, Culek 1996, Chytrý et al. 1999).

The delimitation of the Carpathian oak-hornbeam forests obtained using cluster analysis (cluster IV) is similar to the traditional association *Carici pilosae-Carpinetum*. Compared to the geographical distribution cited by Neuhäuslová (in Moravec et al. 2000), it is more common on the south-eastern fringes of the Bohemian Massif in the area to the south-west of the city of Brno. These transitional forests types on the fringes of the Bohemian Massif were recognized by Neuhäusl & Neuhäuslová (1968) but assigned to the Hercynian association as a separate geographical variant.

Polonian oak-hornbeam forests: a phantom of the traditional Czech vegetation classification?

The most striking differences between the results of the cluster analysis and traditional associations were found for the Polonian oak-hornbeam forests of the association *Tilio-Carpinetum*. Neuhäuslová (in Moravec et al. 2000) and previous treatments (Neuhäusl & Neuhäuslová-Novotná 1972, Neuhäusl in Moravec et al. 1982, Neuhäuslová in Neuhäuslová et al. 1998) assigned this association to the oak-hornbeam forests growing on soft sedimentary rocks in low-altitude basins and valleys of northern Moravia and Silesia, as well as on hard rocks on the fringes of the Bohemian Massif in the same area. Cluster analysis, however, suggests that oak-hornbeam forests on hard rocks in that area (*Tilio-Carpinetum luzuletosum*) belong to the Hercynian group. Clusters V and VI are mainly separated due to wetter soils, but also show a remarkable geographical pattern. Besides the low-altitude areas of northern Moravia and Silesia, forests belonging to these clusters are frequently found on Cretaceous sediments in eastern Bohemia and occasionally other sites in Bohemia. Neuhäuslová (in Moravec et al. 2000) assigned wet Bohemian oak-hornbeam forests to the subassociations *Melampyro nemorosi-Carpinetum stachyetosum* and *molinietosum arundinaceae*, despite their similarity to the northern Moravian and Silesian forests on wet soils, which she assigned to *Tilio-Carpinetum.* Several stands of *Carici pilosae-Carpinetum primuletosum elatioris* (sensu Neuhäuslová in Moravec et al. 2000) growing on wet soils in northern Moravia and Silesia were also assigned to clusters V and VI. This suggests that there is no geographically delimited association of Polonian oak-hornbeam forests in the Czech Republic. Most of the stands that were assigned to the *Tilio-Carpinetum* in the traditional classification (Neuhäuslová in Moravec et al. 2000) belong to an ecologically delimited type growing on wet soil that is transitional to either floodplain forests (cluster V) or wet acidophilous oak forests (cluster VI).

In Traczyk's (1962) original description and recent Polish literature (Matuszkiewicz 2001), the *Tilio-Carpinetum* association concept differs from that used in the traditional Czech classification (Neuhäuslová in Moravec et al. 2000). As shown in Table 4, the *Tilio-Carpinetum* association in its original delimitation shares some diagnostic species with *Carici pilosae-Carpinetum*, as described by Neuhäusl & Neuhäuslová-Novotná (1964) and accepted in recent treatments of Czech forest vegetation (Neuhäuslová in Moravec et al. 2000). In particular the variant growing in the Malopolska Uplands, an area adjacent to northeastern Moravia, is very similar to the Carpathian *Carici pilosae-Carpinetum* through the occurrence of *Abies alba, Fagus sylvatica* and *Euphorbia amygdaloides.* The more northern Mazovian and Mazurian variants have progressively fewer southern and montane species. However, Polish authors do not consider the *Tilio-Carpinetum* as an association of wet habitats; they do include some wetter types but most stands are on mesic soils. Generally, they characterize this association by subcontinental species of eastern central and southeastern European mountain ranges, which are also widely distributed in the nemoral zone of eastern Europe, e.g. *Carex pilosa, Euonymus verrucosa* and *Galium schultesii.* All of these species are included in the original description of the *Carici pilosae-Carpinetum* (Neuhäusl & Neuhäuslová-Novotná 1964). This suggests that the *Tilio-Carpinetum* of Polish authors and the *Carici pilosae-Carpinetum* of Czech authors are overlapping, if not identical associations. If we accept that they are synonymous, the older valid name, *Tilio-Carpinetum*, would have to be accepted for Czech and Slovak Carpathian oak-hornbeam forests with *Carex pilosa.* By contrast, if we accepted these associations as two separate vegetation units, the geographical dividing line would be most probably situated north of the Malopolska Uplands, because of high similarity of stands in the Carpathians and the Malopolska Upland. Such a division would, however, require a detailed revision of the current Polish classification (Matuszkiewicz 2001), which follows the concept outlined by Traczyk (1962).

