Vegetation diversity of mesic meadows and pastures in the West Carpathians

Diverzita vegetace mezofilních luk a pastvin v Západních Karpatech

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A phytosociological study of the West Carpathian mesic hay meadows and pastures (order *Arrhenatheretalia elatioris*) was performed and is the first unified investigation into the vegetation diversity in the area, which is situated in three countries (Slovakia, Czech Republic and Poland). Because of the differences in the current classification systems used in different countries it was not possible to make a single selection of the *Arrhenatheretalia* relevés from the databases, so a data set containing relevés originally assigned to three orders encompassing this vegetation in hay meadows and pastures in the area (*Arrhenatheretalia elatioris*, *Molinietalia* and *Nardetalia strictae*) was established. This data set was classified using cluster analysis. Only the cluster corresponding to the order *Arrhenatheretalia elatioris* at the level of three clusters was further classified in the same way as the whole data set. The ecological interpretation of the classification was based on altitude, Ellenberg indicator values and geological bedrock. The clusters were also compared with the syntaxonomical assignment of the relevés by their authors. The classification at the level of 12 clusters reflected the most widespread vegetation types of mesic meadows and pastures recorded in the area. The vegetation of extensive pastures, corresponding to the association *Anthoxantho odorati-Agrostietum tenuis,* seemed to be more similar in floristic composition to the mesic meadows of *Arrhenatherion elatioris* than to the intensive pastures of *Cynosurion cristati,* where it was traditionally classified, which has important conservation consequences because of the different position of these units in conservation systems such as Natura 2000. Higher altitude meadows were divided into four vegetation types including meadows corresponding to the association *Gladiolo imbricati-Agrostietum capillaris*, which is a frequent community in the Polish Carpathians that does not occur in the other regions. Montane meadows currently classified in *Polygono bistortae-Trisetion flavescentis* were less clearly distinguished, probably because of their patchy distribution in the West Carpathians. The differences in vegetation diversity of meadows and pastures between particular countries were confirmed, with *Gladiolo imbricati-Agrostietum capillaris* occurring predominantly in the northern part of the West Carpathians and *Anthoxantho odorati-Agrostietum tenuis* virtually absent here. The ecological determinants of variation in montane meadows are discussed.

K e y w o r d s: hay meadow, mesic pasture, vegetation classification, vegetation diversity, West Carpathians

Introduction

Meadows and pastures are the most widespread semi-natural habitats in the West Carpathians, have a long history and are of great importance to conservation (Šeffer et al. 2002, Jongepierová 2008). Because these habitats were created by man, their existence has been conditioned by traditional management and their diversity mirrors not only edaphic and climatic conditions (Critchley et al. 2002, Kalusová et al. 2009) but also historical and present management (Schaffers 2002, Gustavsson et al. 2007, Klimek et al. 2007, Chýlová & Münzbergová 2008, Başnou et al. 2009, Karlík & Poschlod 2009). Meadows and pastures are the only habitat of many endangered species and because they are frequently species-rich they greatly enhance local species diversity. As a consequence of management intensification or abandonment, meadows and pastures have diminished (Šeffer et al. 2002). The decline in traditional meadows and pastures has resulted in the loss of refuges for many rare species.

At the beginning of the 20th century several studies were made of the vegetation of West Carpathian meadows and pastures, some of which resulted in the description of new vegetation units (e.g. Braun-Blanquet 1930, Sillinger 1933). Further studies were published recently (e.g. Hadač et al. 1969, Ružičková 2002, 2004). The results are only valid at a regional scale as these studies were mostly of small areas. There have been syntheses of current knowledge and overviews of vegetation units for particular countries (Matuszkiewicz 1982, Moravec et al. 1983, Mucina & Maglocký 1985, Jarolímek et al. 2008), however, the classification systems used were rather uncritically compiled. The development of large phytosociological databases in the 1990s resulted in the revision of previous classification systems (Schaminée et al. 2009). Parts of the West Carpathians were surveyed as part of the projects "Plant communities of Slovakia" (Valachovič 1995) and "Vegetation of the Czech Republic" (Chytrý 2007a). In addition to unifying the classification for a particular country, the studies also revealed that classification conceptions differ between the countries. It means that the grassland vegetation is classified in three different ways in the West Carpathians (compare Chytrý 2007b for the Czech Republic, Janišová 2007a for Slovakia and Matuszkiewicz 2007 for Poland).

The vegetation of mesic meadows and pastures (order *Arrhenatheretalia elatioris* Tüxen 1931) is similarly classified in the Czech Republic and Slovakia. The major difference is in the concept of the association *Anthoxantho odorati-Agrostietum tenuis* Sillinger 1933, which is widely distributed in extensive pastures (Hájková et al. 2007, Uhliarová et al. 2007). There are bigger discrepancies between these two classifications and the Polish classification, which is still based on regional studies. Mesic meadows in the submontane and montane zone of the Polish West Carpathians are classified in the association *Gladiolo imbricati-Agrostietum capillaris* Br.-Bl. 1930 ex Pawłowski et Walas 1949. Rich hay meadows with *Gladiolus imbricatus* in the Polish Tatra Mts were first described by Szafer et al. (1923) as *Agrostidetum vulgaris*. Nevertheless, these authors did not differentiate this vegetation from that of meadows with *Agrostis capillaris* in the Alps and mountains of central France. This community was delimited as a separate association by Braun-Blanquet (1930), who recorded it in the Belianské Tatry Mts (Slovakia). The Polish regional phytosociological research in the 1950s and 1960s resulted in a detailed description of the floristic and ecological features of the association and its delimitation into several subassociations and varieties (Pawłowski et al. 1960, Grodzińska 1961, Kornaś & Medwecka-Kornaś 1967, Stuchlikowa 1967). It is considered to be endemic to the West Carpathian territory, occurring in the northern part of the Carpathians (Pawłowski et al. 1960, Kornaś 1967). Nevertheless, the short note in Braun-Blanquet (1930) and one record for the Slovenské Rudohorie Mts (Šimurdová & Šomšák 2000) are the only records of *Gladiolo-Agrostietum* in Slovakia. Montane meadows in the Slovakian Carpathians are assigned to several associations with local distributions (Hegedüšová & Ružičková 2007). Because of the wide altitudinal and ecological amplitude of *Gladiolo-Agrostietum* there was no need to delimitate it from *Poo-Trisetetum flavescentis* Knapp ex Oberdorfer 1957 in the Polish classification system. Another association not distinguished in Poland is *Anthoxantho odorati-Agrostietum tenuis*. Therefore, the distributions of the above mentioned vegetation units are partly determined by state borders. These inconsistencies within the West Carpathians result from the different traditions of classification in particular countries. However, they might have a real basis in environmental conditions or management history and it is worth testing whether differences in vegetation really mirror state borders.

The coordination of the classification of vegetation at an international level is not only an academic matter because the classification is the basis for the interpretation of the habitats of European conservation interest within the Natura 2000 network (Council Directive 92/43/EEC 1992). Although the problems caused by the inconsistencies in the classification sytems used in different countries have been studied in the case of central European lowland wet meadows and dry grasslands (Botta-Dukát et al. 2005, Illyés et al. 2007, Dúbravková et al. 2010), this is not the case for mesic and montane meadows and pastures. Studies using relevés from the entire area of the West Carpathians could be used to review current national classifications in order to determine whether geographically distinct distributions of some vegetation units really exist depending on specific environmental conditions.

Supervised classification seems to be the most appropriate method of producing a classification system for the vegetation of an area (Chytrý 2007a). This method is based on using formal definitions to select appropriate relevés from a large phytosociological database in order to obtain a classification consisting of well defined units of vegetation. In contrast to traditional classifications based on unsupervised methods, supervised formalized classification is independent of the data set being classified and therefore more applicable to different data sets when the goal is to obtain a classification system of similar structure or reproduce an already established classification (Bruelheide & Chytrý 2000). By contrast, unsupervised methods can reveal the diversity of vegetation at a particular place and time based on similarities in species composition or the main vegetation gradients, which can reveal the floristic similarities of the vegetation units. Therefore, there is a complementary relationship between traditional and formalized classifications (Roleček 2007).

In this study, we use an actual set of relevés of grassland vegetation in the West Carpathians. The intention is to describe the diversity of vegetation of meadows and pastures in the area. The aims of the study are: (i) to determine the main types of vegetation growing in mesic meadows and pastures in the West Carpathians; (ii) to compare the resulting classification with that used traditionally in particular countries; and (iii) to interpret ecologically particular vegetation types, in particular that of meadows at high altitudes.

