Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe

Vegetace vlhkých nížinných luk podél gradientu klimatické kontinentality ve střední Evropě

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Central European lowland wet meadows are habitats of great conservation interest, however, their phytosociological status has been to a large extent dependent on specific phytosociological traditions in different countries. In order to bridge the gaps between different national schemes of vegetation classification, a statistical analysis of variation in species composition of these meadows in the Czech Republic, E Austria, Slovakia, Hungary and NE Croatia was performed, using a data set of 387 geographically stratified vegetation relevés sampled at altitudes < 350 m. Principal coordinates analysis was used to identify and partial out the noise component in the variation in this data set. The relevés were classified by cluster analysis. A new method for identifying the optimal number of clusters was developed, based on species fidelity to particular clusters. This method suggested the optimum level of classification with three clusters and secondary optimum levels with five and nine clusters. Classification based on three clusters separated the traditional phytosociological alliances of *Calthion palustris* and *Molinion caeruleae*, both with a suboceanic phytogeographical affinity, and a group of flooded meadows of large river alluvia, with a continental affinity. The latter group included the traditional alliances of *Agrostion albae, Alopecurion pratensis, Cnidion venosi, Deschampsion cespitosae* and *Veronico longifoliae-Lysimachion vulgaris*; however, the internal heterogeneity of this group did not reflect putative boundaries between these alliances as proposed in the phytosociological literature. Therefore we suggest to unite these alliances in a single alliance *Deschampsion cespitosae* Horvatić 1930 (the oldest valid name). Classification with nine clusters was interpreted at the level of broad phytosociological associations. Particular clusters were characterized by statistically defined groups of diagnostic species and related to macroclimatic variables.

Keywords: Czech Republic, fidelity, Hungary, *Molinio-Arrhenatheretea*, numerical analysis, optimal number of clusters, phytosociological classification, Slovakia, vegetation survey

Introduction

During the 20th century, Central Europe witnessed a boom in phytosociological studies that proposed various vegetation typologies. Many of these studies focused on small areas and resulted in local classification systems, while syntheses have mainly concentrated on the national level (Mucina et al. 1993). The challenge of unifying the different national vegetation typologies was recently addressed by the international working group European Vegetation Survey (Rodwell et al. 1995). The first move towards a European synthesis was the compilation of vegetation units from different synthetic studies at national and regional levels (Mucina 1997, Rodwell et al. 2002). Such compilations, however, could not overcome the inconsistencies that resulted from incompatible classification systems used for some vegetation types in different countries. Recent developments in compilation of vegetation-plot databases (Ewald 2001, Hennekens & Schaminée 2001) provide a unique opportunity for linking previously incompatible national classification schemes by analysing large data sets that span national boundaries (Bruelheide & Chytrý 2000).

The existing incompatibility of national classifications is exemplified by the case of lowland wet meadows in Central Europe. While the classification of Central European meadow types of suboceanic distribution is more or less stable, based on internationally well-established and widely recognized alliances such as *Arrhenatherion elatioris*, *Polygono-Trisetion*, *Calthion palustris* and *Molinion caeruleae* (Oberdorfer 1993, Ellmauer & Mucina 1993, Pott 1995, Dierschke 1995, Kučera & Šumberová 2001, Stanová & Valachovič 2002, Burkart et al. 2004, Havlová et al. 2004), there is little consensus on the classification of lowland wet meadows, which occur on a broad geographic gradient from the suboceanic to subcontinental areas of Central Europe. The subcontinental lowland wet meadows are mainly assigned to the alliances *Agrostion albae*, *Alopecurion pratensis*, *Cnidion venosi*, *Deschampsion cespitosae* and *Veronico longifoliae-Lysimachion vulgaris*, but the conceptual bases of these alliances vary among countries and authors (Passarge 1964, Špániková 1975, Oberdorfer 1993, Ellmauer & Mucina 1993, Dierschke 1995, Kučera & Šumberová 2001, Stanová & Valachovič 2002, Borhidi 2003, Burkart et al. 2004). The largest difference in these occurs between the suboceanic part of Central Europe, e.g. Germany and W Czech Republic, and subcontinental areas, e.g. Hungary. These meadows are of great conservation interest, as they are the habitat of a number of rare plant species (Hölzel 2003). At the same time they are increasingly endangered due to changes in land use (Joyce & Wade 1999, Šeffer & Stanová 1999). Therefore these habitats are included in the European Union Habitats Directive, which is the legislative basis for creating a pan-European network of protected areas called NATURA 2000. This legal document stresses the need for the development of a robust international classification of these meadows.

The aims of this paper are to: (1) assess the variation in species composition within lowland wet meadows over a broad-scale gradient of climate continentality from the Czech Republic through E Austria and Slovakia to Hungary and NE Croatia, using a large international data set of phytosociological relevés, (2) identify major vegetation types and (3) outline syntaxonomic interpretations.

Materials and methods

Vegetation data

Phytosociological relevés of lowland wet meadows over a NW-SE geographic gradient across Central Europe were collected from national databases of vegetation plots (e.g. Valachovič 1999, Chytrý & Rafajová 2003) and local literature. Only relevés sampled at altitudes below 350 m in the Czech Republic, E Austria, Slovakia, Hungary and NE Croatia, and assigned to the phytosociological order of wet meadows (*Molinietalia*) by their original authors, were used. Relevés from plots of unusual size (smaller than 4 m^2 or larger than 100 m^2) and from slopes of an inclination greater than 10° were excluded. In order to avoid the effect of oversampling of some localities on the data analysis, a stratified resampling of the data set was performed. If there were two or more relevés from the same locality originally assigned to the same traditional phytosociological association or subassociation, only one of them was randomly selected. For this purpose, locality was defined by the name of the nearest village or town. This selection yielded a total of 387 relevés, including 178 from the Czech Republic, 11 from E Austria, 115 from Slovakia, 76 from Hungary and 7 from N Croatia. A list of bibliographic references to these relevés can be obtained from the senior author of this paper upon request. Bryophyte records were deleted, since they were missing from some relevés (note that bryophytes do not play a significant role in this vegetation type). Nomenclature of plants was that of Ehrendorfer (1973).

Climatic data

Climatic data for relevé locations, including the mean annual precipitation, mean annual temperature and mean temperature in January and July, were taken from climatic maps of former Czechoslovakia (Vesecký et al. 1958) and Hungary (Ambrózy & Béll 1989). In areas with varying temperature, however, the amount of precipitation alone does not provide a reliable measure of the moisture that is available to the plants. Therefore, we used the aridity/humidity index of de Martonne, which is close to precipitation/evaporation indices (Tuhkanen 1980). It is calculated as $P / (T + 10)$, where P is the annual precipitation in mm and T the annual mean temperature in °C. In order to characterize the temperature component of continentality, the temperature difference between the coldest (January) and warmest (July) month was used as a separate climatic variable.

Data analysis

In most of the relevés species cover was estimated on the Braun-Blanquet 7-degree scale or similar scales using categories instead of exact values. These categories were replaced by mid percentage values, which were square-root transformed in order to reduce the importance of dominant species (van der Maarel 1979).

Based on the comparative study of Faith et al. (1987), the relativized Manhattan distance was chosen to measure the dissimilarities between relevés. This has the advantage that total cover values of the relevés are not considered and dominant species are not over-weighted. We performed principal coordinates analysis (PCoA; Legendre & Legendre 1998) using SYNTAX 2000 package (Podani 2000) and the relativized Manhattan distances to determine the main gradients in the data set. Ordination biplots of PCoA, with passively projected species and climatic variables, were prepared in the CanoDraw program (ter Braak & Šmilauer 2002). Possible number of ordination axes in such analysis equals the number of relevés minus 1, but usually only the first few ordination axes contain interpretable ecological information, while the others contain largely noise. To establish the number of interpretable axes, the eigenvalues were compared with random expectations based on the broken-stick model (Jackson 1993, Legendre & Legendre 1998: 410). In our case the first 13 axes proved to be significant. They explained 47.5% of the total variation in the data set; hence more than half of the total variation proved to be noise. As the number of significant axes was rather high, only the first three axes, which explained 23.8% of total variation, were interpreted.

Because of the high percentage of noise in the total variation, the coordinates along the 13 significant axes of PCoA were used instead of the raw data as input for the classification. In this way, we were able to avoid the low robustness of agglomerative classification methods when used on noisy data sets (Lambert & Williams 1966, Gauch 1982: 208). This negative property results from the fact that these methods do not consider the complete dissimilarity relationship among clusters, but only individual dissimilarity values for couples of clusters or objects in each step (Hill et al. 1975, Pielou 1977: 316). Ward's algorithm of minimum increment of sum of squares was used for dendrogram construction (Ward 1963, Legendre & Legendre 1998).

A crucial point in the interpretation of hierarchical clustering results is deciding the levels to be interpreted. Based on an extensive review, Dale (1988) concluded that there are no generally applicable rules. In our opinion, fidelity, which is a central concept of the Zürich-Monpellier phytosociological school (Westhoff & van der Maarel 1973), can be used to determine the optimal number of clusters. Therefore, we developed a new method, which uses a generalization of statistical fidelity measures.

