Phytocoenologia	**34** (4)	551–567	Berlin–Stuttgart, December 8, 2004

Diversity of hay meadows in the Czech Republic: major types and environmental gradients

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with 3 figures and 4 tables

Abstract. A stratified data set of 3102 relevés of meadows and mesic pastures of the Czech Republic was analysed by detrended correspondence analysis and cluster analysis. Major gradients and clusters were interpreted using Ellenberg indicator values. The major gradient in species composition was associated with soil moisture and the second most important gradient with available nutrients. Clusters proposed by numerical classification reproduced some of the traditional phytosociological alliances, namely Arrhenatherion, Molinion and Polygono-Trisetion, while some other alliances were less clearly differentiated (e.g. Alopecurion, Cnidion and Cynosurion). Wet meadows of the Calthion alliance were divided among several clusters, which corresponded to the main associations recognized in traditional phytosociological literature. This patterns suggests that wet meadows have a higher beta-diversity than mesic meadows. We tested this hypothesis by calculating mean pair-wise Sörensen dissimilarity for bootstrap subsamples of meadow relevés for partitions of the moisture gradient, and confirmed that beta-diversity of meadows increases with increasing soil moisture. In traditional phytosociological literature, this fact is reflected by higher numbers of associations distinguished within wet meadows than in mesic meadows.

Keywords: beta-diversity, classification, Ellenberg indicator values, grassland vegetation, ordination, phytosociology.

Introduction

Hay meadows are the most widespread type of semi-natural vegetation in Central Europe. Due to socio-economic changes in agriculture, which took place in the second half of the 20th century, areas of species-rich meadows have been increasingly reduced by abandonment of some meadow tracts and introduction of intensive management systems with massive application of artificial fertilizers in other tracts (ELLENBERG 1996, LINUSSON et al. 1998, DUPRÉ & DIEKMANN 2001, JENSEN et al. 2001). Hay meadow ecosystems have therefore appeared in the focus of nature conservation authorities and many applied projects have been initiated with the aim of creating meadow inventories or re-establishing traditional management (PRACH 1996, DZWONKO & LOSTER 1998, JOYCE & WADE 1999, ŠEFFER & STANOVÁ 1999, KRAHULEC et al. 2001, SEDLÁKOVÁ & FIALA 2001, VECRIN et al. 2002, LOSVIK & AUSTAD 2002).

Nature conservation survey projects are in need of a robust classification of meadow vegetation. Phytosociological classification is perfectly suited

DOI: 10.1127/0340-269X/2004/0034-0551 0340-269X/04/0034-0551 $ 4.25
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for this purpose, as it is based on floristic composition and thus directly linked to biodiversity. In Central Europe, there is a long tradition of phytosociological study of meadows (Dierschke 1995), which has resulted in a general agreement as to the major types of meadow vegetation (Oberdorfer 1993, Ellmauer & Mucina 1993, Ellmauer 1994, Dierschke 1995, 1997, Blažková & Balátová in Moravec et al. 1995, Zuidhoff et al. 1996, Kučera & Šumberová 2001). The main environmental gradient responsible for variation in species composition of Central European meadows is moisture, as recognized in "ecograms" of Ellenberg (1996). This gradient is used for the primary division of meadows in the classification studies. Secondary gradients include altitude, nutrient availability, soil pH and water fluctuations. At the level of phytosociological alliances, the major types of meadow vegetation include mesic meadows of low altitudes (Arrhenatherion), manured pastures of low altitudes (Cynosurion), mesic meadows of montane belt (Polygono-Trisetion), mesic meadows of subalpine belt (Poion alpinae), manured wet meadows (Calthion) and unmanured wet meadows (Molinion). Less agreement has been achieved upon justification of separate alliances for tall-forb vegetation replacing wet meadows after abandonment (Filipendulion, Veronico longifoliae-Lysimachion vulgaris) and for wet meadows of lowland river floodplains (Alopecurion, Cnidion). Even less agreement is found at the association level, where delimitations of individual syntaxa often greatly vary among different authors. It is striking that wet meadows, namely those of the Calthion alliance, are usually divided into more associations than mesic meadows in phytosociological surveys (Balátová-Tuláčková 1984).

Most of the phytosociological classifications of Central European meadow vegetation produced so far have been largely based on expert knowledge, and so was the estimation of main environmental gradients (Ellenberg 1996). Some classification exercises involved manual editing of synoptic tables taken from individual studies and some others did not involve data analysis at all. It is therefore important to test whether the major types and gradients recognized in the expert-based phytosociological studies can also be recognized by numerical analysis of large data sets of vegetation relevés (Bruelheide & Chytrý 2000, Studer-Ehrensberger 2000). In this study, we use a large data set of meadow vegetation relevés from the Czech Republic and analyse it with respect to the following objectives: (1) to reveal the major environmental gradients responsible for variation in floristic composition of meadow vegetation; (2) to establish the major vegetation types resulting from numerical classification and to compare them with the major types recognized in the traditional expert-based classification; (3) to test whether beta-diversity of wet meadows is higher than of mesic meadows, a pattern which would justify finer differentiation of wet meadows at the association level, as accepted in phytosociological tradition.

Materials and methods

The basic source of the data were relevés of the Molinio-Arrhenatheretea class from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). Relevés for the current analysis were selected according to their assignment to this class by the original authors. Relevés of extreme size (i.e. < 4 m^2 or > 100 m^2), relevés without recorded bryophytes and relevés lacking sufficiently accurate indication of locality were deleted. With respect to geographical coverage of the national territory, some areas appeared to be oversampled while there were gaps in some other areas. Possible negative effects of spatial autocorrelation resulting from this pattern were therefore reduced, although not entirely eliminated, by performing a geographically stratified selection of relevés from the database. Only one relevé of each association (according to original author's assignment) per grid square of 1.25 longitudinal × 0.75 latitudinal minute (ca. 1.5 × 1.4 km) was selected at random. This selection yielded 3102 relevés which were used for the analysis. Species cover values recorded on ordinal scales (mostly Braun-Blanquet or Domin) were replaced by percentages and square-root transformed.

Major gradients in species composition of meadow vegetation were analysed by ordination of this data set, using detrended correspondence analysis (DCA) from the CANOCO 4.5 package (ter Braak & Šmilauer 2002). For ecological interpretation of the ordination axes, average Ellenberg indicator values (Ellenberg et al. 1992) for relevés were plotted onto DCA ordination diagram as supplementary environmental data.