Materials and Methods

Study area

For a definition of the area of the West Carpathians, the geomorphological concepts of Mazúr & Lukniš (1986) and Demek & Mackovčin (2006) were used as the main guides. The Western Carpathian province comprises subprovinces of the Outer Western Carpathians and Inner Western Carpathians. In the north and west, the area is surrounded by the Outer Carpathian depressions. The eastern margin is formed by the Wiśnicz Piedmont, the Beskid Wyspowy Mts, the Beskid Sądecki Mts, the Čergov Mts and the Šarišská vrchovina Highlands. In the south, the Western Carpathians are surrounded by the Pannonian Basin. Three geomorphological areas in the south of the Western Carpathians, the South-Moravian Carpathians, the Lučenec-Košice Depression and the Mátra-Slanec Area, were not included in the study area. From the floristic point of view, these regions are in the Pannonian flora area, which occupies an outlying position in the West Carpathians (Futák 1972, Szafer & Zarzycki 1972).

Vegetation data

Relevés were collected from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) and the Central Database of the Phytosociological Data in Slovakia (Hegedüšová 2007). Published relevés from Poland were digitalized (Electronic Appendix 1). A few of the relevés came from the authors' field research. In this study, the vegetation of mesic meadows and pastures falling within the order *Arrhenatheretalia elatioris* was of particular interest. The simple selection of relevés assigned to this order by the original authors was nevertheless not applicable because of the different classification systems (e.g. different higher rank classification of *Holcetum lanati* Issler 1934 or different conception of *Anthoxantho odorati-Agrostietum tenuis*) used in the national databases (Moravec et al. 1995, Jarolímek et al. 2008). Because these discrepancies resulted in overlaps mainly between mesic meadows and wet meadows, and mesic pastures and grasslands with *Nardus stricta*, the large initial data set contained relevés originally assigned to the vegetation of meadows and mesic pastures (orders *Arrhenatheretalia elatioris* and *Molinietalia* Koch 1926 from the class *Molinio-Arrhenatheretea*) and submontane and montane grasslands (order *Nardetalia strictae* Oberdorfer ex Preising 1949 from the class *Calluno-Ulicetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944). Only relevés with an accurate geographic location and sampled using plots from 9 to 100 m^2 were included. The relevé selection was further defined by an upper altitude limit of 1500 m, which corresponds to the natural timberline in the West Carpathians (Král 1999). Relevés were imported into the program JUICE (Tichý 2002). Different species abundance scales were transformed into percentages. The initial data set contained 8040 relevés.

Preliminary analyses of the initial data set revealed that some relevés originally assigned to the vegetation of meadows and grasslands recorded transitional vegetation or other vegetation types. The most often misinterpretations of syntaxa concerned the vegetation of dry grasslands, saline grasslands, mires, ruderal habitats and subalpine tall-herb vegetation. The noise in the data was at least partly eliminated in the following two steps:

(1) Dominance of negative diagnostic species. In this step it is assumed that plant communities of meadows and pastures could harbour many species typical of other communities but these species should not dominate. Therefore, relevés that included species considered diagnostic of other vegetation units than that of *Arrhenatheretalia elatioris*, *Molinietalia* and *Nardetalia strictae* with a cover > 25% were removed. The negative diagnostic species were selected following Chytrý & Tichý (2003) and Jarolímek & Šibík (2008). These papers present diagnostic, constant and dominant species of higher vegetation units of the Czech Republic and Slovakia, respectively. Diagnostic species were determined in the same way in both papers, by calculating a phi coefficient (Sokal & Rohlf

1995, Chytrý et al. 2002) as a measure of fidelity (Chytrý et al. 2002). The negative diagnostic species were arbitrarily defined as the species with a phi > 0.24 in the other vegetation units. At the same time, a species could not be diagnostic, constant and/or dominant in vegetation units of the three above mentioned orders.

(2) Reassignment of relevés to associations following supervised classification. The "electronic expert system for identification of syntaxa of grassland vegetation of the Slovak Republic" was used to assign relevés in the initial data set to associations (Janišová 2007a). If a relevé was not assigned to any association on the basis of a formal definition or was assigned to more than one association, it was classified in one of the already defined relevé groups of given associations according to the frequency positive fidelity index (FPFI; Tichý 2005). Relevés that were assigned or closest in species composition to other associations than that of the three above mentioned orders were removed. Furthermore, relevés with a FPFI value < 0.15, i.e. relevés with very low similarity to relevés already assigned on the basis of a formal definition were removed. This value was determined arbitrarily in order to remove outlying relevés but keep the variability of the vegetation in the area. In this way, 139 relevés were removed (78 from Slovakia, 33 from the Czech Republic and 28 from Poland). Among them relevés of abandoned meadows, forest edges and of vegetation transitional to other vegetation types dominated. This selection can have a negative effect as it eliminates variability in vegetation that is not included in the Slovakian supervised classification. In this study it resulted in the removal of several relevés but nevertheless did not markedly affect the variability in the data set.

The geographical distribution of relevés in the study area was not equal as some regions were sampled more intensively. To reduce the effect of oversampling on the analyses the relevés were geographically stratified (Knollová et al. 2005). One relevé of each association (according to the supervised classification) was randomly selected from a grid square of 1.25' longitude and 0.75' latitude (approximately 1.5 × 1.4 km). The final data set contained 4461 relevés (3215 from Slovakia, 695 from Czech Republic and 551 from Poland).

Taxa determined at the genus level were deleted from the data set. Mosses and lichens were also deleted. They were recorded in only about half of relevés and the data set, therefore, is incomplete in terms of the variation in the moss-layer. Juvenile trees and tall shrubs were deleted because they also were not recorded in all relevés. Multiple records of species in different layers were combined. In this way, all species appeared in the data set only once. Nomenclature of taxa follows Marhold & Hindák (1998). In several cases, when a narrow concept of the species listed in the checklist was not possible to apply, taxa were defined as broader aggregates and marked with the abbreviation s.l. (sensu lato). Records of critical taxa that might have been incorrectly determined were combined at the genus level. This was the case for *Alchemilla* spec. div., *Crocus discolor* (*C. discolor* and *C. heuffelianus*) and *Soldanella* spec. div. (*S. carpatica*, *S. hungarica*, *S. montana*).

Data analysis

The final data set (4461 relevés) was subjected to cluster analysis performed in the program PC-ORD 5 (McCune & Mefford 1999). The percentage covers of species were log-transformed. The cluster analysis was completed using a relative Euclidean (chord) distance measure and Ward's group linkage method. Classification proceeded in two steps. At the level of three clusters, the classification reflected the separation of the three orders included

Table 1. – Differential species of orders *Nardetalia strictae*, *Molinietalia* and *Arrhenatheretalia elatioris* determined using the phi coefficient and the West Carpathian data set (4461 relevés). Note that only relevés from altitudes ≤ 1500 m were included in the data set. Species in bold type have phi ≥ 0.5, the others a phi ≥ 0.3.

Nardetalia strictae 732 relevés	*Molinietalia* 1462 relevés	*Arrhenatheretalia elatioris* 2267 relevés
Acetosa arifolia, *Agrostis capillaris*, *Antennaria dioica*, *Avenella flexuosa*, *Carex pilulifera*, *Carlina acaulis*, *Hieracium lachenalii*, *Pilosella officinarum*, *Homogyne alpina*, *Hypericum maculatum*, *Luzula luzuloides*, ***Nardus stricta***, *Phleum rhaeticum*, *Poa chaixii*, *Potentilla aurea*, *Potentilla erecta*, ***Vaccinium myrtillus***, *Veronica officinalis*	*Angelica sylvestris*, ***Caltha palustris***, *Cardamine pratensis* agg., *Carex flava* agg., *Carex hirta*, *Carex nigra*, *Carex panicea*, *Cirsium oleraceum*, *Cirsium palustre*, ***Cirsium rivulare***, *Crepis paludosa*, *Dactylorhiza majalis*, ***Equisetum palustre***, ***Filipendula ulmaria***, *Galium palustre* agg., *Galium uliginosum*, *Juncus articulatus*, *Juncus conglomeratus*, *Juncus effusus*, *Lathyrus pratensis*, *Lychnis flos-cuculi*, *Lysimachia nummularia*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Mentha arvensis*, *Mentha longifolia*, ***Myosotis scorpioides* agg.**, *Poa trivialis*, *Ranunculus repens*, ***Scirpus sylvaticus***, *Valeriana simplicifolia*	*Achillea millefolium* agg., *Arrhenatherum elatius*, *Campanula patula*, *Crepis biennis*, ***Dactylis glomerata* agg.**, *Daucus carota*, *Galium mollugo* agg., *Knautia arvensis* agg., *Leontodon hispidus*, *Leucanthemum vulgare* agg., *Lotus corniculatus* agg., *Pimpinella saxifraga* agg., *Plantago lanceolata*, *Plantago media*, *Poa pratensis* agg., *Ranunculus bulbosus*, *Salvia pratensis*, ***Taraxacum* sect. *Ruderalia***, *Tragopogon orientalis*, *Trifolium pratense*, *Trifolium repens*, ***Trisetum flavescens***, *Veronica chamaedrys* agg., *Vicia cracca*