For the calculation of fidelity measures, Chytrý et al. (2002) used a 2 × 2 contingency table:

Number of relevés ...	in the cluster	not in the cluster
containing the species	$F_{1/1}$	$F_{1/0}$
not containing the species	$F_{0/1}$	$F_{0/0}$

In our generalized approach, this contingency table is extended to a 2 × *c* contingency table, where *c* is the number of clusters:

Number of relevés ...	in the 1st cluster	…	in the *j*-th cluster	…	in the last (*c*-th) cluster
containing the species	$F_{1/1}$	…	$F_{1/j}$	…	$F_{1/c}$
not containing the species	$F_{0/1}$	…	$F_{0/j}$	…	$F_{0/c}$

Some of the fidelity indices reviewed by Chytrý et al. (2002) can be calculated only for 2 × 2 tables, but chi^2 and *G* statistics can be easily calculated for contingency tables of any size (Sokal & Rohlf 1995). We used the *G* statistic. Calculated for a 2 × *c* contingency table, the *G* statistic does not measure the fidelity of species to individual clusters, but species capacity to distinguish the clusters within a given partition. We call this measure the "separation power" of species. The higher the average separation powers for all species (which we call the "crispness of classification"), the better the clusters can be distinguished by the diagnostic species, i.e. the better the classification.

The problem is that the expected separation power and consequently the crispness of classification increase with increasing number of clusters, even if relevés are assigned randomly to clusters (Fig. 1). This effect has to be eliminated before comparing partitions with different numbers of clusters. In a random classification, separation powers have approximately a chi-square distribution with $c–1$ degrees of freedom (Sokal & Rohlf 1995). According to the central limit theorem (e.g. Zar 1999: 76–77), if the number of species is high, which is the case in most data sets, the crispness of classification has approximately a normal distribution with expected value = $c–1$ and standard deviation = $\sqrt{2 \cdot (c - 1)/S}$, where S is the number of species. Therefore, we removed the effect of the number of clusters by subtracting this expected value and dividing the difference between the observed and expected value by the standard deviation. In this way we standardized the crispness values, which can then be compared among partitions with different numbers of clusters. In the vegetation data, there may be several "optimal" levels of classification and the hierarchy of syntaxonomical systems reflects this hierar-

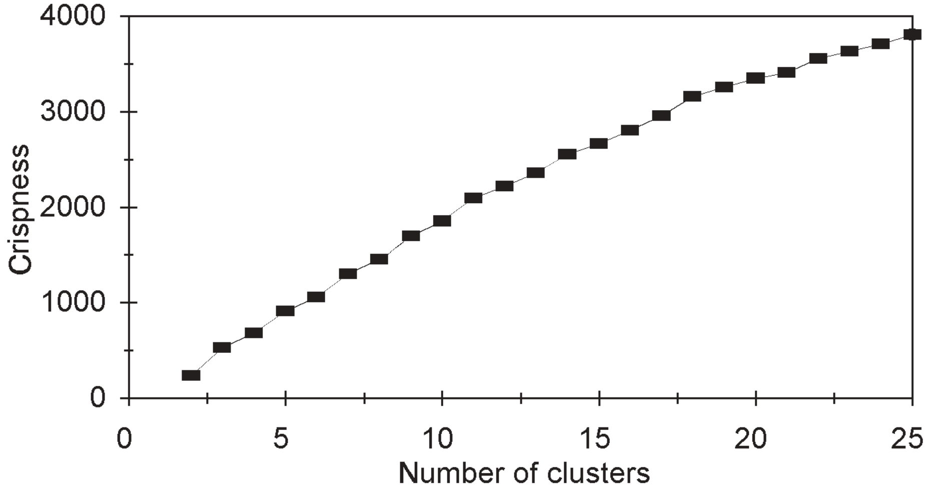

Fig. 1. – Changes in crispness with increasing number of clusters in random classification.

chic property of vegetation. Local maxima of crispness indicate these “optimal” levels (Feoli & Lausi 1980). Since differences between clusters are most pronounced at the highest level, subsequent peaks are smaller. Rare species (those occurring in less than 10 relevés) were excluded from this analysis, because our pilot studies suggested that they decreased the ability of this method to recognize all optimal levels.

Diagnostic species for the clusters were determined a posteriori, by calculating the fidelity of all species to each cluster, using the u_{hyp} statistic as a measure of fidelity (Chytrý et al. 2002). In these calculations, each cluster was compared with the rest of the relevés, which were taken as a single undivided group. In such a way, divisions of the rest of the data set did not influence the fidelity of species to the target cluster. The threshold u_{hyp} value for a species considered to be diagnostic was set to 5.3, because this value produced a total of 100 diagnostic species for all clusters. The results of the classification were summarized in a synoptic table, in which both percentage species frequencies (constancies) and u_{hyp} values (fidelities) are shown, and diagnostic species are ranked by decreasing fidelity, i.e. by decreasing u_{hyp} value (Chytrý et al. 2002). Fidelity calculations were performed with the JUICE 6.1 program (Tichý 2002).

Differences in the climatic variables between clusters were tested by Kruskal-Wallis nonparametric ANOVA and subsequently by Dunn's post-hoc test (Zar 1999: 195–200, 223–224).

Results and discussion

Classification of relevés

The peak of the curve of crispness of classification (Fig. 2) indicates that the optimal number of clusters is three. The contents of these three clusters basically correspond to the alliances of traditional phytosociology. Secondary optimal numbers of clusters, which would provide more detailed classifications, are five and nine. These levels roughly correspond to phytosociological suballiances and associations, respectively.

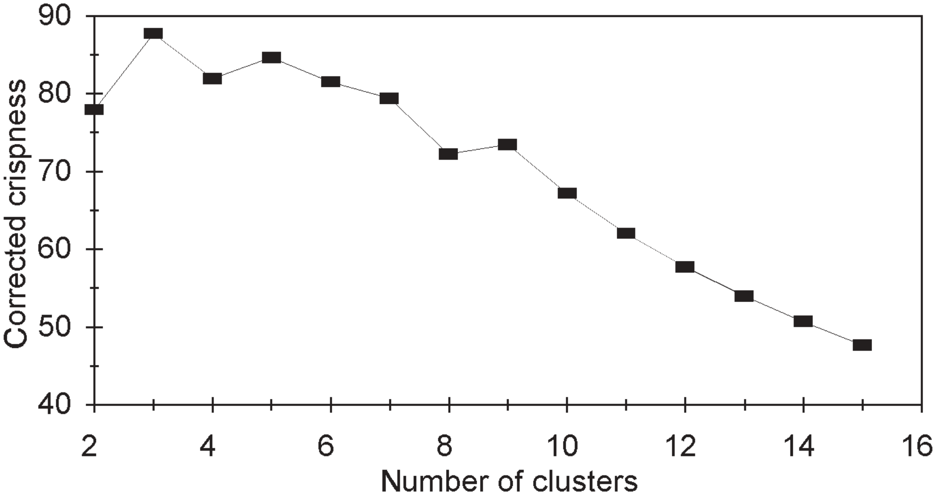

Fig. 2. – Changes in corrected crispness with increasing number of clusters. Global maximum at the level of three clusters indicates the optimal classification, local maxima at five and nine clusters indicate secondary optimal classifications.

Higher-level clusters: alliances

Two of the three clusters of the optimal classification (Fig. 3) clearly correspond to alliances well established in traditional phytosociology: *Calthion* (Cluster 2) and *Molinion* (Cluster 3) (Rybníček et al. 1984, Ellmauer & Mucina 1993, Oberdorfer 1993, Dierschke 1995, Moravec et al. 1995, Kučera & Šumberová 2001, Stanová & Valachovič 2002, Borhidi 2003, Burkart et al. 2004).

Calthion meadows are dominated by large dicots, while graminoids are of secondary importance in many stands. They are found on alluvia of small brooks, near springs and in seepage areas, where soil is moist throughout the year, and usually well supplied with nutrients (Hájek & Hájková 2004). The centre of their distribution is in submontane and montane areas, and are only rarely present in lowlands. In Central Europe they tend to have a subatlantic distribution, being rather common in Germany and the Czech Republic (Oberdorfer 1993, Kučera & Šumberová 2001, Burkart et al. 2004, Havlová et al. 2004), but rare in Hungary (Borhidi 2003).

Molinion meadows are usually dominated by *Molinia arundinacea* or *M. caerulea* and found on nutrient-poor soils, which often contain a high proportion of organic matter. An important habitat feature is an abundant moisture in spring followed by drying out in summer. These meadows are widespread across Central Europe, although not very common in some areas. In the W part of Central Europe they are found from the lowlands to submontane areas (Oberdorfer 1993, Kučera & Šumberová 2001, Burkart et al. 2004), while in Hungary they are typical of lowlands, where they usually occur on organic substrata and often form vegetation complexes in base-rich fens (Kovács 1962, Borhidi 2003).