Classification of the data set was performed by cluster analysis in the program PC-ORD 4 (McCune & Mefford 1999), using relative Euclidean (chord) distance as a resemblance measure and flexible beta group linkage method with parameter $\beta = -0.3$. Two classifications were done. The first classification used all 3102 relevés as input data. In this classification, ten clusters at the highest level of classification hierarchy were accepted, because this number roughly corresponds to the number of alliances traditionally recognized in phytosociological literature. The second classification was done with 900 relevés, including 300 randomly selected relevés from each of the three most common alliances, Calthion, Arrhenatherion and Molinion. Assignment of relevés to the alliances followed the expert opinion of the original authors of these relevés. This second classification was done in order to evaluate validity of the first classification, because the larger data set (3102 relevés) contained unequal numbers of relevés from different habitats. For example, wet meadows, assigned by their original authors to the Calthion alliance, were represented by 53 % of relevés in that data set, and this fact could result in a disproportionately more detailed division of the Calthion meadows in the cluster analysis dendrograms of the first classification.

Diagnostic species for the clusters were determined *a posteriori*, by calculating the fidelity of each species to each cluster, using the phi coefficient of association (Sokal & Rohlf 1995, Chytrý et al. 2002) in the program

JUICE 6.1 (Tichý 2002). In these calculations, each cluster was compared with the rest of the relevés in the data set, which were taken as a single undivided group. In this way, partitioning of the rest of the data set did not influence fidelity of species to the target cluster. The threshold Φ value for a species to be considered as diagnostic was set to 0.20. The results of the classification were summarized in a synoptic table, in which both percentage species frequencies (constancies) and Φ values (fidelities) were shown, and diagnostic species were ranked by decreasing fidelity, i.e. by decreasing Φ value (Chytrý et al. 2002).

Syntaxonomical interpretation of each cluster in terms of the standard national vegetation classification of the Czech Republic (Moravec et al. 1995) was made, using the list of diagnostic species for alliances of this classification, as produced by Chytrý & Tichý (2003) on the basis of statistical calculations applied to a large data set extracted from the Czech National Phytosociological Database. This list represents the collective ideas of Czech vegetation scientists about delimitation of alliances and provides statistically reliable sets of diagnostic species for each alliance. Diagnostic species of each cluster were compared with diagnostic species from the national list, which enabled interpretation of the clusters in terms of phytosociological alliances. As different alliances contained different numbers of diagnostic species and also our clusters included different numbers of diagnostic species, we standardized this comparison by calculating Sörensen similarity index between each group of diagnostic species for a phytosociological alliance and each group of diagnostic species for one of the clusters identified in the current analysis:

$$S = 2a/(2a + b + c),$$

where a is the number of shared (diagnostic) species, b and c are numbers of species present in one of the two groups of diagnostic species but absent in the other. In this paper, values of the Sörensen coefficient were multiplied by 100, thus the range is from 0 to 100.

For further interpretation of the clusters, average Ellenberg indicator values for relevés of each cluster were subjected to principal components analysis (PCA from CANOCO 4.5; ter Braak & Šmilauer 2002) to show the ecological relationships among these clusters.

In order to compare beta-diversity between wet and mesic meadows, we divided the relevés into groups according to average Ellenberg moisture value. The groups were defined by Ellenberg value intervals 3.0–4.9, 5.0–5.9, 6.0–6.9, 7.0–7.9, and 8.0–9.4. The extreme values 3.0 and 9.4 were the lowest and the highest values found in the data set. Relevés with values 3.0–4.0 or 9.0–9.4 were few and therefore they were merged with adjacent categories. For each of these relevé groups, we calculated beta-diversity as the mean Sörensen dissimilarity between all pairs of relevés (100 – S, where S is Sörensen similarity; Magurran 1988, Koleff et al. 2003), using the JUICE 6.1 program (Tichý 2002). Confidence intervals for beta-diversity were obtained from 100 bootstrap samples (Efron 1979) taken from relevés of each interval.

Nomenclature follows Kubát et al. (2002) for vascular plants, Frey et al. (1995) for bryophytes and Moravec et al. (1995) for syntaxa.

Results

Fig. 1 shows species scatter plot of detrended correspondence analysis based on individual relevés (eigenvalues of the first two axes are 0.514 and 0.314). Ellenberg indicator values, plotted *a posteriori* onto ordination diagram, show that the major variation in species composition of the meadows corresponds to two major gradients, the moisture gradient and the gradient of soil nutrient availability, the latter combined with the soil reaction gradient.

Clusters distinguished by the classification of the data set of 3102 relevés are shown in Table 1, along with their diagnostic species. Using the externally defined list of diagnostic species (Chytrý & Tichý 2003), there is a clear interpretation for clusters 4, 5, 6 and 7, which in turn represent vegetation of the alliances Molinion, Calthion, Polygono-Trisetion and Arrhenatherion (Table 2). Cluster 8 is transitional between the alliances Arrhenatherion, Polygono-Trisetion and Cynosurion. Clusters 2, 3, 9 and 10 possess a less clear interpretation in terms of diagnostic species, but all of them are most closely related to the Calthion alliance. They are mainly defined by dominants, including *Cirsium rivulare* in cluster 2, *Cirsium oleraceum* and *Carex cespitosa* in cluster 3, *Scirpus sylvaticus* in cluster 9 and *Filipendula ulmaria* in cluster 10. Cluster 1 is characterized by species of lowland alluvial meadows, but is poorly characterized in terms of both diagnostic and dominant species.

Individual clusters strikingly differ in their relationships to major ecological factors. The most important factors, as revealed by principal components analysis of the mean Ellenberg indicator values and clusters (eigenvalues of the first two axes are 0.615 and 0.326), are identical with those identified in DCA ordination of individual relevés, i.e. moisture, soil reaction and nutrients (Fig. 2). Clusters 10, 9, 2 and 3, i.e. monodominant grasslands of the Calthion alliance, occupy the wettest sites, while clusters 7 and 8, related to the Arrhenatherion alliance are confined to the driest sites. The gradients of soil reaction and nutrients are mutually correlated, with clusters 1, 2, 3, 7 and 10 associated with high values and clusters 4, 5 and 6 with low values.

The second cluster analysis with equal numbers of relevés originally assigned to Calthion, Arrhenatherion and Molinion resulted in ten clusters, of which five corresponded to Calthion, three to Arrhenatherion and two to Molinion (results are not shown here).

Beta-diversity varied along the moisture gradient (Fig. 3). Mean Sörensen dissimilarity was comparatively low for relevés with an average Ellenberg moisture value lower than 6.0, i.e. for relevés from mesic sites, and increased towards wetter sites.