in the data set: grasslands with *Nardus stricta* (*Nardetalia strictae*), wet meadows (*Molinietalia*) and mesic meadows and pastures (*Arrhenatheretalia elatioris*; see Table 1). The last cluster (2267 relevés) was then classified separately using the same parameters. The number of final clusters was chosen in such way as to obtain easily interpretable major vegetation types of mesic meadows and pastures, using the OptimClass method (Tichý et al. 2010). The clusters were identified by their diagnostic species using the JUICE program (Tichý 2002). The diagnostic species were those with a high fidelity to a given cluster using the phi coefficient as the fidelity measure. The phi coefficient was calculated for clusters standardized to a particular size (Tichý & Chytrý 2006). The species with phi ≥ 0.2 were considered diagnostic. The significance of species occurrence concentration in the relevés of a particular cluster was calculated using Fisher's exact test (Chytrý et al. 2002), and species with a random occurrence in the cluster ($P < 0.001$) were excluded from the set of diagnostic species. The results of the classification are summarized in a synoptic table where the diagnostic species of the final clusters are ranked by decreasing phi value and percentage frequencies of the species are displayed. The species cannot be regarded as diagnostic in terms of Chytrý (2007a) and Janišová (2007b) because they were calculated only for the data set corresponding to the order *Arrhenatheretalia elatioris*. Instead, they are regarded as differential species. Furthermore, dominant species are those species with a cover > 25% in at least 20% of relevés of the respective cluster. The clusters were floristically interpreted using the actual guidebooks of grassland vegetation for the area of the West Carpathians (Chytrý 2007b, Janišová 2007a, Matuszkiewicz 2007).

To review the vegetation units traditionally used for the area of the West Carpathians, the classification of relevés into clusters using cluster analysis was compared with their assignment to vegetation units by the original authors. The ecological interpretation of the classification was done using altitude, average Ellenberg indicator values for nutrients, moisture and continentality (Ellenberg et al. 1992) calculated for relevés and geological bedrock. Digitalized geological maps of the Czech Republic (Zoubek et al. 1998) and Slovakia (Biely et al. 2002), respectively and a geological map of the Western Carpathians (for Polish relevés; Lexa et al. 2000) served as a basis for establishment of the last variable. For purposes of this study, the great diversity of geological substrates was converted into seven categories. Within the Carpathian flysch belt, the nappe of the Biele Karpaty unit was considered separately because it is formed from mineral-rich mostly claystone beds, whereas the bedrock of the other units is formed predominantly from mineral-poor sandstones. The border between the Outer Carpathian flysch belt and the Inner Carpathians is formed by a klippen belt composed of limestone and other base-rich sediments. The Inner Carpathian rocks were divided into Paleozoic units (mostly magmatic and metamorphic rocks), Mezozoic units (formed mostly by base-rich sedimentary rocks) and Neogene volcanic rocks. The sediments of the Inner Carpathian Paleogene were merged with Neogene-Quaternary sediments, which are only marginally represented. Inner-Carpathian Paleogene has the same rock composition and chemistry as Outer-Carpathian flysch; the two geological units differ mostly in morphogenetic properties. Generally, the categories can be divided according to prevalence of base-rich and acid rock into basic (Inner Carpathian Mezozoic rocks, klippen belt sediments, flysch of the Biele Karpaty unit, Neogene volcanic rocks) and acid rocks (Inner Carpathian Paleozoic rocks, Outer Carpathian flysch, Paleogene sediments). Differences in the environmental variables between the two clusters at each level of clustering were tested using the Mann-Whitney test for continuous variables and Chi-squared test for categorical variables. The statistical problem of multiple comparisons, made for eleven levels of clustering, was managed by using the Bonferroni correction. The tests were done in the STATISTICA 9 program (www.statsoft.com).

Results

The cluster analysis of the final set of relevés, which correspond to the order *Arrhenatheretalia elatioris* (2267 relevés), indicated 12 interpretable clusters (Table 2). First, the classification was checked at the level of three clusters. The three alliances of the order – *Arrhenatherion elatioris*, *Cynosurion cristati* and *Polygono bistortae-Trisetion flavescentis* – can be recognized in the clusters (see Table 2 for diagnostic species). From an ecological point of view, cluster A contains communities of low altitudes varying in nutrient availability and soil moisture. The vegetation in cluster B is characterized by higher nutrient availability and soil moisture compared to cluster A. Cluster C harbours communities of high altitudes (Fig. 1).

The classification structure, visualized by the dendrogram (Fig. 1), demonstrates the floristic similarity of the 12 clusters and their position within the three above-mentioned clusters. Except for the first one, these clusters are well differentiated by diagnostic species (Table 2) and, except for clusters 4 and 12, are distinguished by one or two species that are dominant at least in 20% of the relevés (Table 3). The original syntaxonomical assignment of relevés to particular clusters is summarized in Table 4. The classification can be interpreted also ecologicaly (Fig. 1). Significant differences in geological bedrock were found between the two respective clusters at all levels of clustering but one: between cluster 1 and 2 ($P < 0.01$; Fig. 2).

Table 2. – Synoptic table of the vegetation of mesic meadows and pastures based on cluster analysis of relevés. Percentage frequencies of species are displayed. Diagnostic species of particular clusters are ranked by decreasing fidelity to each cluster measured by the phi coefficient. Dark-shaded values indicate phi ≥ 0.3, light-shaded values phi ≥ 0.2. Letters A, B, C by species indicate species diagnostic of one of the three clusters associating meadows and extensive pastures at low altitudes (A), intensive pastures and trampled habitats (B) and high altitude meadows (C).

Cluster (3 cluster level)	A	A	A	A	A	A	B	B	C	C	C	C
Cluster (12 cluster level)	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Cluster 2: Extensive pastures												
Pilosella officinarum	8	61	12	18	5	3	–	2	19	22	4	14
Carlina vulgaris s.l.	2	33	12	–	1	–	1	3	1	–	1	1
Juniperus communis	3	24	9	1	–	–	–	–	–	2	–	1
Euphrasia rostkoviana agg.	17	45	31	9	3	5	2	11	17	21	8	17
Thymus pannonicus s.l.	1	9	–	1	–	–	1	–	–	–	–	–
Asperula cynanchica	1	16	13	1	1	1	–	–	–	–	–	2
Achillea nobilis	1	7	–	–	–	–	–	2	–	–	–	–
Cluster 3: Dry meadows in transition to semi-dry grasslands of *Festuco-Brometea*												
Salvia verticillata	2	4	35	4	2	2	1	–	2	–	1	1
Brachypodium pinnatum	11	14	51	16	3	3	1	–	2	1	1	12
Sanguisorba minor (A)	10	26	57	28	12	5	3	–	1	4	3	20
Medicago falcata	8	7	42	16	10	7	8	3	2	1	1	3
Colymbada scabiosa	4	2	35	14	4	9	3	–	5	3	2	5
Gentiana cruciata	1	–	18	1	1	1	1	–	–	–	1	5
Anthyllis vulneraria	10	21	55	27	11	5	3	–	7	12	5	38
Securigera varia (A)	7	10	43	28	23	6	2	–	1	1	1	7
Clinopodium vulgare	6	3	27	7	4	3	1	2	2	1	1	3
Bupleurum falcatum	1	–	11	1	–	1	1	–	–	–	–	–
Fragaria vesca	16	30	49	14	20	10	6	2	13	11	4	17
Plantago media (A)	46	62	87	69	44	40	29	35	19	23	16	59
Campanula glomerata agg.	7	2	35	19	14	8	4	–	6	2	3	20
Linum catharticum	18	36	49	19	13	9	2	3	13	9	5	38
Libanotis pyrenaica	1	–	9	–	–	1	2	–	–	–	–	–
Calamagrostis varia	1	–	7	–	–	–	–	–	–	–	–	1
Carex tomentosa	1	1	16	5	2	1	–	2	1	1	–	9
Knautia maxima	1	–	9	–	1	1	–	–	–	–	–	3
Parnassia palustris	–	–	9	–	–	1	–	–	2	1	1	2
Helianthemum nummularium agg.	2	19	26	5	3	1	2	–	2	4	1	23
Trifolium medium agg.	14	7	36	15	8	4	2	–	31	6	6	23
Agrimonia eupatoria	23	30	37	24	13	10	16	3	1	1	1	3
Carex flacca	5	2	19	5	1	1	2	5	4	2	–	10
Potentilla heptaphylla	6	23	33	27	11	6	2	2	–	4	3	17
Hypericum perforatum	17	38	44	36	19	12	14	5	4	12	1	14
Cluster 4: Dry meadows with *Arrhenatherum elatius*												
Festuca rupicola (A)	15	19	17	56	14	11	10	2	1	3	–	9
Salvia pratensis (A)	8	20	27	63	40	24	8	3	–	1	1	16
Steris viscaria	3	9	9	33	8	2	2	–	1	9	–	10
Ranunculus bulbosus	11	32	18	49	14	18	14	–	2	8	4	13
Dianthus carthusianorum s.l.	6	12	34	49	13	12	15	2	2	7	4	32
Fragaria viridis	8	14	4	30	10	4	4	–	2	3	–	4
Bromus erectus s.l. (A)	5	7	8	26	14	5	1	–	–	–	–	8
Primula veris (A)	11	6	27	37	17	11	4	–	2	1	4	14
Pimpinella saxifraga agg. (A)	44	67	64	83	45	41	23	18	24	68	18	50
Silene nutans	3	3	16	24	3	2	2	–	1	7	2	15
Avenula pubescens	10	4	12	34	7	15	3	–	2	10	12	28