Cluster 1 includes meadows in large lowland river floodplains, which are regularly flooded but unlike the *Calthion* meadows dry out in summer due to dry continental climate. From the *Molinion* meadows they differ in that they develop on mineral soils with a good

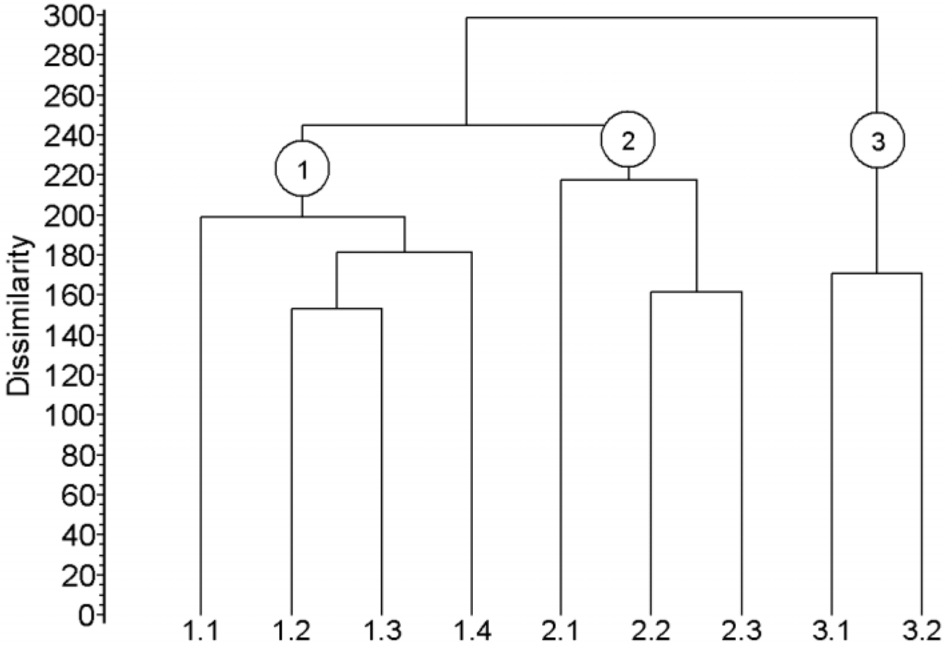

Fig. 3. – Dendrogram made by Ward's method. For simplicity, the bottom part is not drawn.

supply of nutrients. These meadows are traditionally classified into different alliances: *Agrostion albae* (Soó 1941), *Alopecurion pratensis* (Passarge 1964), *Cnidion venosi* (Balátová-Tuláčková 1966, 1969), *Deschampsion cespitosae* (Horvatić 1930) and *Veronico longifoliae-Lysimachion vulgaris* (Balátová-Tuláčková 1981a). In national vegetation surveys of Central European countries the interpretation of these alliances varies considerably and in the absence of comparative studies the use of some of these alliance names is restricted to certain countries. The *Alopecurion pratensis* alliance is sometimes considered as characteristic of the northern, suboceanic part of Central Europe, while the other alliances are considered as typical of the Pannonian floristic province of SE Central Europe (Moravec et al. 1995, Kučera & Šumberová 2001, Stanová & Valachovič 2002). The *Veronico longifoliae-Lysimachion vulgaris* alliance was originally proposed for tall-herb vegetation of abandoned meadows in continental areas, however, such stands are rare and very similar in species composition to mown meadows (Ellmauer & Mucina 1993, Šumberová 1997, Kučera & Šumberová 2001). The *Cnidion* alliance was delimited by Balátová-Tuláčková (1969) to include all floodplain meadows of Central and E Europe where continental species occur that are distributed from S Russia and the Ukraine to Poland and E Germany, in the Pannonian basin and in the Rhine valley of SW Germany. In this delimitation, the *Cnidion* alliance concept overlaps with that of the *Deschampsion cespitosae* alliance, described earlier from NE Croatia (Horvatić 1930). Ellmauer & Mucina (1993) interpreted *Deschampsion* and *Cnidion* as Illyrian and Pannonian alliances, respectively, however, the original description of *Deschampsion cespitosae* (Horvatić 1930) is not from the Illyrian but the Pannonian floristic province in Croatia and does not contain Illyrian species.

Cluster 1 is rather heterogeneous, but its internal variation, revealed by numerical analysis, does not support any of the concepts in the earlier literature that tried to outline boundaries between some of the above mentioned alliances. A significant proportion of the species typical of this cluster have continental distribution ranges, which is not the case for the *Calthion* and *Molinion* clusters (Table 1). However, species with the most pronounced continental affinities, e.g. *Allium angulosum, Carex melanostachya*, *C. praecox*, *Cnidium dubium*, *Galium boreale*, *Scutellaria hastifolia*, *Veronica longifolia* and *Viola pumila*, are only found in some stands of this cluster (namely lower-level Clusters 1.1 and 1.2; see Table 3). Stands lacking these species are much more common; they are poorly characterized in terms of diagnostic species and have some features of mesic hay meadows of the *Arrhenatherion* alliance (Clusters 1.3 and 1.4 in suboceanic and subcontinental areas, respectively; see Table 3).

Based on our analysis of the internal variation in the structure of Cluster 1, we suggest considering this cluster as a single alliance, for which the oldest valid name, *Deschampsion cespitosae* Horvatić 1930 should be used. The name *Agrostion albae* (Soó 1941) is a nomenclatural synonym of the *Deschampsion cespitosae* alliance and the other alliances (*Alopecurion pratensis*, *Cnidion venosi* and *Veronico longifoliae-Lysimachion vulgaris*) are syntaxonomical synonyms in our concept. Unlike Kovács (1975) or Borhidi (2003) we do not accept that these units are suballiances, because our analysis does not support such a subdivision.

Table 1. – Representation of oceanic and continental species among the diagnostic species of alliances, as defined in the present classification. Only the species with fidelity values of $u_{hyp} > 5$ were considered as diagnostic. Categories of oceanity/continentality, taken from Rothmaler et al. (1990), are ranked from the most oceanic = oz, to the most continental = k.

	Deschampsion	*Calthion*	*Molinion*
oz	–	–	4 (15%)
(oz)	4 (33%)	6 (33%)	14 (52%)
suboz	–	4 (22%)	2 (7%)
(suboz)	1 (8%)	3 (17%)	3 (11%)
(subk)	1 (8%)	–	–
subk	1 (8%)	–	1 (4%)
(k)	1 (8%)	–	1 (4%)
k	–	–	–
indifferent	4 (33%)	5 (28%)	2 (7%)

Lower-level clusters: associations

The clusters at nine-cluster level are close to associations recognized in the traditional phytosociological literature. However, as our analysis emphasized the species composition, some of these clusters are slightly broader than the traditional associations that were often delimited based on dominant species. Our aim was to describe major broad-scale variation patterns rather than testing differences between traditional associations. Therefore, we did not pay much attention to the syntaxonomy and nomenclature of associations, nonetheless, our results can be used in future syntaxonomic revisions. Relationships to the traditional associations are indicated in Table 2.

Table 2. – Traditional phytosociological classification of relevés assigned to clusters resulting from cluster analysis. Only frequently used names and important references are given.

	Czech Republic	Slovakia and adjacent areas of Austria	Hungary and adjacent areas of Croatia
Cluster 1.1	• *Agrostion: Alopecuretum pratensis, Deschampsietum croato-pannonicum* (Vicherek 1960) • *Cnidion: Lathyro palustris-Gratioletum* (Vicherek et al. 2000)	• *Alopecurion*: *Alopecuretum pratensis* (Řehořek 1969, Špániková 1971) • *Deschampsion*: *Cirsio cani-Deschampsietum cespitosae* (Řehořek 1969) • *Molinion* (Zahradníková-Rošetzká 1965, Bosáčková 1971) • *Cnidion*: *Cnidio-Violetum pumilae* (Maťašová 1987, Šeffer & Stanová 1999), *Lathyro palustris-Gratioletum, Gratiolo-Caricetum suzae* (Balátová-Tuláčková & Hübl 1974)	• *Agrostion*: *Carici vulpinae-Alopecuretum pratensis* (Kovács & Máthé 1967), *Agrostietum albae* (Simon 1960) • *Cnidion*: *Veronica longifolia-Euphorbia lucida* (Balátová-Tuláčková & Knežević 1975), *Gratiola officinalis-Carex praecox-suzae* (Balátová-Tuláčková & Knežević 1975), *Serratulo-Plantaginetum altissimae* (Balátová-Tuláčková & Knežević 1975)
Cluster 1.2	• *Molinion*: *Cnidium venosum-Jacea vulgaris* ssp. *angustifolia* as. (Vicherek 1960), *Serratulo-Festucetum commutatae* (Blažková 1993) • *Cnidion: Gratiolo-Caricetum suzae, Cnidio venosi-Jaceetum angustifoliae, Cnidio-Violetum pumilae* (Vicherek et al. 2000)	• *Cnidion*: *Gratiolo-Caricetum suzae* (Balátová-Tuláčková 1968, Balátová-Tuláčková & Hübl 1974, Šeffer & Stanová 1999, Zlinská & Kubalová 2001), *Cnidio-Violetum pumilae* (Balátová-Tuláčková & Hübl 1974) • *Molinion*: *Serratulo-Festucetum commutatae* (Zlinská & Kubalová 2001)	• *Agrostion: Festucetum pratensis anthoxanthetosum* (Jeanplong 1960)
Cluster 1.3	• *Alopecurion*: *Alopecuretum pratensis* (Kovář 1981, Balátová-Tuláčková 1997a, Duchoslav 1997), *Holcetum lanati* (Kovář 1981, Duchoslav 1997) • *Calthion*: *Angelico-Cirsietum oleracei* (Kovář 1981, Neuhäusl & Neuhäuslová 1989), *Scirpo-Cirsietum cani* (Neuhäusl & Neuhäuslová 1989, Balátová-Tuláčková 1997a) • *Cnidion*: *Pseudolysimachio-Alopecuretum* (Blažková 1993) • *Molinion*: *Serratulo-Festucetum commutatae* (Kovář 1981), *Sanguisorbo-Festucetum commutatae* (Duchoslav 1997)	• *Deschampsion*: *Cirsio cani-Deschampsietum cespitosae* (Řehořek 1969)	