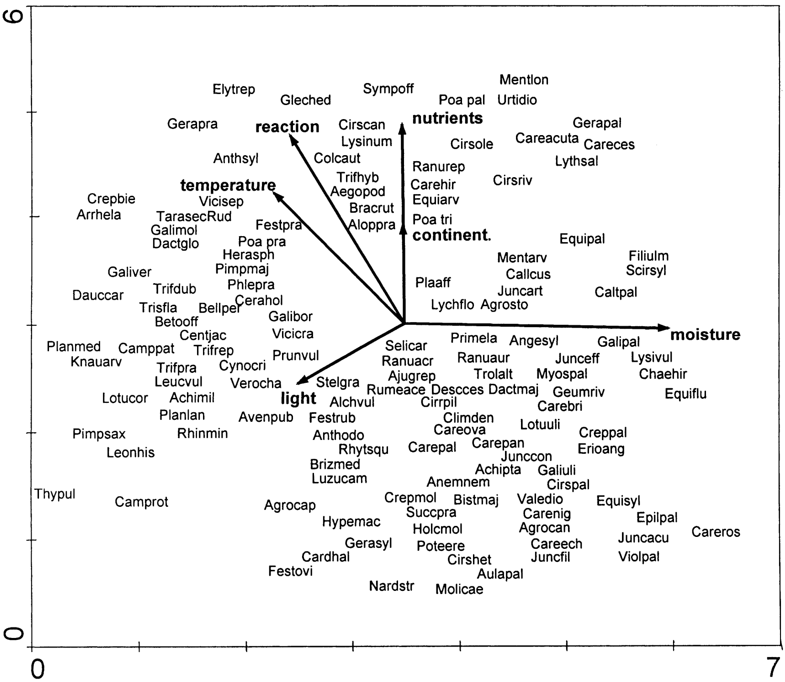
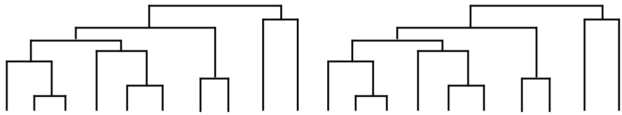


Fig. 1. Detrended correspondence analysis (DCA) ordination diagram of meadow data set. Species list: *Achillea millefolium* s. lat., *A. ptarmica*, *Aegopodium podagraria*, *Agrostis canina*, *A. capillaris*, *A. stolonifera*, *Ajuga reptans*, *Alchemilla vulgaris* s. lat., *Alopecurus pratensis*, *Anemone nemorosa*, *Angelica sylvestris*, *Anthoxanthum odoratum* s. lat., *Anthriscus sylvestris*, *Arrhenatherum elatius*, *Aulacomnium palustre*, *Avenula pubescens*, *Bellis perennis*, *Betonica officinalis*, *Bistorta major*, *Brachythecium rutabulum*, *Briza media*, *Calliergonella cuspidata*, *Caltha palustris*, *Campanula patula*, *C. rotundifolia* s. lat., *Cardaminopsis halleri*, *Carex acuta*, *C. brizoides*, *C. cespitosa*, *C. echinata*, *C. hirta*, *C. nigra*, *C. ovalis*, *C. pallescens*, *C. panicea*, *C. rostrata*, *Centaurea jacea*, *Cerastium holosteoides* ssp. *triviale*, *Chaerophyllum hirsutum*, *Cirriphyllum piliferum*, *Cirsium canum*, *C. heterophyllum*, *C. oleraceum*, *C. palustre*, *C. rivulare*, *Climacium dendroides*, *Colchicum autumnale*, *Crepis biennis*, *C. mollis*, *C. paludosa*, *Cynosurus cristatus*, *Dactylis glomerata*, *Dactylorhiza majalis*, *Daucus carota* ssp. *carota*, *Deschampsia cespitosa*, *Elytrigia repens*, *Epilobium palustre*, *Equisetum arvense*, *E. fluviatile*, *E. palustre*, *E. sylvaticum*, *Eriophorum angustifolium*, *Festuca ovina*, *F. pratensis*, *F. rubra* s. lat., *Filipendula ulmaria*, *Galium boreale* ssp. *boreale*, *G. mollugo*, *G. palustre* s. lat., *G. uliginosum*, *G. verum* s. lat., *Geranium palustre*, *G. pratense*, *G. sylvaticum*, *Geum rivale*, *Glechoma hederacea* s. lat., *Heracleum sphondylium*, *Holcus mollis*, *Hypericum maculatum*, *Juncus acutiflorus*, *J. articulatus*, *J. conglomeratus*, *J. effusus*, *J. filiformis*, *Knautia arvensis* s. lat., *Leontodon hispidus*, *Leucanthemum vulgare* s. lat., *Lotus corniculatus*, *L. uliginosus*, *Luzula campestris* s. lat., *Lychnis flos-cuculi*, *Lysimachia nummularia*, *L. vulgaris*, *Lythrum salicaria*, *Mentha arvensis*, *M. longifolia*, *Molinia caerulea* s. lat., *Myosotis palustris* s. lat., *Nardus stricta*, *Phleum pratense* s. lat., *Pimpinella major*, *P. saxifraga*, *Plagiomnium affine* s. lat., *Plantago lanceolata*, *P. media*, *Poa palustris*, *P. pratensis* s. lat., *P. trivialis*, *Potentilla erecta*, *Primula elatior*, *Prunella vulgaris*, *Ranunculus acris*, *R. auricomus* s. lat., *R. repens*, *Rhinanthus minor*, *Rhytidiadelphus squarrosus*, *Rumex acetosa*, *Scirpus sylvaticus*, *Selinum carvifolia*, *Stellaria graminea*, *Succisa pratensis*, *Symphytum officinale* s. lat., *Taraxacum* sect. *Ruderalia*, *Thymus pulegioides*, *Trifolium dubium*, *T. hybridum*, *T. pratense*, *T. repens*, *Trisetum flavescens*, *Trollius altissimus*, *Urtica dioica*, *Valeriana dioica*, *Veronica chamaedrys* s. lat., *Vicia cracca*, *V. sepium*, *Viola palustris*.

Table 1. Synoptic table produced by cluster analysis, with the corresponding dendrogram. Values are percentage frequencies in the left-hand part of the table and fidelities (Φ values multiplied by 1000) in the right-hand part. Diagnostic species for the clusters (defined as those with $\Phi > 0.20$) are shaded and ranked by decreasing Φ values, i.e. decreasing fidelities to each cluster. Negative Φ values are not shown.