Cluster (3 cluster level)	A	A	A	A	A	A	B	B	C	C	C	C
Cluster (12 cluster level)	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Cluster 5: Mesic meadows with *Arrhenatherum elatius*												
Pastinaca sativa	4	–	2	3	25	11	5	5	2	–	–	–
Cluster 6: Eutrophic meadows with *Trisetum flavescens*												
Crepis biennis (A)	31	2	26	34	42	61	15	6	31	7	30	11
Trisetum flavescens (A)	60	9	67	88	68	97	43	8	42	53	89	56
Bromus hordeaceus	5	2	–	5	14	29	18	6	5	1	6	1
Anthriscus sylvestris	13	3	6	17	21	39	15	2	5	3	21	5
Glechoma hederacea s.l.	10	1	3	14	23	32	14	6	4	3	11	3
Cluster 7: Intensive pastures and eutrophic meadows with *Festuca pratensis*												
Capsella bursa-pastoris (B)	1	–	–	1	1	3	15	8	1	–	1	–
Rumex crispus (B)	8	1	2	1	5	7	24	11	6	2	4	1
Tripleurospermum perforatum (B)	1	–	–	–	1	1	13	9	–	–	–	–
Trifolium hybridum (B)	5	1	3	1	5	3	22	3	14	7	1	2
Cluster 8: Trampled habitats with perennial species												
Lolium perenne (B)	16	17	–	2	5	8	28	100	3	1	1	–
Poa annua (B)	1	1	–	–	1	–	6	57	4	–	–	–
Plantago major (B)	17	5	1	2	6	6	26	75	7	3	–	1
Potentilla anserina (B)	5	1	2	–	1	3	12	45	2	–	–	1
Bellis perennis (B)	15	11	1	8	13	26	15	63	12	3	17	3
Polygonum aviculare agg.	–	–	–	1	1	–	3	12	1	–	–	1
Ranunculus repens (B)	17	6	–	2	18	24	31	55	36	12	26	2
Matricaria discoidea	–	–	–	–	–	–	–	8	–	–	–	–
Odontites vulgaris agg.	4	1	–	1	–	1	1	12	1	–	–	–
Carduus acanthoides	2	2	2	–	–	–	2	11	–	–	1	1
Sagina procumbens	1	–	–	–	–	–	–	11	9	–	–	–
Cluster 9: High altitude meadows with *Agrostis capillaris*												
Gladiolus imbricatus (C)	1	–	2	1	1	5	–	–	44	11	11	9
Omalotheca sylvatica	1	3	–	–	1	1	–	2	17	4	2	1
Holcus mollis	1	1	–	–	3	1	–	2	19	13	6	1
Agrostis capillaris (C)	73	91	57	52	26	26	35	58	98	87	63	78
Phleum pratense	33	11	21	13	16	34	47	31	67	44	60	16
Rhinanthus serotinus agg.	4	1	7	2	1	3	3	2	23	6	11	8
Gentiana asclepiadea (C)	1	–	–	–	1	–	–	–	14	6	11	3
Jacea pratensis s.l.	31	34	34	39	45	35	17	11	64	39	18	21
Cluster 10: High altitude nutrient-poor meadows with *Festuca rubra*												
Carex pilulifera	2	1	4	1	–	1	–	–	2	20	–	7
Luzula campestris s.l. (C)	39	50	37	73	37	43	12	12	60	91	62	68
Polygala vulgaris (C)	18	38	37	22	9	10	2	2	23	56	7	45
Carex pallescens (C)	23	9	19	24	6	9	7	2	38	52	15	46
Nardus stricta (C)	15	31	7	10	–	1	3	8	28	44	10	38
Stellaria graminea (C)	42	27	26	28	27	48	38	15	71	77	46	46
Festuca rubra agg. (C)	80	79	71	64	65	48	40	23	68	98	74	80
Cluster 11: Montane meadows with *Trisetum flavescens*												
Myosotis scorpioides agg. (C)	5	1	–	3	4	8	5	2	28	14	49	15
Lychnis flos-cuculi	12	3	–	9	18	31	19	2	31	26	50	12
Vicia sepium (C)	16	1	8	10	17	17	8	–	28	13	43	21
Rhinanthus pulcher	1	–	–	–	–	1	–	–	–	–	7	1
Alchemilla spec. div. (C)	66	47	66	56	31	56	47	48	86	92	99	91
Cluster 12: Semi-dry montane meadows on base-rich bedrock												
Primula elatior (C)	8	1	10	2	1	8	3	–	15	17	29	56

Cluster (3 cluster level)	A	A	A	A	A	A	B	B	C	C	C	C
Cluster (12 cluster level)	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Trollius altissimus (C)	1	–	1	2	–	–	1	–	1	1	2	19
Phyteuma orbiculare	1	–	9	–	1	1	1	–	–	1	1	21
Campanula serrata (C)	7	–	8	3	–	2	–	–	2	1	2	24
Colchicum autumnale	22	5	31	39	26	29	17	–	9	17	26	65
Luzula luzuloides (C)	2	1	4	2	2	1	1	–	7	18	16	31
Cruciata glabra (C)	53	47	65	68	17	39	22	5	57	69	71	93
Cirsium erisithales	1	–	2	–	–	2	–	–	1	–	1	12
Potentilla aurea (C)	1	1	–	–	–	–	2	–	9	17	20	24
Gymnadenia conopsea (C)	1	2	13	1	1	1	–	–	12	11	7	22
Thesium alpinum	–	1	–	–	–	–	–	–	–	–	–	5
Geranium sylvaticum (C)	4	–	6	1	–	2	2	–	6	1	19	20
Viola canina (C)	13	35	22	29	7	7	2	–	7	32	3	41
Jacea phrygia agg.	21	5	22	33	6	16	20	5	17	28	25	47
Species diagnostic for two clusters												
Tithymalus cyparissias (A)	18	59	51	30	24	3	6	14	5	3	1	9
Thymus pulegioides	29	77	75	51	17	8	8	15	20	41	8	62
Leontodon autumnalis	27	46	3	4	18	10	18	51	30	12	6	2
Carlina acaulis (C)	11	42	69	25	7	7	6	–	14	34	8	53
Trifolium montanum	11	16	60	36	12	10	4	–	9	7	4	60
Briza media (C)	43	64	93	74	51	30	12	6	38	68	27	83
Viola hirta (A)	12	18	44	42	19	10	4	–	2	2	1	12
Arrhenatherum elatius (A)	46	10	66	91	99	72	28	3	9	18	20	34
Tragopogon orientalis (A)	29	7	51	66	36	44	14	–	6	13	21	59
Alopecurus pratensis (B)	13	2	1	34	24	37	48	5	9	7	46	8
Hypericum maculatum (C)	38	9	22	24	7	16	19	9	81	83	64	64
Senecio subalpinus (C)	–	–	–	–	–	–	–	–	16	1	17	2
Cardaminopsis halleri (C)	1	–	2	1	1	4	1	–	26	13	30	16
Potentilla erecta (C)	21	41	26	15	8	3	6	9	54	68	12	63
Crepis mollis (C)	3	–	1	–	–	3	1	–	9	8	26	27
Other species with frequency ≥ 20% in at least one cluster												
Achillea millefolium agg.	89	90	83	92	86	88	83	92	85	93	77	79
Plantago lanceolata	83	87	79	94	79	79	50	74	82	94	66	74
Trifolium pratense	81	82	47	88	71	94	80	49	70	79	86	79
Lotus corniculatus agg. (A)	78	89	83	89	64	55	44	32	49	71	38	84
Dactylis glomerata agg.	76	26	73	90	90	90	78	43	57	61	76	71
Trifolium repens	75	74	36	80	50	88	80	95	72	88	87	61
Veronica chamaedrys agg.	73	55	52	80	73	85	56	29	68	83	90	67
Taraxacum sect. *Ruderalia* (B)	71	32	55	72	70	94	86	85	62	53	84	54
Leontodon hispidus (C)	71	74	85	92	63	69	34	34	70	93	70	82
Leucanthemum vulgare agg.	70	68	57	88	78	81	47	23	73	88	74	78
Festuca pratensis	68	35	58	62	58	78	79	52	60	48	56	58
Ranunculus acris agg. (C)	67	34	48	63	65	77	66	51	81	87	92	76
Poa pratensis agg. (B)	61	30	54	80	69	74	84	49	38	32	39	42
Prunella vulgaris	53	60	37	29	32	34	23	65	56	46	34	43
Cerastium holosteoides	52	53	21	52	51	74	43	55	53	62	51	36
Anthoxanthum odoratum s.l. (C)	63	78	64	82	58	65	21	17	84	92	83	82
Acetosa pratensis (C)	62	27	42	84	64	84	51	11	71	83	87	75
Campanula patula (C)	62	45	39	67	56	77	33	3	78	85	75	66
Galium mollugo agg. (A)	42	26	60	55	68	64	26	15	34	30	32	36
Rhinanthus minor (C)	29	30	38	51	31	35	27	11	51	54	60	47
Knautia arvensis agg.	27	32	66	65	45	33	21	6	38	43	20	55
Cynosurus cristatus	48	34	24	18	18	25	33	52	48	31	32	27
Vicia cracca (C)	42	14	51	57	39	57	36	14	64	66	67	56