Cluster 1.4		• *Deschampsion*: *Cirsio cani-Deschampsietum cespitosae* (Špániková 1971)	• *Agrostion*: *Cirsio cani-Festucetum pratensis* (Siroki 1956, 1958, 1962), *Carici vulpinae-Alopecuretum pratensis* (Bodrogközy 1962), *Agrostietum albae* (Kovács 1955, Siroki 1958)
Cluster 2.1	• *Calthion*: *Angelico-Cirsietum oleracei* (Balátová-Tuláčková 1981b, Duchoslav 1997), *Cirsietum rivularis* (Balátová-Tuláčková 1997a, Duchoslav 1997), *Polygono-Cirsietum palustris* (Balátová-Tuláčková 1981b), *Scirpo-Cirsietum cani* (Balátová-Tuláčková 1981b, 1997a), *Caricetum cespitosae* (Balátová-Tuláčková 1981b), *Scirpetum sylvatici* (Kovář 1981b)	• *Calthion*: *Cirsietum rivularis* (Balátová-Tuláčková 1968, Špániková 1971), *Scirpetum sylvatici* (Špániková 1971), *Filipendulo-Menthetum longifoliae* (Zlinská 1989) • *Arrhenatherion*: *Holcetum lanati* (Špániková 1971, Kováčová 1976)	
Cluster 2.2	• *Calthion*: *Filipendulo-Geranietum palustris* (Balátová-Tuláčková 1979, 1997b), *Lysimachio vulgaris-Filipenduletum* (Balátová-Tuláčková 1997b, Kolbek et al. 1999)	• *Calthion*: *Filipendulo-Geranietum palustris* (Klika 1958, Balátová-Tuláčková 1968)	
Cluster 2.3	• *Calthion*: *Scirpetum sylvatici* (Kolbek et al. 1999, Hájková 2000)	• *Calthion*: *Angelico-Cirsietum oleracei* (Sitášová 1995), *Scirpetum sylvatici* (Sitášová 1999)	
Cluster 3.1	• *Molinion*: *Junco-Molinietum caeruleae* (Balátová-Tuláčková 1997b)	• *Molinion*: undetermined at association level (Zahradníková-Rošetzká 1965, Špániková 1971, Bosáčková 1975)	• *Molinion*: *Succiso-Molinietum*, *Junco-Molinietum*, *Molinio-Salicetum rosmarinifoliae* (Kovács 1962)
Cluster 3.2	• *Molinion*: *Molinietum caeruleae* (Duchoslav 1997), *Gentiano pneumonanthis-Molinietum litoralis* (Balátová-Tuláčková 1993)	• *Molinion*: *Selino-Molinietum caeruleae* (Balátová-Tuláčková 1968, Bosáčková 1975), *Silaëtum pratensis* (Balátová-Tuláčková 1968) • *Calthion*: *Cirsietum rivularis* (Bosáčková 1975)	• *Molinion*: *Succiso-Molinietum* (Kovács 1962)

Cluster 1.1 Wet *Deschampsion* meadows

These meadows are dominated by different species, most frequently *Alopecurus pratensis*, but in places also *Deschampsia cespitosa, Agrostis stolonifera, Poa palustris* or *Carex vulpina*. Diagnostic species (Table 3) indicate that the soil is wetter than in Cluster 1.3, which also includes many relevés dominated by *Alopecurus pratensis*. Species of tall-sedge beds with high fidelity values indicate a high ground-water table, even in summer. Such situations can develop on low terraces of river floodplains and in depressions. These meadows occur in the SE Czech Republic, S Slovakia, Hungary and in the Croatian part of the Pannonian floristic province along the Drava river. At the five-cluster level, this cluster is separated from the other *Deschampsion* clusters.

Table 3. – Shortened synoptic table of the diagnostic (most faithful) species for the nine clusters resulting from the cluster analysis. The left-hand part of the table contains percentage frequencies and the right-hand part fidelities, expressed as adjusted *u*-values for hypergeometric distribution. Diagnostic species are ranked by decreasing fidelities within particular clusters. Negative fidelity values are not shown. Hundred diagnostic species are listed, followed by non-diagnostic species whose occurrence frequency in the data set exceeds 10%.

	Percentage frequency									Fidelity (u_{hyp} value)								
	Deschampsion				*Calthion*			*Molinion*		*Deschampsion*				*Calthion*			*Molinion*	
Cluster	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2
Number of relevés	59	30	57	26	81	23	12	60	39	59	30	57	26	81	23	12	60	39
1.1. Wet *Deschampsion* meadows																		
Poa palustris	54	13	2	–	14	–	8	–	5	10	–	–	–	–	–	–	–	–
Galium palustre agg.	68	23	5	15	26	9	25	8	18	8.6	–	–	–	–	–	–	–	–
Iris pseudacorus	29	3	–	–	2	–	–	2	–	8.6	–	–	–	–	–	–	–	–
Gratiola officinalis	34	30	–	15	1	–	–	2	–	7.2	4.2	–	1.2	–	–	–	–	–
Rumex crispus	44	40	18	12	6	9	–	–	–	6.8	4.0	–	–	–	–	–	–	–
Carex vulpina	41	13	9	23	12	–	–	2	3	6.8	–	–	1.5	–	–	–	–	–
Mentha pulegium	19	3	–	–	–	–	–	3	–	6.7	–	–	–	–	–	–	–	–
Eleocharis palustris agg.	34	20	4	8	4	–	–	13	5	6.0	1.6	–	–	–	–	–	–	–
1.2. Summer-dry, continental *Deschampsion* meadows																		
Cnidium dubium	10	67	2	4	2	–	–	–	5	–	12	–	–	–	–	–	–	–
Viola pumila	–	40	2	–	–	–	–	–	3	–	11	–	–	–	–	–	–	–
Carex praecox	22	73	9	12	4	–	–	–	5	2.4	11	–	–	–	–	–	–	–
Inula salicina	2	53	2	8	–	4	–	3	26	–	9.1	–	–	–	–	–	–	4.0
Veronica arvensis	–	30	4	–	1	–	–	–	–	–	8.8	–	–	–	–	–	–	–
Serratula tinctoria	31	97	11	4	5	–	–	53	44	–	8.8	–	–	–	–	–	4.8	2.3
Carex melanostachya	15	37	–	–	–	–	–	–	–	3.8	8.1	–	–	–	–	–	–	–
Clematis integrifolia	–	20	–	4	–	–	–	–	–	–	7.8	–	–	–	–	–	–	–
Valerianella locusta	–	20	2	–	–	–	–	–	–	–	7.8	–	–	–	–	–	–	–
Veronica longifolia	17	43	5	–	2	–	–	–	3	3.0	7.8	–	–	–	–	–	–	–
Agropyron repens	19	57	23	23	–	–	–	2	–	1.6	7.6	2.6	1.7	–	–	–	–	–
Glechoma hederacea	15	73	39	19	20	9	17	2	–	–	7.5	3.7	–	–	–	–	–	–
Scutellaria hastifolia	5	23	–	–	–	–	–	–	–	1.3	7.4	–	–	–	–	–	–	–
Lythrum virgatum	10	33	–	12	–	–	–	–	3	1.9	7.2	–	1.5	–	–	–	–	–
Vicia tetrasperma	5	27	–	8	1	–	–	–	–	–	7.0	–	1.2	–	–	–	–	–
Myosotis ramosissima	–	17	2	–	–	–	–	–	–	–	7.0	–	–	–	–	–	–	–
Allium angulosum	15	40	4	–	–	–	–	12	3	2.2	6.7	–	–	–	–	–	1.1	–
Potentilla reptans	44	67	14	23	6	–	–	12	21	4.8	6.5	–	–	–	–	–	–	–
Euphorbia esula	–	17	4	–	–	–	–	–	–	–	6.3	1.0	–	–	–	–	–	–
Calamagrostis epigejos	–	20	–	4	–	–	–	–	8	–	6.3	–	–	–	–	–	–	2.1
Rumex thyrsiflorus	–	13	2	–	–	–	–	–	–	–	6.1	–	–	–	–	–	–	–
Vicia angustifolia	–	10	–	–	–	–	–	–	–	–	6.0	–	–	–	–	–	–	–
Iris sibirica	12	30	–	–	1	–	–	2	10	2.2	6.0	–	–	–	–	–	–	1.3
Festuca rupicola	–	20	5	–	–	–	–	–	5	–	5.9	1.2	–	–	–	–	–	–
Cirsium arvense	7	43	28	15	5	–	–	–	8	–	5.7	4.3	–	–	–	–	–	–
Symphytum officinale agg.	41	67	37	15	26	9	–	3	5	3.1	5.5	2.3	–	–	–	–	–	–
1.3. Suboceanic *Deschampsion* meadows																		
Geranium pratense	3	3	60	–	19	–	–	3	3	–	–	11	–	1.2	–	–	–	–
Trisetum flavescens	–	–	42	–	10	–	–	–	3	–	–	9.8	–	–	–	–	–	–
Cerastium holosteoides	5	40	81	38	41	4	–	8	28	–	1.1	8.7	–	2.1	–	–	–	–
Dactylis glomerata	5	10	63	12	19	17	–	12	46	–	–	7.8	–	–	–	–	–	3.6
Campanula patula	8	27	40	–	7	–	–	5	3	–	2.6	7.2	–	–	–	–	–	–
Veronica chamaedrys agg.	2	17	46	4	25	9	8	–	13	–	–	6.7	–	2.5	–	–	–	–
Galium mollugo agg.	15	40	54	15	14	9	8	13	13	–	2.6	6.6	–	–	–	–	–	–