Cluster number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Number of relevés	**475**	**268**	**130**	**435**	**410**	**85**	**360**	**384**	**265**	**290**	**475**	**268**	**130**	**435**	**410**	**85**	**360**	**384**	**265**	**290**
Trifolium hybridum	28	5	14	15	6	.	6	3	5	1	265	.	30	70	.	.	.	.	.	.
Phalaris arundinacea	17	.	5	1	3	1	1	1	4	8	258	.	.	.	.	.	.	.	.	48
Carex vulpina	14	3	2	3	2	.	.	.	3	1	246	.	.	.	.	.	.	.	.	.
Symphytum officinale s. lat.	21	7	11	4	1	.	8	1	6	7	239	.	31	.	.	.	.	.	.	.
Ranunculus repens	63	41	55	30	41	14	21	22	46	16	237	32	85	.	39	.	.	.	64	.
Rumex crispus	17	7	6	1	1	.	2	3	8	1	231	23	10	.	.	.	.	.	34	.
Cirsium canum	26	12	26	11	2	.	10	1	6	4	230	18	115	11	.	.	.	.	.	.
Cirsium rivulare	4	69	8	6	5	.	.	.	22	9	.	565	.	.	.	.	.	.	102	.
Mentha longifolia	2	34	7	1	1	.	1	.	10	4	.	403	18	.	.	.	.	.	68	.
Juncus inflexus	1	26	3	2	1	.	1	.	6	2	.	382	.	.	.	.	.	.	41	.
Eupatorium cannabinum	1	17	2	1	1	.	.	.	2	1	.	325	.	.	.	.	.	.	.	.
Cruciata glabra	1	29	5	4	2	.	1	7	5	2	.	318	.	.	.	.	.	27	.	.
Epipactis palustris	1	12	.	1	1	.	.	.	.	1	.	310	.	.	.	.	.	.	.	.
Campylium stellatum s. lat.	1	15	.	1	1	.	1	.	2	.	.	305	.	.	.	.	.	.	.	.
Carex flava	1	21	2	4	3	.	.	1	3	1	.	293	.	12	.	.	.	.	.	.
Brachythecium rivulare	1	18	4	1	2	.	.	.	6	2	.	277	12	.	.	.	.	.	51	.
Eriophorum latifolium	1	15	.	2	3	.	.	.	1	1	.	275	.	.	33	.	.	.	.	.
Calliergonella cuspidata	11	49	30	19	27	2	1	2	21	7	.	270	78	29	115	.	.	.	38	.
Carex flacca	1	20	2	6	3	.	1	1	1	1	.	270	.	63	.	.	.	.	.	.
Cratoneuron commutatum	.	9	.	1	.	.	.	.	.	.	.	267	.	.	.	.	.	.	.	.
Cratoneuron filicinum	.	12	2	1	1	.	.	.	3	1	.	266	.	.	.	.	.	.	29	.
Tussilago farfara	1	15	3	1	1	.	2	.	5	1	.	260	.	.	.	.	.	.	43	.
Bryum pseudotriquetrum	1	18	3	2	9	1	.	.	2	.	.	252	.	.	110	.	.	.	.	.
Cardamine amara	3	20	5	.	2	.	.	.	15	7	.	224	.	.	.	.	.	.	159	36
Valeriana simplicifolia	1	11	1	1	1	.	.	.	4	2	.	216	.	.	.	.	.	.	58	.
Carex paniculata	.	7	.	1	1	.	.	.	.	1	.	213	.	.	.	.	.	.	.	.
Carex tomentosa	1	10	1	3	1	.	.	1	1	1	.	209	.	50	.	.	.	.	.	.
Carex cespitosa	4	3	42	1	2	.	.	.	2	4	.	.	429	.	.	.	.	.	.	.
Cirsium oleraceum	21	22	75	9	9	.	6	1	18	34	55	49	333	.	.	.	.	.	20	157
Succisa pratensis	9	12	5	52	18	5	1	3	3	1	.	.	.	463	55	.	.	.	.	.
Molinia caerulea s. lat.	6	8	8	47	18	1	1	1	2	11	.	.	.	424	63	.	.	.	.	.
Nardus stricta	4	1	1	43	24	13	1	18	1	1	.	.	.	369	137	.	.	62	.	.
Potentilla erecta	10	37	6	59	47	42	4	27	13	5	.	74	.	307	186	63	.	.	.	.
Luzula campestris s. lat.	16	15	15	68	50	35	37	55	7	2	.	.	.	297	135	.	29	178	.	.
Briza media	11	33	18	60	40	32	28	44	5	1	.	25	.	278	95	10	.	121	.	.
Carex pallescens	9	19	8	39	23	35	2	8	8	2	.	38	.	275	89	95	.	.	.	.
Festuca ovina	1	1	.	19	2	5	6	5	1	.	.	.	.	273	.	.	18	.	.	.
Scorzonera humilis	2	1	.	14	4	4	.	1	.	1	.	.	.	259	18	.	.	.	.	.
Sanguisorba officinalis	56	31	48	74	46	36	35	17	35	36	110	.	21	251	23	.	.	.	.	.
Galium boreale ssp. *boreale*	11	4	2	23	2	.	7	2	1	4	71	.	.	250	.	.	.	.	.	.
Holcus lanatus	55	44	56	79	64	12	48	35	32	20	50	.	30	244	117	.	.	.	.	.
Centaurea jacea	23	20	7	42	7	1	38	26	1	1	25	.	.	218	.	.	164	55	.	.
Viola canina	1	1	1	16	1	1	1	15	.	.	.	.	.	216	.	.	.	179	.	.
Climacium dendroides	15	35	30	45	40	11	9	8	20	8	.	91	35	214	156	.	.	.	.	.
Danthonia decumbens	2	2	.	13	3	.	1	4	.	.	.	.	.	214	.	.	.	14	.	.
Calluna vulgaris	1	.	.	7	1	.	.	1	.	.	.	.	.	212	.	.	.	.	.	.
Deschampsia cespitosa	53	44	46	71	70	68	13	31	36	31	59	.	.	200	184	74	.	.	.	.
Betonica officinalis	6	2	2	16	1	.	9	5	.	.	10	.	.	200	.	.	61	.	.	.
Carex panicea	18	48	38	59	60	24	1	2	25	10	.	131	44	269	268	.	.	.	.	.
Aulacomnium palustre	2	3	2	21	24	.	.	1	2	1	.	.	.	220	258	.	.	.	.	.
Anthoxanthum odoratum s. lat.	39	41	33	77	61	34	54	80	22	3	.	.	.	226	95	.	37	232	.	.
Carex nigra	21	35	22	49	80	28	.	2	44	18	.	27	.	156	415	.	.	.	84	.
Juncus filiformis	5	5	7	12	44	25	.	1	14	2	.	.	.	.	408	72	.	.	27	.
Agrostis canina	7	11	5	19	45	13	1	1	12	3	.	.	.	79	377	.	.	.	.	.
Cirsium palustre	23	16	34	51	79	36	1	7	50	36	.	.	.	152	372	10	.	.	108	18
Galium uliginosum	22	18	54	48	76	76	1	3	44	50	.	.	83	108	332	146	.	.	56	103
Viola palustris	3	5	1	9	36	26	.	1	22	11	.	.	.	.	321	83	.	.	107	.
Valeriana dioica	5	17	20	26	43	21	1	1	11	6	.	21	34	129	318	33	.	.	.	.
Epilobium palustre	3	7	3	3	28	6	1	.	14	6	.	.	.	.	311	.	.	.	82	.
Eriophorum angustifolium	2	18	5	5	27	2	.	.	4	1	.	137	.	.	302	.	.	.	.	.