Cluster (3 cluster level)	A	A	A	A	A	A	B	B	C	C	C	C
Cluster (12 cluster level)	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Carum carvi	35	7	17	22	25	42	44	18	45	31	62	45
Daucus carota (A)	37	42	44	54	49	37	22	20	7	5	3	9
Heracleum sphondylium	25	3	21	21	35	42	7	2	44	13	43	21
Lathyrus pratensis (C)	25	–	21	21	35	42	14	3	37	16	46	45
Galium verum agg.	22	35	29	44	29	17	21	3	7	12	10	25
Medicago lupulina	15	20	38	20	33	29	15	34	3	1	5	9
Holcus lanatus	28	11	7	29	29	27	6	11	10	21	6	11
Ranunculus polyanthemos	24	12	30	31	18	15	7	–	11	25	5	41
Carex caryophyllea	6	24	22	32	3	4	1	2	1	11	2	29
Poa trivialis	9	1	1	4	18	23	29	8	34	7	37	4
Deschampsia cespitosa	14	6	–	3	6	6	21	9	22	17	26	20
Cirsium arvense (B)	27	13	10	8	14	13	33	38	15	4	9	6
Ajuga reptans	8	7	8	18	22	20	4	–	5	12	11	27
Pimpinella major (C)	10	3	11	3	17	12	6	–	35	13	28	23
Veronica officinalis	13	30	9	16	6	2	7	8	14	32	7	18
Dianthus deltoides	9	26	2	14	8	3	6	3	3	22	–	4
Silene vulgaris	8	5	24	26	9	9	5	–	1	2	2	17
Filipendula vulgaris	13	11	21	31	10	10	7	–	1	4	4	16
Convolvulus arvensis	14	9	15	19	21	21	16	8	1	1	–	1
Hypochaeris radicata	11	15	1	8	2	7	1	12	22	22	6	7
Phyteuma spicatum (C)	8	1	4	3	1	6	1	–	18	9	26	25
Ranunculus auricomus agg.	8	1	4	11	7	15	8	–	5	6	26	24
Danthonia decumbens	8	23	15	6	1	1	–	2	12	8	–	13
Rosa canina s.l.	14	21	18	14	10	4	7	–	6	6	–	7
Pilosella bauhinii	3	9	19	21	1	3	2	–	4	2	1	5
Trifolium dubium	12	11	1	15	18	27	14	17	14	8	12	6
Lysimachia nummularia	8	1	4	18	19	25	7	3	1	1	5	5
Elymus repens (B)	10	4	4	5	10	10	21	11	16	–	3	1
Potentilla reptans	15	11	15	6	10	10	10	26	1	–	–	2
Veronica serpyllifolia	6	2	–	5	3	10	14	20	15	7	7	1
Viola tricolor agg.	6	7	1	5	2	3	5	2	22	9	12	11
Chaerophyllum aromaticum	12	–	6	6	6	9	1	2	17	21	14	7

Cluster 1 has no diagnostic species. It can be characterized by a high frequency of the low growing grasses *Festuca rubra* agg. and *Agrostis capillaris*, and from cluster 2 by a high frequency of indicators of more productive stands such as *Dactylis glomerata* agg., *Festuca pratensis*, *Trisetum flavescens*, *Taraxacum* sect. *Ruderalia* or *Acetosa pratensis*. The original assignment of relevés is heterogenous. Cluster 1 falls within the nutrient-poorer and drier part of cluster A, but is more mesic than cluster 2.

Cluster 2 is well differentiated by diagnostic species, including indicators of grazing management and nutrient-poor conditions and low growing species of dry grasslands. Dominant species are *Festuca rubra* agg. and *Agrostis capillaris*. The species combination corresponds to the association *Anthoxantho odorati-Agrostietum tenuis*, i.e. the vegetation of extensive pastures on dry, rather nutrient-poor and base-rich soils. This syntaxonomical interpretation accords with the original assignment of relevés. Distribution of relevés is concentrated in the Czech and Slovak Carpathians, whereas the sporadic occurrence in Poland is connected with a rather warm climate or base-rich soils in the foothills or the Pieniny Mts, respectively (Fig. 3).

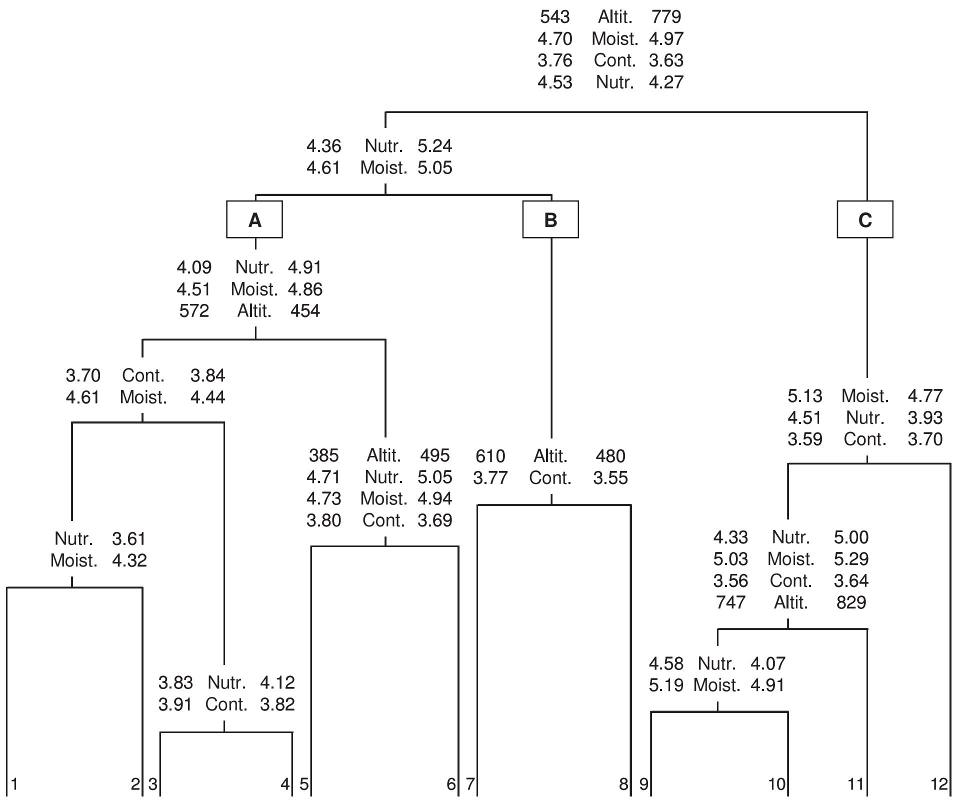

Fig. 1. – Classification dendrogram up to the level of 12 final clusters. Ecological differences between clusters at a particular level of clustering were tested for altitude (Altit.) and Ellenberg indicator values for nutrients (Nutr.), moisture (Moist.) and continentality (Cont.) using Mann-Whitney test. Only differences significant at $P < 0.001$ are displayed. The variables are ordered according to their significance, accompanied by medians for two respective clusters.

Cluster 3 is an outlying cluster within the vegetation of mesic grasslands. It is distinguished by many diagnostic species, most of which are specific to semi-dry grasslands. *Brachypodium pinnatum* is the dominant species. The relevés were originally classified mostly into high-rank syntaxa. At the level of associations, only *Anthoxantho-Agrostietum* is more widely represented. Together with cluster 4, this vegetation develops on dry soils with a low nutrient availability. A high number of relevés comes from the area on Inner Carpathian base-rich rocks.

The common diagnostic taxon of clusters 4 and 5, which occurs with a high frequency, is *Arrhenatherum elatius*. Cluster 4 can be differentiated by numerous dry-grassland species, diagnostic of dry meadows of *Ranunculo bulbosi-Arrhenatheretum elatioris* Ellmauer in Mucina et al. 1993 (e.g. *Festuca rupicola*, *Salvia pratensis*, *Ranunculus bulbosus*, *Dianthus carthusianorum* s.l.). The original assignment of relevés to cluster 4 was divaricated. Nearly half of the relevés were originally assigned to the broad association *Arrhenatheretum elatioris* Braun 1915, with some also assigned to *Anthoxantho-*

Table 3. – Percentage dominance of dominant species (i.e. species with cover > 25 % in at least 20 % of relevés) in particular clusters.