Cluster	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2
Pimpinella major	5	3	28	–	9	–	–	3	3	–	–	6.2	–	–	–	–	–	–
Anthriscus sylvestris	–	–	18	–	4	4	8	–	–	–	–	5.8	–	–	–	–	–	–
Poa pratensis agg.	32	97	88	77	53	35	25	12	64	–	5.0	5.7	2.6	–	–	–	–	1.5
Vicia sepium	–	3	26	–	16	4	–	–	–	–	–	5.7	–	3.1	–	–	–	–
1.4. Mesic, continental *Deschampsion* meadows																		
Medicago lupulina	2	–	5	50	4	–	–	5	10	–	–	–	8.9	–	–	–	–	–
Bromus commutatus	–	–	–	12	–	–	–	–	–	–	–	–	6.5	–	–	–	–	–
Daucus carota	7	13	11	54	4	–	–	28	10	–	–	–	6.2	–	–	–	3.7	–
2.1. Suboceanic *Calthion* meadows																		
Myosotis palustris agg.	15	7	11	–	56	–	58	7	10	–	–	–	–	9.0	–	3.4	–	–
Holcus lanatus	14	3	67	15	83	13	–	33	44	–	–	4.3	–	8.6	–	–	–	–
Alchemilla vulgaris agg.	–	–	19	–	36	13	–	2	3	–	–	2.0	–	7.6	–	–	–	–
Cirsium rivulare	–	–	2	–	35	–	8	3	31	–	–	–	–	7.4	–	–	–	4.0
Anthoxanthum odoratum	–	17	46	–	59	–	–	17	44	–	–	3.3	–	7.2	–	–	–	2.4
Caltha palustris	25	3	2	15	54	48	58	10	21	–	–	–	–	6.8	2.6	2.7	–	–
Angelica sylvestris	2	–	16	8	46	39	25	12	18	–	–	–	–	6.7	2.5	–	–	–
Juncus effusus	14	–	5	4	33	4	25	10	3	–	–	–	–	6.2	–	1.3	–	–
Lotus uliginosus	–	–	5	–	23	26	–	3	–	–	–	–	–	5.9	3.4	–	–	–
Cardamine pratensis agg.	41	67	39	15	62	39	8	2	5	1.1	3.9	–	–	5.8	–	–	–	–
Dactylorhiza majalis	–	–	4	–	17	4	–	–	5	–	–	–	–	5.8	–	–	–	–
Equisetum palustre	7	–	9	19	52	70	50	23	31	–	–	–	–	5.7	4.8	1.8	–	–
Lychnis flos-cuculi	61	77	63	62	77	4	25	2	38	1.9	3.1	2.2	1.2	5.4	–	–	–	–
2.2. Suboceanic unmown *Calthion* grasslands dominated by *Filipendula ulmaria*																		
Geranium palustre	–	–	2	–	11	57	–	–	–	–	–	–	–	2.2	11	–	–	–
Anemone nemorosa	–	–	4	–	–	26	–	–	–	–	–	–	–	–	8.3	–	–	–
Chaerophyllum hirsutum	–	–	–	–	–	17	–	–	–	–	–	–	–	–	8.0	–	–	–
Crepis paludosa	–	–	–	–	15	48	–	–	10	–	–	–	–	3.1	7.9	–	–	–
Filipendula ulmaria	14	43	28	–	56	96	58	–	31	–	1.4	–	–	5.2	6.8	2.0	–	–
Cirsium oleraceum	–	–	19	–	30	57	25	3	3	–	–	1.3	–	4.6	6.1	1.1	–	–
Galium aparine	–	7	2	–	9	30	8	–	–	–	–	–	–	1.9	6.0	–	–	–
2.3. Suboceanic unmown *Calthion* grasslands dominated by *Scirpus sylvaticus*																		
Urtica dioica	10	7	14	4	11	30	67	–	–	–	–	–	–	–	3.2	6.4	–	–
3.1 and 3.2. *Molinion* meadows																		
Achillea aspleniifolia	10	–	–	–	–	–	–	33	5	–	–	–	–	–	–	–	8.5	–
Festuca pseudovina	–	3	–	4	–	–	–	22	3	–	–	–	–	–	–	–	7.4	–
Nardus stricta	–	–	–	–	–	–	–	18	3	–	–	–	–	–	–	–	7.4	–
Gentiana pneumonanthe	3	–	–	–	1	–	–	25	8	–	–	–	–	–	–	–	7.3	–
Hieracium lactucella	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	6.2	–
Centaurium littorale ssp. *uliginosum*	–	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	5.8	–
Tetragonolobus maritimus	3	–	–	–	–	–	–	22	21	–	–	–	–	–	–	–	5.6	4.1
Briza media	–	3	7	–	26	–	–	28	74	–	–	–	–	1.9	–	–	2.1	9.4
Trifolium montanum	–	3	–	–	1	–	–	–	28	–	–	–	–	–	–	–	–	9.1
Dianthus superbus	2	–	–	–	1	–	–	–	26	–	–	–	–	–	–	–	–	8.6
Carex davalliana	–	–	–	–	–	–	–	13	31	–	–	–	–	–	–	–	3.1	7.6
Galium verum agg.	5	37	23	15	7	9	–	35	69	–	1.9	–	–	–	–	–	2.5	7.4
Filipendula vulgaris	–	17	9	–	2	–	–	–	33	–	2.4	–	–	–	–	–	–	7.2
Galium boreale	8	63	42	–	6	–	–	23	72	–	5.1	3.3	–	–	–	–	–	7.2
Carex hostiana	–	–	–	–	–	–	–	10	26	–	–	–	–	–	–	–	2.5	7.1
Carex hartmanii	–	–	–	–	–	–	–	3	18	–	–	–	–	–	–	–	–	6.8
Gymnadenia conopsea	–	–	–	–	–	–	–	2	15	–	–	–	–	–	–	–	–	6.7
Valeriana dioica	5	–	–	–	19	13	–	17	46	–	–	–	–	1.8	–	–	1.0	6.6