Table 1. (cont.)

Cluster number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Number of relevés	**475**	**268**	**130**	**435**	**410**	**85**	**360**	**384**	**265**	**290**	**475**	**268**	**130**	**435**	**410**	**85**	**360**	**384**	**265**	**290**
Carex echinata	3	10	2	8	26	2	.	1	9	1	.	38	.	14	291	.	.	.	30	.
Juncus conglomeratus	10	23	18	23	40	15	.	1	15	9	.	63	18	90	261	.	.	.	.	.
Mentha x *verticillata*	5	3	8	5	20	1	.	1	11	2	.	.	16	.	235	.	.	.	66	.
Lotus uliginosus	11	10	17	21	35	11	1	1	20	14	.	.	15	80	230	.	.	.	52	.
Carex canescens	1	4	3	4	16	.	.	1	9	1	.	.	.	.	229	.	.	.	69	.
Angelica sylvestris	29	37	57	36	61	48	2	5	46	51	.	20	102	19	221	51	.	.	76	114
Potentilla palustris	1	1	.	1	10	.	.	.	2	2	.	.	.	.	216	.	.	.	.	.
Myosotis palustris s. lat.	33	61	48	43	68	78	2	13	69	36	.	126	30	21	216	127	.	.	179	.
Tephroseris crispa	1	5	2	4	15	8	.	1	5	2	.	17	.	.	211	35	.	.	18	.
Juncus acutiflorus	1	1	2	2	10	1	.	.	3	3	.	.	.	.	205	.	.	.	12	.
Bistorta major	14	11	48	19	53	81	2	27	20	32	.	.	107	.	245	215	.	11	.	50
Juncus effusus	20	42	36	28	55	33	1	1	66	34	.	87	32	.	224	14	.	.	247	34
Caltha palustris	27	59	52	17	60	14	1	1	64	58	.	167	82	.	222	.	.	.	200	168
Galium palustre s. lat.	19	34	22	14	44	11	.	1	57	21	.	92	.	.	211	.	.	.	260	.
Cirsium heterophyllum	1	1	2	2	5	100	1	6	1	5	.	.	.	.	.	717	.	.	.	.
Crepis mollis	4	5	9	13	17	45	1	18	1	3	.	.	.	51	99	206	.	114	.	.
Imperatoria ostruthium	.	.	.	.	.	6	.	1	.	1	.	.	.	.	.	200	.	.	.	.
Geranium sylvaticum	2	4	7	.	5	40	2	23	2	5	.	.	.	.	.	232	.	259	.	.
Hypericum maculatum	5	9	5	19	15	64	8	51	8	6	.	.	.	22	.	212	.	343	.	.
Agrostis capillaris	16	12	18	44	45	91	26	84	8	4	.	.	.	92	97	205	.	409	.	.
Arrhenatherum elatius	14	8	12	11	2	4	90	30	3	4	.	.	.	.	.	.	631	98	.	.
Crepis biennis	2	1	4	2	1	.	39	7	1	1	.	.	.	.	.	.	479	13	.	.
Plantago media	3	1	1	9	1	.	42	14	1	.	.	.	.	.	.	.	436	71	.	.
Galium mollugo s. lat.	25	21	13	13	4	9	74	42	9	12	.	.	.	.	.	.	418	157	.	.
Securigera varia	1	1	1	1	.	.	24	6	.	.	.	.	.	.	.	.	391	48	.	.
Tragopogon orientalis	1	1	.	2	1	.	22	3	.	.	.	.	.	.	.	.	370	.	.	.
Taraxacum sect. *Ruderalia*	51	13	22	29	12	2	81	57	10	3	157	.	.	.	.	.	367	193	.	.
Salvia pratensis	1	1	.	1	.	.	20	7	.	.	.	.	.	.	.	.	326	65	.	.
Festuca rupicola	1	1	.	1	.	.	20	6	1	.	.	.	.	.	.	.	322	44	.	.
Daucus carota ssp. *carota*	3	6	2	5	.	.	29	12	2	.	.	.	.	.	.	.	321	87	.	.
Medicago lupulina	1	2	2	3	.	.	19	3	.	.	.	.	.	.	.	.	318	.	.	.
Geranium pratense	22	4	15	5	.	.	37	5	4	3	158	.	33	.	.	.	309	.	.	.
Pastinaca sativa	3	2	2	1	.	.	17	.	1	.	13	.	.	.	.	.	306	.	.	.
Heracleum sphondylium	17	13	22	11	12	31	50	32	6	10	.	.	.	.	.	45	275	111	.	.
Sanguisorba minor	1	1	.	.	.	.	12	3	.	1	.	.	.	.	.	.	265	30	.	.
Poa pratensis s. lat.	65	22	57	56	46	31	87	59	22	20	128	.	28	50	.	.	264	69	.	.
Convolvulus arvensis	3	.	3	1	.	.	13	1	1	.	26	.	.	.	.	.	257	.	.	.
Abietinella abietina	1	.	.	1	.	.	11	2	.	.	.	.	.	.	.	.	257	14	.	.
Galium verum s. lat.	13	5	15	17	1	.	34	16	1	2	22	.	23	59	.	.	254	50	.	.
Bromus erectus	1	1	.	3	.	.	13	3	.	.	.	.	.	.	.	.	250	21	.	.
Cerastium holosteoides ssp. *triviale*	47	28	25	48	21	4	70	59	14	3	87	.	.	92	.	.	245	170	.	.
Trifolium dubium	9	4	5	12	2	.	30	19	1	.	.	.	.	31	.	.	244	118	.	.
Hypericum perforatum	2	1	2	2	1	2	18	11	1	.	.	.	.	.	.	.	242	116	.	.
Campanula rapunculoides	.	.	1	.	1	.	10	3	.	.	.	.	.	.	.	.	238	51	.	.
Cerastium arvense	1	.	.	1	1	.	15	12	1	.	.	.	.	.	.	.	233	174	.	.
Fragaria viridis	2	1	.	2	.	.	12	3	.	.	.	.	.	.	.	.	232	10	.	.
Vicia sepium	10	3	8	3	4	7	27	12	4	6	24	.	.	.	.	.	230	47	.	.
Brachythecium albicans	1	1	.	2	1	.	13	8	.	.	.	.	.	.	.	.	210	115	.	.
Pimpinella major	11	1	15	11	4	21	27	11	2	4	11	.	36	18	.	61	205	.	.	.
Vicia hirsuta	2	.	.	1	.	.	9	1	1	1	.	.	.	.	.	.	204	.	.	.
Dactylis glomerata	30	25	19	20	7	24	91	66	9	12	.	.	.	.	.	.	450	265	.	.
Knautia arvensis s. lat.	4	1	1	13	1	2	55	37	.	1	.	.	.	.	.	.	437	257	.	.
Trisetum flavescens	19	12	25	22	9	24	78	56	2	2	.	.	.	.	.	.	430	253	.	.
Campanula patula	14	7	11	23	4	14	64	48	4	1	.	.	.	19	.	.	382	249	.	.
Leontodon hispidus	7	9	4	25	3	5	61	58	1	.	.	.	.	48	.	.	370	353	.	.
Plantago lanceolata	30	17	17	60	18	12	85	78	5	1	.	.	.	183	.	.	350	310	.	.
Lotus corniculatus	11	6	1	29	3	1	52	41	1	.	.	.	.	113	.	.	326	229	.	.
Leucanthemum vulgare s. lat.	25	20	15	50	12	11	74	64	5	1	.	.	.	159	.	.	323	254	.	.
Achillea millefolium s. lat.	42	23	22	61	33	73	89	93	13	5	.	.	.	110	.	84	302	338	.	.
Pimpinella saxifraga	2	1	.	18	1	.	40	43	1	.	.	.	.	62	.	.	288	335	.	.
Trifolium pratense	30	15	18	44	13	5	66	62	8	1	.	.	.	118	.	.	274	259	.	.
Veronica chamaedrys s. lat.	31	26	32	46	37	75	78	77	14	6	.	.	.	30	.	114	262	270	.	.
Ranunculus bulbosus	1	.	.	1	.	.	18	15	.	.	.	.	.	.	.	.	249	203	.	.
Trifolium repens	31	9	15	40	16	2	57	62	6	1	18	.	.	100	.	.	227	277	.	.
Campanula rotundifolia s. lat.	1	.	.	7	1	9	19	43	.	.	.	.	.	.	.	.	121	445	.	.
Phyteuma spicatum	1	.	.	1	1	16	1	22	1	1	.	.	.	.	.	109	.	354	.	.
Hieracium pilosella	1	.	.	3	1	.	8	20	.	.	.	.	.	.	.	.	72	306	.	.