Cluster	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Festuca rubra agg.	20	20	–	–	–	–	–	–	–	55	–	–
Agrostis capillaris	–	23	–	–	–	–	–	–	51	–	–	–
Brachypodium pinnatum	–	–	20	–	–	–	–	–	–	–	–	–
Arrhenatherum elatius	–	–	–	–	61	–	–	–	–	–	–	–
Trisetum flavescens	–	–	–	–	–	32	–	–	–	–	33	–
Festuca pratensis	–	–	–	–	–	–	28	–	–	–	–	–
Trifolium repens	–	–	–	–	–	–	21	52	–	–	–	–
Lolium perenne	–	–	–	–	–	–	–	65	–	–	–	–
Alchemilla spec. div.	–	–	–	–	–	–	–	–	–	–	36	–

Table 4. – Original assignment of relevés to syntaxonomical units and number of relevés from particular West-Carpathian countries in particular clusters. Only alliances and associations of the order *Arrhenatheretalia* are presented. Association *Ranunculo bulbosi-Arrhenatheretum elatioris* was combined with *Arrhenatheretum elatioris*. Higher-rank syntaxa are shown in bold.

Cluster	1	2	3	4	5	6	7	8	9	10	11	12
Number of relevés	248	148	89	262	207	231	214	65	162	180	140	321
Czech Republic	70	27	25	12	75	21	17	8	9	4	3	12
Poland	17	5	2	0	9	22	7	19	104	27	20	5
Slovakia	161	116	62	250	123	188	190	38	49	149	117	304
Arrhenatheretalia elatioris	244	146	88	261	207	228	190	65	161	162	137	290
Arrhenatherion elatioris	93	13	35	194	193	181	67	1	125	90	74	64
Arrhenatheretum elatioris	25	1	9	71	142	60	7	0	0	3	4	16
Cirsio cani-Festucetum pratensis	0	0	0	0	0	2	0	0	0	1	0	0
Festucetum pratensis	9	0	0	0	2	1	23	0	1	0	1	0
Viscario-Festucetum rubrae	1	4	0	0	1	0	0	0	0	1	0	1
Trifolio-Festucetum rubrae	2	1	0	1	1	1	1	0	0	2	6	4
Poo-Trisetetum flavescentis	0	1	0	6	2	24	4	1	0	3	21	1
Lilio bulbiferi-Arrhenatheretum elatioris	0	0	1	5	0	2	0	0	0	0	0	0
Gladiolo imbricati-Agrostietum capillaris	4	2	0	0	0	1	2	0	77	3	6	2
Cynosurion cristati	123	129	26	32	2	6	73	64	27	61	19	104
Lolio perennis-Cynosuretum cristati	11	14	0	0	0	0	22	40	0	0	1	0
Anthoxantho odorati-Agrostietum tenuis	30	100	19	19	1	3	1	1	4	48	3	74
Festuco-Cynosuretum cristati	24	4	0	1	0	0	16	0	2	7	6	3
Luzulo-Cynosuretum cristati	10	2	0	0	0	0	1	0	1	1	6	2
Lolietum perennis	0	0	0	0	0	0	0	14	0	0	0	0
Polygono bistortae-Trisetion flavescentis	9	1	2	8	1	14	5	0	6	7	37	92
Geranio-Alchemilletum crinitae	0	0	0	0	0	0	0	0	0	0	9	0
Trisetetum flavescentis	2	0	0	4	1	11	1	0	0	0	4	2
Geranio sylvatici-Trisetetum flavescentis	0	0	0	0	0	0	0	0	1	0	1	0
Molinietalia	3	0	0	0	0	3	24	0	1	2	1	17
Nardetalia strictae	1	2	1	1	0	0	0	0	0	16	2	14

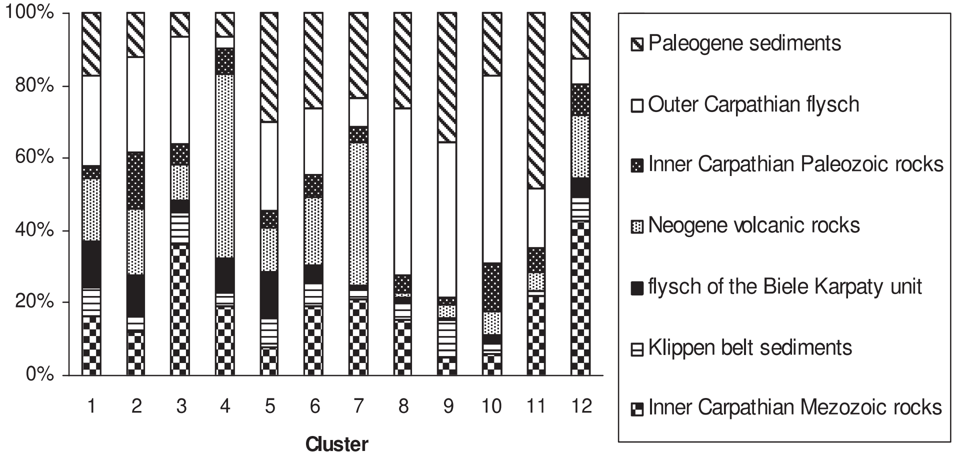

Fig. 2. – Representation of categories of geological bedrock in particular clusters.

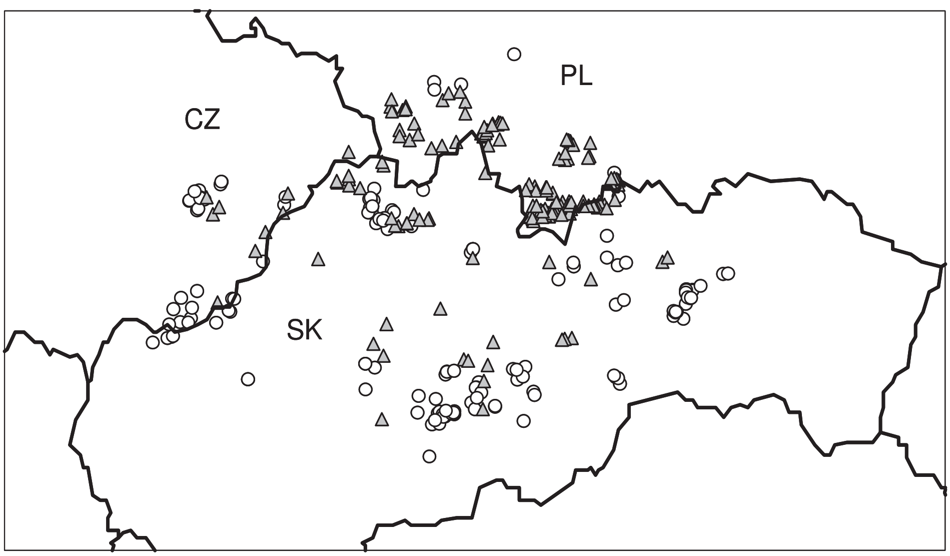

Fig. 3. – Map showing the distribution of the relevés included in cluster 2 (extensive pastures corresponding largely to the association *Anthoxantho odorati-Agrostietum tenuis*; white circles) and 9 (meadows with *Agrostis capillaris* corresponding largely to the association *Gladiolo imbricati-Agrostietum capillaris*; grey triangles).

Agrostietum. This cluster is distinguished by the high representation of relevés from base-rich bedrock, mainly consisting of Neogene volcanic rocks.

There are few species that can be used to differentiate cluster 5, and they are diagnostic of mesic meadows with *Arrhenatherum elatius* of *Pastinaco sativae-Arrhenatheretum elatioris* Passarge 1964. Most of the relevés were originally assigned to the core association *Arrhenatheretum elatioris*. Within cluster A, cluster 5 is distinguished by high nutrient availability and soil moisture and occurs at low altitudes.

Cluster 6 is differentiated by the high frequency and dominance of *Trisetum flavescens* and by species of nutrient-rich sites (*Anthriscus sylvestris*, *Bromus hordeaceus*, *Glechoma hederacea* s.l.). The species composition of relevés indicates this cluster is also associated with nutrient-rich and moist habitats within cluster A.

Cluster 7 is defined by weed species and species of wet or disturbed places. The species of nutrient-rich stands are very frequent. Of them, *Festuca pratensis* and *Trifolium repens* dominate. The original assignment of the relevés is heterogeneous, 23 relevés were assigned to the order *Molinietalia*. Clusters 7 and 8 contain the most nutrient-demanding communities.