Cluster	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1	3.2
Carex tomentosa	7	10	2	–	4	–	–	7	31	–	–	–	–	–	–	–	–	6.1
Danthonia decumbens	–	–	–	–	2	–	–	13	26	–	–	–	–	–	–	–	3.1	6.1
Selinum carvifolia	2	13	19	–	9	4	–	15	44	–	–	1.6	–	–	–	–	–	6.0
Molinia arundinacea et *caerulea*	5	3	–	–	11	9	–	100	87	–	–	–	–	–	–	–	13	8.6
Succisa pratensis	–	7	9	–	11	–	–	77	72	–	–	–	–	–	–	–	11	7.6
Potentilla erecta	–	–	2	4	14	–	–	52	69	–	–	–	–	–	–	–	7.2	8.6
Carex panicea	10	10	5	27	42	4	–	72	87	–	–	–	–	1.7	–	–	6.7	7.4
Leontodon hispidus	5	17	9	12	2	–	–	45	49	–	–	–	–	–	–	–	6.4	5.7
Linum catharticum	2	3	–	–	1	–	–	30	41	–	–	–	–	–	–	–	5.8	7.0
Carex flacca	–	–	–	–	5	–	–	28	41	–	–	–	–	–	–	–	5.4	7.0
Species diagnostic for more than one cluster																		
Taraxacum officinale agg.	37	77	79	92	14	–	8	15	18	–	4.7	7.2	6.1	–	–	–	–	–
Rumex acetosa	20	53	89	31	86	22	–	15	49	–	–	6.6	–	7.5	–	–	–	–
Scirpus sylvaticus	3	–	9	–	58	52	100	3	5	–	–	–	–	9.1	3.7	6.8	–	–
Other species with frequency > 10 %																		
Ranunculus acris	32	80	82	77	84	17	–	78	95	–	1.4	2.4	–	3.3	–	–	1.7	3.7
Ranunculus repens	88	67	65	62	77	26	25	33	36	4.9	–	–	–	3.5	–	–	–	–
Alopecurus pratensis	83	97	88	69	63	48	67	3	10	4.3	4.5	5.0	1.3	1.1	–	–	–	–
Sanguisorba officinalis	19	77	82	8	64	22	25	60	62	–	2.8	4.9	–	2.4	–	–	1.3	1.2
Festuca pratensis agg.	36	50	79	85	65	13	–	28	64	–	–	4.4	3.4	2.7	–	–	–	1.6
Lathyrus pratensis	20	93	68	8	73	70	25	18	54	–	5.0	3.1	–	4.7	2.0	–	–	–
Lysimachia nummularia	59	80	61	19	70	13	8	17	36	2.0	3.7	2.3	–	4.6	–	–	–	–
Deschampsia cespitosa	32	37	60	12	56	13	8	43	82	–	–	2.4	–	2.2	–	–	–	4.9
Poa trivialis	44	23	68	50	60	39	75	3	10	–	–	4.6	1.0	4.0	–	2.4	–	–
Plantago lanceolata	25	80	51	27	36	–	–	47	64	–	4.6	1.7	–	–	–	–	1.0	3.2
Centaurea jacea agg.	22	57	33	42	25	–	–	58	74	–	2.3	–	–	–	–	–	3.7	5.1
Achillea millefolium agg.	15	50	63	58	32	4	8	28	59	–	1.5	4.4	2.3	–	–	–	–	3.0
Cirsium canum	22	23	51	42	38	–	–	35	51	–	–	2.9	–	–	–	–	–	2.4
Trifolium pratense	27	30	39	65	33	–	8	25	41	–	–	1.2	3.8	–	–	–	–	1.3
Prunella vulgaris	15	37	26	19	26	9	–	55	54	–	–	–	–	–	–	–	4.5	3.4
Vicia cracca	27	57	40	23	19	30	8	7	54	–	3.6	2.2	–	–	–	–	–	3.7
Festuca rubra agg.	5	17	53	–	51	17	–	13	49	–	–	4.4	–	5.0	–	–	–	3.0
Ranunculus auricomus agg.	19	57	49	4	37	70	–	2	13	–	3.6	3.8	–	2.0	4.5	–	–	–
Leucanthemum vulgare agg.	24	57	40	23	27	–	–	13	46	–	3.7	2.3	–	–	–	–	–	2.7
Agrostis stolonifera	49	33	12	38	28	–	8	32	18	4.1	–	–	1.3	–	–	–	–	–
Carex gracilis	37	37	16	8	25	43	25	22	28	2.1	1.4	–	–	–	2.0	–	–	–
Carex hirta	19	57	28	50	40	–	8	3	21	–	4.0	–	2.9	3.2	–	–	–	–
Lysimachia vulgaris	34	13	7	–	21	57	42	12	56	2.0	–	–	–	–	3.8	1.5	–	5.0
Lythrum salicaria	37	33	5	–	26	17	42	30	23	2.6	1.3	–	–	–	–	1.5	1.2	–
Lotus corniculatus	8	33	14	31	12	–	–	42	38	–	1.7	–	1.3	–	–	–	4.3	2.8
Equisetum arvense	10	33	16	15	20	22	25	10	36	–	2.1	–	–	–	–	–	–	2.9
Trifolium repens	14	17	32	46	28	–	–	7	3	–	–	2.8	3.8	2.6	–	–	–	–
Colchicum autumnale	7	43	40	8	14	9	–	–	31	–	3.9	5.0	–	–	–	–	–	2.3
Galium uliginosum	–	–	5	–	30	48	25	12	46	–	–	–	–	3.4	4.0	–	–	5.1
Trifolium hybridum	36	30	18	15	23	9	–	–	–	4.2	2.0	–	–	1.8	–	–	–	–
Carex acutiformis	7	13	4	12	17	43	–	22	15	–	–	–	–	–	4.1	–	1.7	–
Phragmites australis	5	–	7	–	16	35	17	30	21	–	–	–	–	–	2.9	–	3.7	1.1
Phalaris arundinacea	32	27	14	4	17	4	17	–	–	4.5	2.1	–	–	1.1	–	–	–	–
Luzula campestris agg.	–	7	19	4	30	–	–	7	21	–	–	1.6	–	5.0	–	–	–	1.5
Rhinanthus minor	12	7	11	8	14	–	–	15	31	–	–	–	–	–	–	–	–	3.6
Stellaria graminea	14	37	18	4	15	9	–	–	8	–	4.3	1.3	–	–	–	–	–	–
Carex nigra agg.	2	–	2	4	27	9	–	10	36	–	–	–	–	4.6	–	–	–	4.8
Juncus articulatus	8	3	–	4	11	–	–	27	18	–	–	–	–	–	–	–	4.6	1.7

Cluster 1.2. Summer-dry, continental *Deschampsion* meadows

These are polydominant meadows, with *Alopecurus pratensis*, *Poa pratensis*, *Carex praecox* and *Serratula tinctoria* having higher cover values in places. This cluster is strongly differentiated from all other clusters by several diagnostic species of continental distribution, such as *Cnidium dubium*, *Carex praecox*, *Viola pumila*, *Veronica longifolia*, *Inula salicina* and *Carex melanostachya*. These meadows are regularly flooded for few weeks in spring, but in summer the water table often drops to approximately 1 m below ground or even deeper due to the dry continental climate (Balátová-Tuláčková 1968). They are usually mown once or twice a year, but never grazed (Šeffer & Stanová 1999). This vegetation occurs mostly in large river floodplains in SE Moravia, E Austria and W and S Slovakia (Vicherek 1962, Balátová-Tuláčková 1966, 1969, Balátová-Tuláčková & Hübl 1974, Šeffer & Stanová 1999, Vicherek et al. 2000, Zlinská & Kubalová 2001). There were no Hungarian relevés of this vegetation type in our data set; however, the "dry *Alopecuretum*" sampled by D. Steták (in preparation) along the Danube and *Carex praecox* facies of *Alopecuretum pratensis* along the Tisza river described by Tímár (1953) are very similar.

Cluster 1.3. Suboceanic *Deschampsion* meadows

These meadows may be dominated by different species, mostly by *Alopecurus pratensis* and less frequently by *Holcus lanatus*, *Poa pratensis*, *Festuca pratensis*, *Sanguisorba officinalis* and *Cirsium canum*. High fidelity values are attained by species of mesic meadows (*Arrhenatherion*), while the absence of species of tall-sedge beds (*Magnocaricion*) indicates that these meadows are less influenced by flooding than those of the previous two clusters. They are only flooded for a short time or not at all. In this respect, they are similar to Cluster 1.4, however, the presence of drought-sensitive species (e.g. *Lysimachia nummularia*, *Chaerophyllum aromaticum*, *Polygonum bistorta*) that are absent from Cluster 1.4 indicates that soils of these meadows do not dry out even in summer. This difference between Clusters 1.3 and 1.4 can be caused by the macroclimatic gradient: these communities are scattered in the Czech Republic and Slovakia but absent from Hungary, except its western part (Jeanplong 1960), while Cluster 1.4 is widespread in Hungary.

Cluster 1.4. Mesic, continental *Deschampsion* meadows

These meadows are mainly dominated by *Festuca pratensis*, which can be replaced by other grasses in some places (e.g. *Alopecurus pratensis, Deschampsia cespitosa* and *Poa pratensis*). The number of species with high fidelity values is extremely low (Table 3); these include several species of mesic hay meadows (*Arrhenatherion* alliance, e.g. *Daucus carota, Trifolium pratense, Pastinaca sativa*). On the other hand, common wet-meadow species that are absent in the *Arrhenatherion* stands occur frequently. This points to the transitional position of these meadows between wet alluvial meadows (Clusters 1.1 and 1.2) and mesic meadows (*Arrhenatherion*); they are slightly drier than the former and slightly wetter than the latter. They often occur on mesic soils above the floodplains, and if found on the floodplains, they are confined to elevated ground which is only weakly affected by floods. These meadows are usually cut once a year and not fertilized (Ružičková 1971). They are widespread across Hungary and S Slovakia, but become rare towards the northwest, where they are gradually replaced by meadows of Cluster 1.3. However, the occurrence of this type of meadow in the Czech Republic may have been underestimated in the current analysis, because some of these stands may have been originally assigned in the *Arrhenatherion* alliance in this country, and were not therefore included in our data set.

Cluster 2.1. Suboceanic *Calthion* meadows

This cluster comprises relevés mainly from the Czech Republic and Slovakia. These meadows have different dominant species and several of their diagnostic species are hygrophilous, e.g. *Caltha palustris, Myosotis palustris* agg., *Scirpus sylvaticus* and *Cirsium rivulare*. This vegetation usually occurs on permanently wet, rather fertile soils (Hájek & Hájková 2004). On alluvia of large lowland rivers, it is found rarely, and then mainly in places with impeded drainage, e.g. on clay deposits (Duchoslav 1997). The centre of distribution of this vegetation type is found in montane and submontane areas with a humid climate, where it is mainly found near springs or on alluvia of small brooks (Rybníček et al. 1984). Compared with the similar Clusters 2.2 and 2.3, this cluster mostly includes stands that are regularly mown and have a higher species richness. At the five-cluster level, this cluster is separated from the other *Calthion* clusters. This distinction is consistent with the division of the *Calthion* alliance into mown, species-rich meadows of the *Calthenion* suballiance (Cluster 2.1) and abandoned, species-poor meadows of the *Filipendulenion* suballiance (Cluster 2.2). Cluster 2.3 also includes species-poor monodominant meadows (*Scirpetum sylvatici* association).

Cluster 2.2. Suboceanic unmown *Calthion* grasslands dominated by *Filipendula ulmaria*

These tall-herb communities are mainly dominated by *Filipendula ulmaria*, but *Geranium palustre*, *Carex acutiformis* or *C. cespitosa* may attain a high percentage cover in some stands. Diagnostic species include those of high-productive wet meadows (*Geranium palustre, Crepis paludosa*, *Cirsium oleraceum*) and shade-tolerant species (*Anemone nemorosa*, *Chaerophyllum hirsutum*). This vegetation often develops after cessation of regular mowing of *Calthion* meadows, often on calcium- and nutrient-rich soils (Hájek & Hájková 2004). The distribution centre of this vegetation type is the submontane and montane belts (Rybníček et al. 1984, Kučera & Šumberová 2001). At low altitudes (below 350 m) these stands only occur in few areas with a suboceanic climate, mainly in N Bohemia.