Table 1. (cont.)

Cluster number	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Number of relevés	475	268	130	435	410	85	360	384	265	290	475	268	130	435	410	85	360	384	265	290
Cardaminopsis halleri	2	1	2	1	2	22	1	21	.	1	.	.	.	.	.	151	.	306	.	.
Thymus pulegioides	1	.	.	6	1	.	18	25	.	.	.	.	.	.	.	.	178	289	.	.
Carlina acaulis	.	1	.	2	.	.	6	16	.	.	.	.	.	.	.	.	73	280	.	.
Euphrasia rostkoviana	1	.	1	7	1	.	6	19	.	.	.	.	.	63	.	.	27	280	.	.
Silene dioica	2	1	.	1	1	8	.	13	.	1	.	.	.	.	.	67	.	263	.	.
Hypochaeris radicata	1	.	.	3	1	.	5	15	.	.	.	.	.	.	.	.	38	257	.	.
Leontodon autumnalis	7	3	1	9	1	1	5	23	1	.	13	.	.	39	.	.	.	257	.	.
Potentilla aurea	.	1	.	1	.	1	.	8	.	.	.	.	.	.	.	.	.	252	.	.
Veronica officinalis	1	1	1	6	2	.	3	16	.	.	.	.	.	54	.	.	.	239	.	.
Alchemilla vulgaris s. lat.	33	46	40	56	45	65	37	75	23	19	.	14	.	103	11	71	.	237	.	.
Polygala vulgaris	1	1	.	9	1	.	5	17	.	.	.	.	.	97	.	.	12	228	.	.
Dianthus deltoides	1	.	.	2	.	.	5	12	.	.	.	.	.	.	.	.	67	228	.	.
Festuca rubra s. lat.	43	57	63	81	85	89	69	92	29	16	.	.	.	155	177	93	51	228	.	.
Hieracium lachenalii	.	.	.	.	.	.	1	6	.	.	.	.	.	.	.	.	.	224	.	.
Thlaspi caerulescens	1	.	.	.	.	.	6	9	.	.	.	.	.	.	.	.	100	204	.	.
Ononis spinosa	1	1	1	1	.	.	1	8	.	.	.	.	.	.	.	.	.	200	.	.
Scirpus sylvaticus	23	56	67	18	49	20	1	1	100	62	.	133	139	.	113	.	.	.	414	183
Epilobium obscurum	2	2	11	.	9	.	.	.	19	6	.	.	67	.	83	.	.	.	227	20
Filipendula ulmaria	33	34	46	29	38	29	5	3	37	99	.	.	58	.	40	.	.	.	23	448
Geranium palustre	6	4	18	2	3	.	1	.	5	28	.	.	112	.	.	.	.	.	.	306
Lysimachia vulgaris	13	27	10	18	21	4	.	1	31	44	.	84	.	.	39	.	.	.	114	232

Table 2. Comparison of diagnostic species for relevé clusters defined in Table 1 (columns) and diagnostic species for phytosociological alliances as defined in the national list (CHYTRÝ & TICHÝ 2003; rows). The upper part of the table shows numbers of common diagnostic species; values in brackets next to alliance names are total numbers of diagnostic species for particular alliances as given in the national list. The lower part of the table reports Sörensen similarity (multiplied by 100) between groups of diagnostic species for each of the ten clusters and groups of diagnostic species for each alliance.

Cluster number	1	2	3	4	5	6	7	8	9	10
Number of relevés	475	268	130	435	410	85	360	384	265	290
Total number of diagnostic species for cluster	7	20	2	22	25	7	44	37	5	3
Number of common diagnostic species										
Arrhenatherion (48)	0	0	0	4	0	0	29	18	0	0
Polygono-Trisetion (10)	0	0	0	0	1	4	0	7	0	0
Cynosurion (5)	0	0	0	0	0	0	1	2	0	0
Alopecurion (5)	0	0	0	0	0	0	0	0	0	0
Calthion (54)	1	2	2	6	17	1	0	3	5	3
Cnidion (19)	1	0	0	2	0	0	0	0	0	0
Molinion (27)	0	0	0	17	2	0	0	2	0	0
Sörensen similarity										
Arrhenatherion	0	0	0	11	0	0	63	42	0	0
Polygono-Trisetion	0	0	0	0	6	47	0	30	0	0
Cynosurion	0	0	0	0	0	0	4	10	0	0
Alopecurion	0	0	0	0	0	0	0	0	0	0
Calthion	3	5	7	16	43	3	0	7	17	11
Cnidion	8	0	0	10	0	0	0	0	0	0
Molinion	0	0	0	69	8	0	0	6	0	0