Cluster 8 is clearly delimited. Species with a high diagnostic value as well as constancy are considered indicators of nutrient-rich intensive pastures and trampled habitats. The combination of diagnostic species closely corresponds to that of the association *Lolietum perennis* Gams 1927. The original syntaxonomical interpretation of relevés is also clear, with a predominant representation of associations from the alliance *Cynosurion cristati*.

Among the diagnostic species of cluster 9, there are common species of both mesic meadows (*Phleum pratense*, *Jacea pratensis*, regionally *Rhinanthus serotinus* agg.) and montane meadows (*Senecio subalpinus*, *Cardaminopsis halleri*). Together with *Gladiolus imbricatus* and *Agrostis capillaris* this combination corresponds to the association *Gladiolo imbricati-Agrostietum capillaris*, as defined by Pawłowski et al. (1960). *Agrostis capillaris* is also the dominant species in half of the relevés. By contrast, *Hypericum maculatum*, *Gentiana asclepiadea* and *Omalotheca sylvatica* are species of high altitudes but are not confined to meadows. Most relevés originally assigned to *Gladiolo-Agrostietum* belong to cluster 9, although they form only about half of all relevés in that cluster. Within cluster C, cluster 9 includes vegetation on rather nutrient-rich soils. Together with cluster 10, the vegetation consists of species with a more oceanic distribution. The majority of relevés come from the area on flysch bedrock and most are located in the Polish Carpathians (Fig. 3).

Cluster 10 is distinguished by species of grassland with *Nardus stricta*. *Festuca rubra* agg. is the most frequent dominant species. The original assignment of relevés differed, with a significant representation of relevés assigned to *Anthoxantho-Agrostietum*. Compared to cluster 9, the vegetation of cluster 10 occurs on drier and nutrient-poorer soils. Furthermore, the proportion of magmatic and metamorphic rocks in the Inner Carpathians is greater.

The diagnostic species of cluster 11 includes species of the *Polygono bistortae-Trisetion flavescentis* association of montane and wet meadows. The vegetation is dominated by *Trisetum flavescens* and *Alchemilla* spec. div. Cluster 11 includes the vegetation that develops on nutrient-rich wet soils. Most of relevés came from sites on Paleogene flysch sediments or base-rich sedimentary rocks in the Inner Carpathians.

Cluster 12 is distinguished by numerous diagnostic species, including high montane elements and tall herbaceous plants of montane meadows. Furthermore, slightly thermophilous and calcicole species have a higher frequency compared to the other species of cluster C. Nearly one-third of the relevés were originally assigned to the alliance *Polygono bistortae-Trisetion flavescentis* and many to *Anthoxantho-Agrostietum*. From an ecological point of view, this cluster is distinguished by a low nutrient availability and soil moisture, and high representation of base-rich bedrock.

Discussion

The present classification includes all the main types of mesic meadow and pasture vegetation in the West Carpathians: extensive nutrient-poor and intensive eutrophic pastures, trampled habitats, dry and mesic meadows with *Arrhenatherum elatius* at low altitudes and montane meadows on acidic as well as base-rich substrates. Although this classification can be interpreted ecologically based on the environmental variables measured, nevertheless this may not include all the factors affecting grassland diversity because it is closely connected with management practice. Furthermore, history, i.e. persistence of grassland in an area and variation in historical land use, is often identified as an important factor determining the present patterns of vegetation on dry grasslands (Pärtel et al. 2007, Karlík & Poschold 2009). Nevertheless, mesic mountain grasslands often originated much later in the mountainous regions of the Carpathians (Rybníček & Rybníčková 2009) and their variation is probably more influenced by recent management practices. For a complete interpretation of the diversity of meadow and pasture vegetation these factors have to be taken into account.

Extensive pastures and low productive meadows

The results of this study are in accord with the current narrow concept of the association *Anthoxantho odorati-Agrostietum tenuis* (Hájková et al. 2007, Uhliarová et al. 2007) as extensive low productive pastures with low growing species of both semi-dry grasslands on calcium-enriched soils and grasslands with *Nardus stricta*, but the cover values for these species are low. Many relevés that were originally classified as *Anthoxantho-Agrostietum* using the traditional and wider concept of this association (Jurko 1974), were classified by the current scheme as a transitional community close to semi-dry grasslands (cluster 3), dry meadows with *Arrhenatherum elatius* (cluster 4), dry montane meadows on base-rich substrates (cluster 12) or even unproductive meadows on acid substrates (cluster 10) and grasslands with *Nardus stricta* (cluster corresponding to the order *Nardetalia strictae* in the first step of the classification process).

Developing on diverse geological substrates, these grasslands seem to be conditioned mainly by extensive management. However, the mineral content of the soil in these stands can be high compared to substrates at high altitudes because of less intense leaching of minerals by rain. This might limit the development of the extensive pastures of *Anthoxantho-Agrostietum* in the more oceanic Polish Carpathians, although many of the characteristic and constant species there occur in the local species pools (Zając & Zając 2001).

Cluster 1 includes the vegetation that develops at more mesic stands. Furthermore, some relevés in this cluster might have been sampled in relatively young meadows re-established naturally in abandoned arable fields or intense, occasionally ploughed pastures. Because it takes some time for grassland species to colonize a restored site (Gustavsson et al. 2007) the lack of specialists might be due to the meadows being at an early stage of succession.

Intensive pastures and trampled habitats

The *Lolio perennis-Cynosuretum cristati* association, Tüxen 1937, though a widely distributed pasture vegetation, was not well distinguished in this study. Cluster 7 was differentiated more by accompanying species, which occupied bare land or nutrient-rich disturbed places, than pasture indicators. Besides intensive pastures, this cluster also includes meadows with *Festuca pratensis* growing in nutrient-rich and rather wet habitats that were originally classified in different vegetation units, which indicates their transitional position between mesic and wet meadows and nutrient-rich pastures.

In contrast, the community of *Lolietum perennis* in trampled habitats (cluster 8) forms a clearly delimited but small cluster because this type of vegetation occured only sporadically in the data set. This was because this community was diversely classified by the former phytosociological classification systems. Therefore, this type of vegetation is not well represented in this study, although it is a widely distributed but rather neglected in the West Carpathians (Hájková et al. 2007, Janišová et al. 2007, Matuszkiewicz 2007).

Meadows at low altitudes

The common feature of clusters representing the vegetation recorded in low altitude meadows was the high frequency of *Arrhenatherum elatius*. Nevertheless, there is an obvious gradient in moisture and nutrient availability from dry and nutrient-poor (clusters 3 and 4) through mesic (cluster 5) to wet meadows on eutrophic soils (cluster 6). Ellmauer & Mucina (1993) divided the widely conceived *Arrhenatheretum elatioris* Braun 1915 into three associations. In the present classification, cluster 4 corresponds well to dry meadows with *Arrhenatherum elatius* of *Ranunculo bulbosi-Arrhenatheretum elatioris,* whereas cluster 3 is rather transitional towards the semi-dry grasslands of alliances *Bromion erecti* Koch 1926 and *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951. However, both clusters also include relevés originally assigned to *Anthoxantho odorati-Agrostietum tenuis*. They might correspond to the subassociation *Anthoxantho-Agrostietum festucetosum rupicolae* Jurko 1971 with dominants *Festuca rupicola* and *Brachypodium pinnatum*, being a link between alliances *Cynosurion cristati* and *Bromion erecti* (Jurko 1971). Furthermore, Jurko (1974) and Uhliarová et al. (2007) describe the *Anthoxantho-Agrostietum* variant with *Primula veris*, with the diagnostic species *Viola hirta*, *Trifolium montanum*, *Primula veris*, *Steris viscaria* and *Silene nutans* growing in the mineral-rich soils of limestone and volcanic ranges. This vegetation was classified in the driest meadows in this study because of the shared occurrence of taller semi-dry grassland species. Anyway, dry meadows and extensive pastures seem to be floristically similar. Both develop on nutrient-poor and dry soils at low altitudes. Dry meadows with *Arrhenatherum elatius* occur more frequently on basic substrates but the main difference is in the way they are managed (mowing versus extensive grazing). It is assumed, at least in some regions, that the development of a given type of vegetation is conditioned by management practices.

In addition to the mesic meadows corresponding to *Pastinaco sativae-Arrhenatheretum elatioris* (cluster 5), a more eutrophic meadow community on wetter substrates (cluster 6) was distinguished. Ellmauer & Mucina (1993) describe eutrophic meadows in which *Alopecurus pratensis* is dominant as the association *Ranunculo repentis-Alopecuretum pratensis* Ellmauer in Mucina et al. 1993. In the Czech Republic and Slovakia, these meadows are classified as *Poo trivialis-Alopecuretum pratensis* Regel 1925 of the alliance *Deschampsion cespitosae* Horvatić 1930 (Hájková et al. 2007, Uhliarová et al. 2007). This association comprises alluvial meadows with *Alopecurus pratensis* in river floodplains, distributed mainly in the lowlands and basins outside the area of the Carpathian mountains. Eutrophic meadows in cluster 6 were distinguished by the high frequency and dominance of *Trisetum flavescens*. They might have included over-fertilized meadows, and also vegetation in transition to the montane meadows in the eutrophic branch of *Poo-Trisetetum flavescentis*.