Cluster 2.3. Suboceanic unmown *Calthion* grasslands dominated by *Scirpus sylvaticus*

All relevés in this cluster are dominated by the tall graminoid *Scirpus sylvaticus*. This vegetation has low species richness and there are very few diagnostic species due to the strong competitive ability of the dominant species. Besides *Scirpus sylvaticus*, only *Urtica dioica* has a high fidelity in our analysis, obviously because of eutrophication and ruderalization. *Scirpus sylvaticus* stands develop after the cessation of moving on carbonate free, waterlogged humus-rich gleyic soils (Hájek & Hájková 2004). These stands are not typical of the floodplains of large lowland rivers; rather they are widespread on water seepage in the submontane and montane belts across the Czech Republic and Slovakia (Rybníček et al. 1984, Špániková 1982).

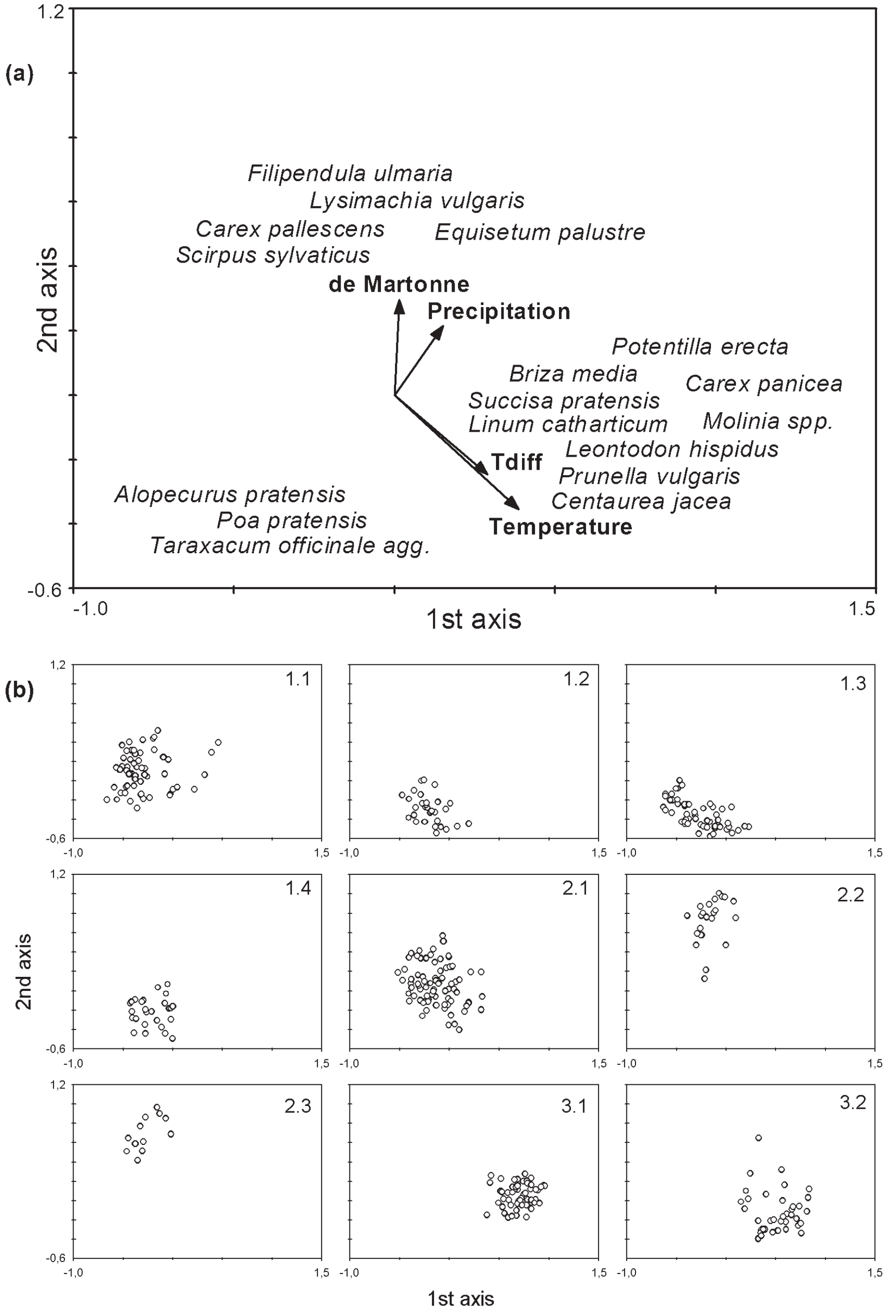

Fig. 4. – Ordination of relevés by PCoA with standardized Manhattan dissimilarity function; 1st and 2nd axis. (a) Species and passive projection of climatic variables (Temperature = mean annual temperature, Tdiff = annual temperature range, Precipitation = annual precipitation, de Martonne = humidity index). Only species, whose variation is best explained by the 1st and 2nd axis, are drawn. (b) Separation of clusters in the ordination space; cluster numbers are the same as in Table 3.

Clusters 3.1 & 3.2. *Molinion* meadows

In the cluster analysis, Cluster 3 is subdivided into two clusters (Fig. 3), which are very similar in their species composition. The basic difference is that Cluster 3.1 is species-poor, with about 25 species per relevé, while Cluster 3.2 is species-rich, with around 40 species. Traditional phytosociological classification usually divides *Molinia* meadows into two groups according to their position on the gradient from calcium-rich to low pH soils (Kovács 1962). Such groups were not distinguished by the current numerical classification. Nevertheless, we do not deny existence of this pattern, since the acidic type, which is more typical of higher altitudes, was only represented by a few relevés in our data set.

These meadows are dominated by *Molinia arundinacea* or *M. caerulea*. They are very clearly distinguished from the other meadow types, as documented by a high number of species with high fidelity values (Table 3). There are some specialist species in *Molinia* meadows (e.g. *Gentiana pneumonanthe*, *Succisa pratensis*), but species of short oligotrophic grasslands (e.g. *Danthonia decumbens*, *Nardus stricta*, *Potentilla erecta*) and base-rich fens (e.g. *Carex davalliana*, *C. hostiana*) are also common. These meadows occur outside the floodplains, are traditionally unmanured and mown only once a year or every second year (Ellenberg 1996, Ellmauer & Mucina 1993, Kučera & Šumberová 2001). This type of *Molinia* meadows is widespread in the lowlands of S Slovakia and Hungary, but very rare in the Czech Republic, where *Molinia* meadows are mainly found on mineral soils at higher altitudes (Kučera & Šumberová 2001).

Ordination and macroclimatic relationships

Separation of the clusters in the space of the first two ordination axes of PCoA is shown in Fig. 4b. Along the first axis *Molinion* clusters (3.1 and 3.2) are separated from the other clusters. Unmown *Calthion* meadows (Clusters 2.2 and 2.3) are far from the *Deschampsion* relevés (1.1 to 1.4), while the cluster of mown *Calthion* meadows (2.1) is closer.

Molinion meadows seem to be confined to the areas with a high mean annual temperature and a high annual temperature range (Fig. 4a). However, this pattern is probably an artifact of the rarity of the *Molinion* meadows in lowlands of the cooler Czech Republic and their higher abundance in the lowlands of the warmer parts of Central Europe, i.e. in Hungary and S Slovakia. In reality, the lowland *Molinion* stands in Hungary and Slovakia usually occur where the mesoclimatic conditions are colder than the macroclimate (Kovács 1957). *Calthion* meadows, on the other hand, are associated with a more oceanic type of climate, which is wetter, with lower mean temperatures and narrower temperature differences (Fig. 4a). *Deschampsion* meadows are found in the macroclimatically driest areas of Central Europe: their soils are wet in spring due to floods but dry out in summer.

Climatic factors, however, explain only a small amount of the variation along the first and second PCoA axes (Table 5). Species whose distribution patterns are best explained by the first or second axis largely overlap with diagnostic species of the three alliances (Fig. 4, Table 3). The first axis can presumably be interpreted as a gradient from mineral soils (left-hand part) to organic soils and fens (right-hand part), while the second axis seems to follow the pattern of soil moisture in summer, ranging from dry soils in the bottom part of the ordination diagram to moist soils in the upper part.