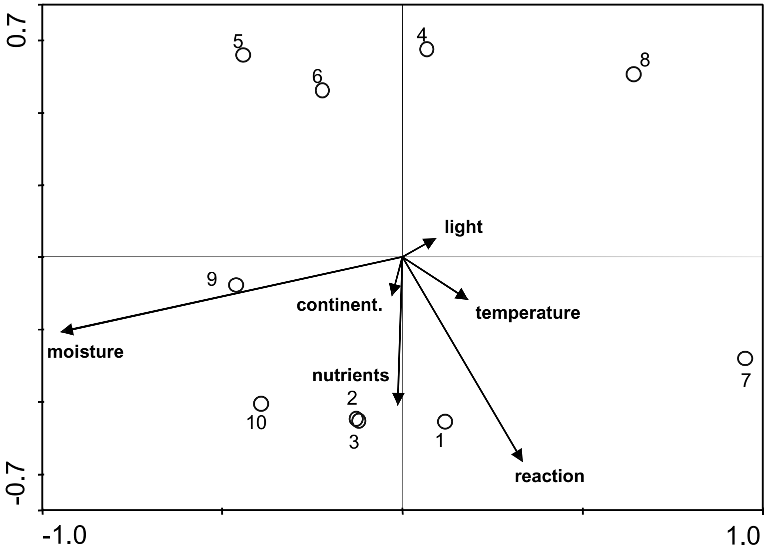


Fig. 2. Principal components analysis (PCA) of ten relevé clusters, based on average Ellenberg indicator values for each cluster. The clusters are numbered as in Table 1.

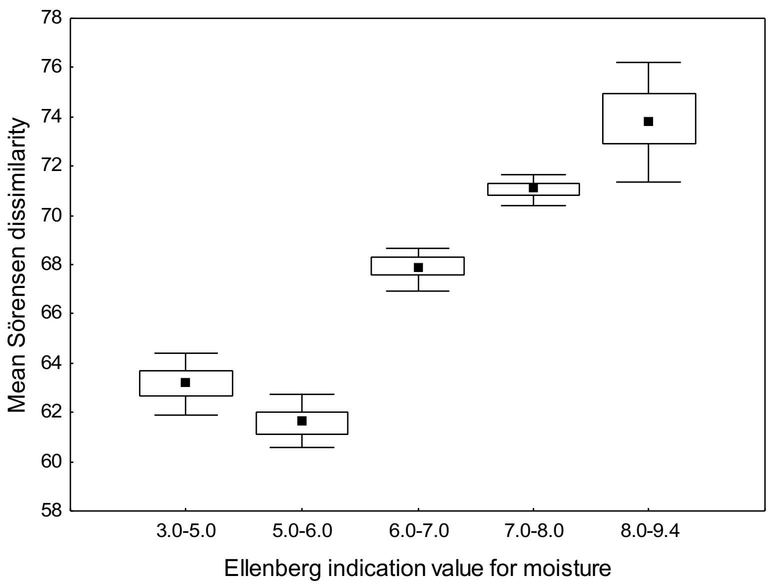


Fig. 3. Beta-diversity pattern in meadows along the soil moisture gradient. Higher values of mean Sörensen dissimilarity indicate higher beta-diversity, i.e. a higher mean degree of change in species composition among different sites. Boxes and whiskers show medians and 50 % and 95 % percentiles.

Discussion

Detrended correspondence analysis of a geographically stratified data set of 3102 relevés of Czech hay meadows and mesic pastures revealed moisture as the main gradient and nutrients, correlated with soil base status, as a secondary gradient controlling species composition (Fig. 1). This result is in accordance with classical expert-based ordination of meadow types of Central Europe, presented in the form of "ecograms" by ELLENBERG (1996), as well as with the results of recent studies based on numerical ordination of phytosociological data sets and measured environmental variables (LOSVIK 1993, SCHAFFERS & SÝKORA 2002, HÁJEK & HÁJKOVÁ 2004). These major gradients identified for Central European meadows are identical with major gradients recognized for Central European forests (ELLENBERG 1996, WOHLGEMUTH et al. 1999). Light availability is a less important factor, and is negatively correlated with moisture, possibly due to the development of higher and denser stands of broad-leaved herbs in moist habitats, which decrease light availability near the soil surface.

Table 3. Syntaxonomical and ecological interpretation of the relevé clusters identified by cluster analysis. Cluster numbers correspond to those used in Table 1 and Fig. 2.

Cluster number	Syntaxonomy	Habitat
1	Alopecurion, Cnidion	wet meadows of inundated floodplains of lowland rivers
2	Calthion: Cirsietum rivularis	wet meadows of nutrient-rich habitats in the Western Carpathians
3	Calthion: Angelico-Cirsietum oleracei and Caricetum cespitosae	wet meadows of nutrient-rich habitats, mostly in the Bohemian Massif
4	Molinion	unmanured intermittently wet meadows
5	Calthion: Angelico-Cirsietum palustris, Polygono-Cirsietum palustris	wet meadows of nutrient-poor habitats, mostly in the Bohemian Massif
6	Polygono-Trisetion: Polygono-Cirsietum heterophylli	wet meadows of montane belt in the Bohemian Massif
7	Arrhenatherion (nutrient-rich types)	mesic meadows of nutrient-rich habitats at lower altitudes
8	Arrhenatherion (nutrient-poor types), Polygono-Trisetion, Cynosurion	mesic meadows of nutrient-poor habitats in submontane and montane belt
9	Calthion: Scirpetum sylvatici	species-poor wet meadows dominated by *Scirpus sylvaticus*
10	Calthion: Filipendulenion	unmown wet meadows dominated by *Filipendula ulmaria*

Cluster analysis of our meadow data set (Table 1) more or less reproduced the alliances traditionally recognized in phytosociological literature (Balátová-Tuláčková et al. in Mucina & Maglocký 1985, Oberdorfer 1993, Ellmauer & Mucina 1993, Ellmauer 1994, Dierschke 1995, 1997, Blažková & Balátová in Moravec et al. 1995, Zuidhoff et al. 1996, Kučera & Šumberová 2001). Syntaxonomical interpretations of clusters are presented in Table 3.