The ecologically delimited type of wet oak-hornbeam forests in northern Moravia, Silesia and eastern Bohemia (clusters V and VI) does not easily fit the concept of geographically delimited associations. However, it is similar to the association *Stellario holosteae-Carpinetum*, proposed by Oberdorfer (1957) for (sub)atlantic, mostly wet oak-hornbeam forests. This association is reported from Germany (Pott 1995, Rennwald 2000, Schubert et al. 2001) and northwestern Poland (Matuszkiewicz 2001), where it includes forests growing on both nutrient-rich and nutrient-poor soils, which correspond to clusters

Table 4. – Comparison of the diagnostic species of the *Carici pilosae-Carpinetum* and *Tilio-Carpinetum* associations in their original diagnoses (Neuhäusl & Neuhäuslová-Novotná 1964, Traczyk 1962) and the recent synthetic treatments of Czech and Polish forest vegetation (Moravec et al. 1982, 2000, Matuszkiewicz 2001). + means that the authors indicate the species as character, differential or diagnostic; (+) means that the species is reported only for the variant of *Tilio-Carpinetum* from the Malopolska Uplands. *Fagus sylvatica* in Neuhäusl & Neuhäuslová-Novotná (1964) was erroneously reported as *F. moesiaca.*

	Carici pilosae-Carpinetum		*Tilio-Carpinetum*		
	Neuhäusl & Neuhäuslová-Novotná (1964)	Neuhäusl (in Moravec et al. 1982), Neuhäuslová (in Moravec et al. 2000)	Traczyk (1962)	Matuszkiewicz (2001)	Neuhäusl (in Moravec et al. 1982), Neuhäuslová (in Moravec et al. 2000)
Carex pilosa	+	+	+	+	.
Euphorbia amygdaloides	+	+	(+)	(+)	.
Fagus sylvatica	+	+	(+)	(+)	.
Glechoma hirsuta	+	.	.	.	.
Dentaria bulbifera	.	+	.	.	.
Symphytum tuberosum	.	+	.	.	.
Galium schultesii	.	.	+	+	.
Euonymus verrucosus	.	.	+	+	.
Ranunculus cassubicus	.	.	+	+	.
Isopyrum thalictroides	.	.	+	.	.
Cruciata glabra	.	.	.	+	.
Abies alba	.	.	(+)	(+)	.
Acer pseudoplatanus	.	.	(+)	.	.
Populus tremula	.	.	.	.	+
Sorbus aucuparia	.	.	.	.	+

V and VI, respectively. While in the moister northwestern areas of Central Europe such forests are widespread on different soil types, in the more continental climate of the Czech Republic they are restricted to soils kept moist by ground water. If we accept that Czech oak-hornbeam forests on wet soils belong to the *Stellario holosteae-Carpinetum* association, this would link the geographical and ecological approach to vegetation classification: it would be a geographically-based association of northwestern Central Europe, which beyond the limits of its continuous distribution is confined to habitats that resemble the environments in the centre of its distribution. Such a pattern corresponds to the classic "rule of relative habitat constancy" (Walter & Walter 1953).

No support found for local associations

Two associations of the traditional classification with a locally restricted distribution in the Czech Republic, *Stellario-Tilietum* and *Tilio-Betuletum*, were not identified by the cluster analysis. This was not an artifact of the small number of relevés of these two associations in the data set, because neither of them formed a coherent group at a lower level of cluster hierarchy. Instead, the relevés assigned to these associations in Neuhäuslová's (in Moravec et al. 2000) classification were divided among clusters I, II and V (Table 3). Fidelity calculations for the relevé groups of the traditional associations (Table 1) indicate that the diagnostic species of the former association are mainly light-demanding calcifuges and of the latter species that indicate disturbance and eutrophication. Both of these species groups probably indicate recent human-made disturbance rather than a stable environment. These results provide poor support for the *Stellario-Tilietum* and *Tilio-Betuletum* associations. The *Stellario-Tilietum* association was described to include *Carpinion* stands dominated by *Tilia cordata* and *Quercus robur* growing in a restricted area of southern Bohemia where *Carpinus betulus* is absent due to migration constraints (Moravec 1964). However, it is questionable if the absence of a single, yet potentially dominant species, is sufficient grounds for separation of an association. An association delimited in this way is impossible to differentiate from the *Melampyro nemorosi-Carpinetum* stands that lack *Carpinus betulus*, but occur within the geographical range of this species.