Unlike the first two axes, the third axis is strongly related to macroclimatic variables (Table 5), i.e. increasing temperature, temperature differences, decreasing humidity and

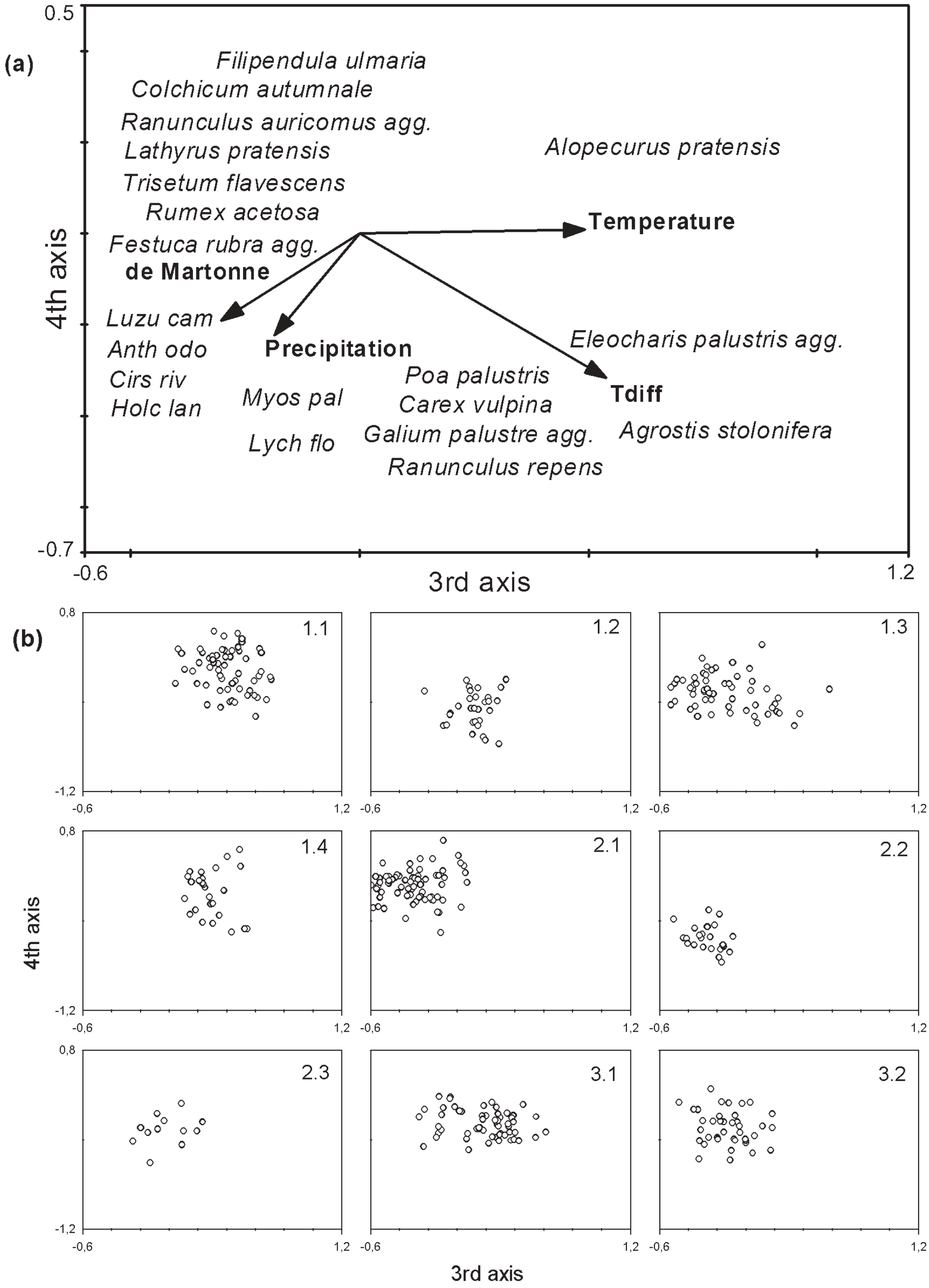

Fig. 5. – Ordination of relevés by PCoA with standardized Manhattan dissimilarity function; 3rd and 4th axis. (a) Species (Anth odo = *Anthoxanthum odoratum*, Cirs riv = *Cirsium rivulare*, Holc lan = *Holcus lanatus*, Luzu cam = *Luzula campestris* agg., Lych flo = *Lychnis flos-cuculi*, Myos pal = *Myosotis palustris* agg.) and passive projection of climatic variables (Temperature = mean annual temperature, Tdiff = annual temperature range, Precipitation = annual precipitation, de Martonne = humidity index) into the ordination space. Only species, whose variation is best explained by the 3rd and 4th axis, are drawn. (b) Separation of clusters in the ordination space; cluster numbers are the same as in Table 3.

precipitation, which account for a high amount of the variation (Fig. 5). The third axis can therefore be interpreted as a climate continentality gradient. This gradient is important within the *Deschampsion* cluster. The subocenic type of *Deschampsion* meadows (Cluster 1.3) is characterized by generalist species of mesic meadows of the *Arrhenatherion* alliance (e.g. *Festuca rubra* and *Trisetum flavescens*), many of which are rare in the Pannonian floristic province due to its continental climate. Several species of this cluster are common in Hungary (e.g. *Anthoxanthum odoratum, Luzula campestris* and *Holcus lanatus*), but are absent from alluvial meadows.

Climatic relationships examined by Kruskal-Wallis analysis (Table 4) showed that the de Martonne humidity index proved to be a better indicator of dry or wet macroclimate than precipitation (Table 4). *Calthion* clusters (except Cluster 2.3, possibly due to its small size) were significantly more humid than *Deschampsion* clusters. Using the mean annual temperature, two main clusters can be distinguished. *Calthion* clusters (2.1, 2.2 and 2.3) and suboceanic *Deschampsion* meadows (1.3) are found in the cooler areas, while the other *Deschampsion* clusters and lowland *Molinion* meadows are confined to warmer areas. The annual temperature range is lowest in the *Calthion* meadows and in the suboceanic *Deschampsion* meadows (Cluster 1.3). It means that the macroclimate of the suboceanic *Calthion* alliance and the most suboceanic subcluster of the continental *Deschampsion* alliance do not differ in the thermic component of continentality but differ in humidity.

Table 4. – Comparison of climatic variables for individual clusters. Values are medians. Clusters in columns with the same letter do not differ significantly in Kruskal-Wallis and Dunn's test at $P < 0.05$.

	Precipitation (mm)	Humidity (de Martonne index)	Mean annual temperature (°C)	Annual temperature range (°C)
Cluster 1.1	625.0^{abc}	32.7^{ab}	9.3^{bcd}	22.0^{b}
Cluster 1.2	525.0^{a}	28.4^{a}	9.5^{cd}	21.5^{ab}
Cluster 1.3	575.0^{ab}	31.1^{ab}	8.5^{abc}	19.5^{a}
Cluster 1.4	612.5^{abc}	31.7^{abc}	9.8^{cd}	22.3^{b}
Cluster 2.1	650.0^{c}	36.1^{cd}	8.0^{a}	20.5^{a}
Cluster 2.2	625.0^{c}	36.8^{d}	7.5^{ab}	19.5^{a}
Cluster 2.3	625.0^{abc}	34.8^{bcd}	7.5^{ab}	19.5^{ab}
Cluster 3.1	600.0^{bc}	30.4^{ab}	9.8^{d}	21.5^{b}
Cluster 3.2	625.0^{bc}	34.2^{bcd}	9.0^{cd}	21.5^{ab}

Table 5. – Correlation coefficients between climatic variables and PCoA axes. *** $P < 0.001$, ** $P < 0.01$, NS – not significant at $P < 0.05$.

	axis			
	1	2	3	4
Precipitation (mm)	0.16^{**}	0.17^{**}	-0.24^{***}	-0.23^{***}
Humidity (de Martonne index)	0.03^{NS}	0.22^{***}	-0.38^{***}	-0.20^{***}
Mean annual temperature (°C)	0.37^{***}	-0.22^{***}	0.60^{***}	0.02^{NS}
Annual temperature range (°C)	0.28^{***}	-0.10^{NS}	0.60^{***}	-0.31^{***}

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Souhrn

Nížinné vlhké louky střední Evropy patří k ohroženým biotopům, ale jejich postavení v systému klasifikace vegetace bylo do značné míry závislé na rozdílných fytocenologických tradicích různých zemí. Za účelem mezinárodního sjednocení jejich klasifikace jsme provedli statistickou analýzu stratifikovaného souboru 387 fytocenologických snímků z České republiky, východního Rakouska, Slovenska, Maďarska a severního Chorvatska, zapsaných v nadmořských výškách pod 350 m. Pomocí analýzy hlavních koordinát (PCoA) jsme odstranili nesystematickou složku variability (šum) v datech a klasifikovali jsme snímky pomocí shlukové analýzy. Byla vyvinuta a použita nová metoda pro určení optimálního počtu shluků, založená na fidelitě druhů k jednotlivým shlukům. Tato metoda identifikovala tři shluky jako optimální úroveň klasifikace a pět, respektive devět shluků jako sekundární optimální úrovně.

Klasifikace se třemi shluky odlišila tradiční fytocenologické svazy *Calthion palustris* a *Molinion caeruleae*, oba se suboceanicky laděnou fytogeografickou tendencí, a skupinu zaplavovaných luk s kontinentální tendencí na aluviích velkých nížinných řek. Tato kontinentální skupina zahrnula vegetaci tradičně řazenou ke svazům *Agrostion albae*, *Alopecurion pratensis*, *Cnidion venosi*, *Deschampsion cespitosae* a *Veronico longifoliae-Lysimachion vulgaris*; její vnitřní rozrůzněnost však neodrážela hranice mezi svazy tak, jak jsou uváděny v tradiční fytocenologické literatuře. Z toho důvodu navrhujeme považovat tuto skupinu za jediný svaz, pro který musí být přijato nejstarší platné jméno *Deschampsion cespitosae* Horvatić 1930. Klasifikace s devíti shluky (tab. 3) byla interpretována na úrovni širokých fytocenologických asociací. Jednotlivé shluky byly charakterizovány statisticky definovanými diagnostickými druhy a vztaženy k makroklimatickým proměnným.

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