Mesic meadows and pastures are included in clusters 7 and 8. Cluster 7 comprises a widespread type of nutrient-rich meadows of the Arrhenatherion alliance (association Arrhenatheretum elatioris sensu lato), which is rich in diagnostic species. Cluster 8 combines submontane types of the Arrhenatherion, often found on nutrient-poor soils, with mesic pastures of the Cynosurion and montane meadows of the Polygono-Trisetion. In the Czech Republic, mesic pastures often contain several species typical of meadows while indicators of grazed habitats are few. This is perhaps due to frequent changes of meadows into pastures and vice versa, intermittent abandonment of pastures in rotational grazing systems (Pavlů et al. 2003) or due to combined management with one hay-cutting and aftermath grazing (Krahulec et al. 2001). Therefore the boundary between submontane mesic meadows, which lack several thermophilous species of the lowland Arrhenatherion, and pastures is rather fuzzy, as evident from the combination of these grassland types into a single cluster.

Drier types of montane meadows of the Polygono-Trisetion are also included in cluster 8, but wetter types with broad-leaved herbs such as *Cirsium heterophyllum* and *Geranium sylvaticum* form separate cluster 6. Many relevés assigned to cluster 6 were originally assigned to the Polygono-Cirsietum heterophylli association, which is transitional between the Polygono-Trisetion and Calthion alliances. Although the medium-high Hercynic ranges of the Czech Republic do not harbour many species of high-mountain meadows, which makes them poorer in diagnostic species when compared with the meadows of the Alps or the Carpathians (Ellmauer 1994, Kliment 1994, Studer-Ehrensberger 2000), our results support the concept of the separate Polygono-Trisetion alliance in these Hercynic ranges.

There is a single distinct cluster that includes the Molinion alliance (cluster 4). This cluster has several diagnostic species, of which some are shared with *Nardus* grasslands of the Violion caninae alliance (e.g. *Nardus stricta*, *Potentilla erecta*, *Viola canina*, *Danthonia decumbens*). Ellenberg values indicate an intermediate position of this cluster on the moisture gradient between the mesic meadows of the Arrhenatherion and the wet meadows of the Calthion. This cluster has also the lowest nutrient requirements of all clusters, which is in accordance with the low productivity of the Molinion meadows. These meadows have been traditionally unmanured, mown only once a year or every second year in July or August (Ellenberg 1996, Ellmauer & Mucina 1993, Kučera & Šumberová 2001). Nowadays they are largely abandoned due to their low hay yields.

Unlike the other alliances, Calthion wet meadows were divided among five clusters. We suspected that this might be an artifact of the rather high proportion of relevés of this alliance included in the data set, which was not eliminated even by the geographically stratified selection of relevés prior to the analysis. Such influence of the data set structure on classification results is an inherent property of unsupervised classification methods such as cluster analysis (Bruelheide & Chytrý 2000, Kočí et al. 2003). However, the second classification of reduced data set with equal numbers of relevés that were originally assigned to the alliances Calthion, Arrhenatherion and Molinion, also produced a partition with five of ten clusters corresponding to the Calthion. This result suggests that the overrepresentation of the Calthion clusters reflects a real pattern existing in the nature rather than just the unbalanced structure of our data set. The Calthion clusters revealed in the analysis (Table 1) correspond to major associations such as Cirsietum rivularis (cluster 2), Angelico-Cirsietum oleracei and Caricetum cespitosae (cluster 3), Angelico-Cirsietum palustris and Polygono-Cirsietum palustris (cluster 5), Scirpetum sylvatici (cluster 9), and the Filipendulenion suballiance (cluster 10).

The high degree of splitting of the Calthion alliance is consistent with expert knowledge summarized in the Central European phytosociological literature, which recognizes more associations within the Calthion than in any other alliance of meadow vegetation. Table 4 shows numbers of associations within different alliances of meadow vegetation, extracted from national lists and monographs of vegetation units from wider Central Europe. Except for Hungary, where the environment is perhaps too dry for the development of diverse Calthion vegetation (Borhidi 2003), rather high numbers of associations within the Calthion are consistently distinguished in all of these publications. Our analysis of beta-diversity in meadows along the moisture gradient (Fig. 3) is consistent with this trend, showing that meadow vegetation in wet habitats exhibits a higher degree of change in species composition among different sites. In wet meadows, there are several tall, broad-leaved herbs with a strong competitive ability, namely *Cirsium* species, *Filipendula ulmaria*, *Scirpus sylvaticus* and *Carex cespitosa*, which become dominants in habitats that correspond to their ecological requirements. Once becoming dominants, these species may alter ecological conditions within their stands and influence species composition. Consequently, phytosociological classification tends to recognize more associations within wet meadows. By contrast, mesic meadows usually contain several co-dominant species, in particular medium-tall grasses, rather than a single dominant.

Wet meadows of lowland river floodplains, traditionally assigned to the alliances Alopecurion and Cnidion, were merged in cluster 1. This points out to the high similarity of both alliances, however, it can also be an artifact of a low number of Cnidion relevés in our data set (1 % according to the original author's assignment) and marginal geographical location of the Czech Republic with respect to the putative geographical distribution of this alliance (Balátová-Tuláčková 1969).

Table 4. Numbers of vegetations units (associations or association-level communities) distinguished in some alliances of the Molinio-Arrhenatheretea class in Central Europe.

	Alliance	Arrhenatherion	Polygono-Trisetion	Phyteumo-Trisetion	Cynosurion	Calthion	Filipendulion	Molinion	Alopecurion	Cnidion	Deschampsion	Veronico longifoliae-Lysimachion vulgaris
Reference	**country/ region**	**Arrhenatheretalia**				**Molinietalia**						
Blažková & Balátová in Moravec et al. (1995)	Czech Republic	5	7	–	5	16	10	7	7	6	–	3
Zuidhoff et al. (1996)	The Netherlands	1	–	–	2	6	–	1	2	–	–	–
Pott (1995)	Germany	8	3	–	3	10	5	8	–	2	–	–
Schubert et al. (2001)	Germany	7	4	–	4	10	3	3	–	–	3	–
Oberdorfer (1993)	southern Germany	3	2	–	3	10	8	3	–	5	–	–
Ellmauer & Mucina (1993)	Austria	8	3	2	4	14	10	9	–	6	1	1
Balátová-Tuláčková et al. in Mucina & Maglocký (1985)	Slovakia	8	8	–	5	10	6	9	2	6	3	–
Borhidi (2003)	Hungary	4	–	1	2	3	5	4	–	–	6	–
Matuszkiewicz (2001)	Poland	4	2	–	2	12	6	2	1	1	–	–
Balevičienė & Tučienė (1998)	Lithuania	3	–	–	2	8	–	2	2	–	–	–

Acknowledgement. We thank Zoltán Botta-Dukát for his advice on bootstrap resampling, Ilona Kuželová for managing our database and Karle Sýkora and Kateřina Šumberová for their valuable comments on the previous version of the manuscript. This research was funded from the grants GA ČR 206/02/0957 and MSM 143100010.

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