Conclusions

Our analysis suggests that the patterns of floristic variation in Czech oak-hornbeam forests are controlled both by phytogeographical and environmental factors. Four major types, corresponding to phytosociological associations, can be distinguished: (1) Hercynian, widespread in the Bohemian Massif (*Melampyro nemorosi-Carpinetum* Passarge 1962 or *Galio sylvatici-Carpinetum* Oberdorfer 1957); (2) Pannonian, confined to southern Moravia (*Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová ex Neuhäuslová-Novotná 1964); (3) Carpathian, common in eastern and central Moravia (*Tilio cordatae-Carpinetum* Traczyk 1962 or *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964); (4) Wet habitat type, occurring mainly on soft bedrocks in eastern Bohemia, northern Moravia and Silesia (*Stellario holosteae-Carpinetum* Oberdorfer 1957).

The Polonian association, fostered in the traditional Czech phytosociological literature, is not supported by the data and should be abandoned. The same is true of the two local associations, *Stellario-Tilietum* and *Tilio-Betuletum*. Unlike the traditional classification, in which geographical boundaries between associations were drawn rather arbitrarily based on geographical land classification, the current analysis suggests a delimitation of vegetation units that follows the most important discontinuities in species composition and permits some overlap in geographical distribution that occurs due to the effects of specific local environmental features. By linking and reconciling the geographical and ecological approaches to the vegetation classification, we arrive at a more natural classification, which is easier to use in habitat mapping projects.

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Souhrn

Klasifikace vegetace by měla odrážet hlavní ekologické nebo fytogeografické gradienty, které podmiňují variabilitu v druhovém složení porostů. Význam jednotlivých gradientů je však závislý na geografickém rozsahu studia. Lokálně definované jednotky odrážejí hlavně lokální gradienty, jako jsou disturbance a půdní podmínky, zatímco jednotky definované v širších oblastech odrážejí rozdíly v geografickém rozšíření druhů, které je výsledkem proměnlivosti makroklimatu a evoluční a migrační historie druhů ve větších územích.

Příkladem fytocenologické klasifikace vycházející ze širokého geografického pojetí jsou dubohabrové lesy svazu *Carpinion*, které jsou v České republice tradičně rozdělovány na pět geograficky vikarizujících skupin (např. Neuhäuslová in Moravec et al. 2000): (1) hercynské dubohabřiny (*Melampyro nemorosi-Carpinetum*), (2) panonské dubohabřiny (*Primulo veris-Carpinetum*), (3) karpatské dubohabřiny (*Carici pilosae-Carpinetum*), (4) polonské dubohabřiny (*Tilio-Carpinetum*) a (5) jihočeské dubolipové háje (*Stellario-Tilietum*) s absencí habru. Poněkud nekonzistentně je součástí této jinak geografické klasifikace také šestá asociace, *Tilio-Betuletum*, která je vymezena ekologicky, specifickými vlastnostmi půd. Cílem naší studie bylo zjistit, na základě numerické analýzy geograficky stratifikovaného souboru 601 fytocenologických snímků, zda variabilita druhového složení dubohabřin České republiky odráží tradiční geograficky pojatou fytocenologickou klasifikaci a jaké jsou hranice, diagnostické druhy a ekologické nároky vymezených typů.

Výsledky potvrdily, že variabilita dubohabřin je do značné míry podmíněná geograficky, ale velmi významný je také gradient od mezických po vlhká stanoviště. Tři ze čtyř velkých a tradičně geograficky pojatých skupin, tj. hercynské, panonské a karpatské dubohabřiny, mají opodstatnění pro klasifikaci dubohabrových lesů České republiky. Tradiční jednotka polonských dubohabřin však není příliš dobře vyhraněná jako geografická skupina; spíš jde o klimaticko-edaficky vymezenou jednotku vlhkých dubohabřin, která má centrum rozšíření na severní Moravě, ve Slezsku a ve východních Čechách a floristickým složením je blízká zčásti k lužním lesům, zčásti k vlhkým acidofilním doubravám. Asociace *Stellario-Tilietum* a *Tilio-Betuletum*, které byly tradičně považovány za lokální asociace některých částí Českého masívu, nemají na základě numerické analýzy opodstatnění, protože nevybočují z rozsahu variability ostatních hercynských dubohabřin. Na základě výsledků numerické klasifikace navrhujeme rozlišovat následující čtyři asociace: (1) Hercynská asociace, rozšířená v Českém masivu, odpovídající asociaci *Melampyro nemorosi-Carpinetum* Passarge 1962*,* případně *Galio sylvatici-Carpinetum* Oberdorfer 1957. (2) Panonská asociace vázaná na jižní Moravu (*Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová ex Neuhäuslová-Novotná 1964). (3) Karpatská asociace, hojná na východní a střední Moravě, tradičně označovaná jako *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964, jejíž správné jméno je však možná *Tilio cordatae-Carpinetum* Traczyk 1962. (4) Asociace vlhkých stanovišť, rozšířená zejména na měkkých sedimentech východních Čech a severní Moravy a Slezska, která je pravděpodobně totožná s atlantskou asociací *Stellario holosteae-Carpinetum* Oberdorfer 1957.

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