Montane meadows

Four types of high altitude meadows were distinguished, varying in nutrient availability, soil moisture and geological bedrock. Meadows with *Agrostis capillaris* (cluster 9) are only sporadically distinguished by montane meadow elements but the species composition clearly differs from mesic meadows with *Arrhenatherum elatius*. In the Polish classification system (Matuszkiewicz 2007), this vegetation is classified as *Gladiolo imbricati-Agrostietum capillaris* and occurs in meadows in the submontane and montane zone. Increasing occurrence of montane elements with increasing altitude is reflected at the level of subassociations (Kornaś 1967). Some diagnostic species of cluster 9 were among the characteristic species of this association as defined by Pawłowski et al. (1960). A closer comparison is difficult because of the narrow concept of some of the characteristic taxa, which could not be followed in this study (e.g. *Jacea pratensis* s.l. including *J. pratensis*/*subjacea*/*macroptilon*, *Alchemilla* spec. div.). Of the other diagnostic species of the cluster, *Hypericum maculatum* or *Holcus mollis* are frequently accompanying grassland species, but their high abundance might nevertheless indicate the degradation of the meadows following the cessation of mowing (Krahulec et al. 1996). The shared occurrence of these species could result in the inclusion of relevés from degraded meadows in cluster 9, which however otherwise represents a well-distinguished community of high altitude meadows with *Agrostis capillaris*.

These meadows occur mainly on flysch bedrock in the Outer Carpathians or the Inner Carpathian basins. Soils that develop by the weathering of flysch rock are acid cambisols, naturally poor in nutrients. The occurrence of a highly productive community in such conditions is due to traditional management, which consists of regular manuring, mowing once or twice a year and slight grazing (Pawłowski et al. 1960, Kornaś 1967). Intense manuring supports the growth of nutrient-demanding species, whereas low manuring intensity leads to the high occurrence of elements chatacteristic of low productive grasslands (Pawłowski et al. 1960). Besides the geological bedrock, the northern area of the flysch Carpathians differs in having a more oceanic climate, which weakens southwards. Unfortunately, it was not possible to test the relationship between the diversity of meadows and climate. The climatic data from Poland could not be compared with that from the Czech Republic and Slovakia because of both the different approximations and ranges in data categories used in climatic maps.

Gladiolo imbricati-Agrostietum capillaris is the most widespread hay meadow community in the Polish Carpathians (Kornaś 1967). Most of the relevés in the final data set that were originally assigned to *Gladiolo-Agrostietum* were included in cluster 9, which indicates this vegetation is floristically homogeneous. Only a few of the relevés were classified as belonging to other vegetation types such as the poor meadows in cluster 10 or the more productive vegetation with *Trisetum flavescens* in cluster 11. In accordance with Pawłowski et al. (1960), the centre of distribution of these meadows is in the Polish part of the West Carpathians and adjacent areas in Slovakia in the northern part of the Spišská Magura and Pieniny Mts. Šimurdová & Šomšák (2000) consider that the vegetation of meadows and pastures with *Gladiolus imbricatus* on pseudogley soils in the Slovenské Rudohorie Mts belongs to *Gladiolo-Agrostietum*. The species composition of these grasslands nevertheless does not correspond to this association because it includes rather low productive species, is similar to grasslands with *Nardus stricta* and lacks montane elements. The development of montane meadows with *Agrostis capillaris* seems to be favoured by several factors: geological substrate formed of flysch sediments, traditional management practices and an oceanic climate. Furthermore, phytogeographical factors such as migration routes might also play a role. Towards the south and west, areas with a similar combination of ecological factors are scarce and patchy. Nevertheless, there are similar meadows in the central part of the West Carpathians, i.e. on the belt of klippen sediments in the northern part of the Malá Fatra Mts.

Cluster 10 includes species of nutrient-poor meadows dominated by *Festuca rubra* and a few species of montane meadows. Similar vegetation in the Krkonoše Mts was classified as *Trifolio-Festucetum rubrae* Oberdorfer 1957 (Krahulec et al. 1996). Recently, it was classified as *Poo-Trisetetum flavescentis* and vegetation in transition from mesic meadows with *Arrhenatherum elatius* to grasslands with *Nardus stricta* (Hájková et al. 2007, Uhliarová et al. 2007). Furthermore, the cluster includes vegetation characteristic of the subassociation *Anthoxantho odorati-Agrostietum tenuis nardetosum* Jurko 1970, i.e. extensive pastures on acidic bedrock. In Poland, these grasslands are considered to be in transition from *Gladiolo-Agrostietum* to *Hieracio lachenalii-Nardetum strictae* Kornaś ex Pawłowski et al. 1960, and these nutrient-poor montane grasslands with *Nardus stricta* are managed by sheep grazing or mowing once a year with occasional autumnal grazing. They also represent the successional stage between these two communities. Both the cessation of manuring and continual mowing of *Gladiolo-Agrostietum* cause a successional change towards nutrient-poor grasslands, whereas manuring of the grasslands leads to nutrient enrichment and a successional change towards productive meadows (Pawłowski et al. 1960). A similar succession was observed in the Krkonoše Mts (Krahulec et al. 1996). The effect of adding nutrients by manuring or grazing is nevertheless bedrock-specific (Başnou et al. 2009).

Montane meadows with *Trisetum flavescens* (cluster 11) differ from the two former types in having a higher frequency of species of the alliance *Polygono bistortae-Trisetion flavescentis*. Analogous vegetation is reported by Ružičková (1997) in the north-western foothills of the Belianske Tatry Mts and classified as *Geranio-Alchemilletum crinitae* Hadač et al. 1969. Occuring in these meadows are species of the West Carpathian montane meadows (*Senecio subalpinus*, *Crocus discolor*) as well as those that do not or only rarely occur in meadows with *Agrostis capillaris* (*Geranium sylvaticum*, *Rhinanthus pulcher*). Furthermore, they characteristically have a high cover of *Trisetum flavescens* and high frequency of species of wet meadows. *Geranio-Alchemilletum crinitae* is recorded by Hadač et al. (1969) in high altitude meadows in the Belianske Tatry Mts, which have a slightly different vegetation structure and are dominated by *Geranium phaeum*. Recently, the latter concept of this association was adopted and its restricted distribution in the highest Slovakian mountain ranges described (Hegedüšová & Ružičková 2007). These meadows are confined to fresh, deep productive soils that typically develop on base-rich substrates.

A specific plant community grows in the semi-dry montane meadows on base-rich bedrock (cluster 12) in the Inner Carpathian mountain ranges. Its species composition indicates that this vegetation is a high altitude equivalent of the association *Anthoxantho* *odorati-Agrostietum tenuis* or *Ranunculo bulbosi-Arrhenatheretum elatioris*. Ružičková (2002) describes species-rich meadows with species of montane and mesic meadows and semi-dry grasslands as *Campanulo glomeratae-Geranietum sylvatici* Ružičková 2002 (*Polygono bistortae-Trisetion flavescentis*) and *Lilio bulbiferi-Arrhenatheretum elatioris* Ružičková 2002 (*Arrhenatherion elatioris*). The specific floristic composition is determined by a combination of a base-rich substrate, montane climate and extensive management (Ružičková 2002). In contrast to the meadows that develop on flysch, they are naturally well supplied with nutrients and not conditioned by manuring (Ružičková 2001).

Ružičková (2001) considers the vegetation that grows on the productive meadows that develop on Paleogene flysch sediments in the Spišská Magura Mts as belonging to *Geranio sylvatici-Trisetetum flavescentis* Knapp ex Oberdorfer 1957. This region is the only Carpathian location of this association, which has a Central European distribution (Dierschke 1981, 1997, Hájková et al. 2007). In the West Carpathians, these meadows are in transition between *Gladiolo-Agrostietum* and *Geranio-Alchemilletum crinitae*. The management of these meadows is the same as that of the *Gladiolo-Agrostietum* meadows (cf. Pawłowski et al. 1960, Ružičková 2001).

No cluster encompassing *Poo-Trisetetum flavescentis* was delimited by the present classification. This confirms the transitional character of this association, which occurs in the middle of the altitudinal gradient in meadow vegetation. In addition, cluster 10 includes *Poo-Trisetetum flavescentis* as transitional vegetation between mesic meadows and grasslands with *Nardus stricta*, and relevés belonging to this association included in other types of vegetation. For example, they can be found in clusters 9 and 11. These meadows have a similar vegetation structure, with *Agrostis capillaris* or *Trisetum flavescens* as the dominant species. Their floristic similarity is due to similar management practices. Nevertheless, the poor species composition of montane meadows is determined by the mountain climate, with long-term snow cover and high precipitation in summer (Ellenberg 1996).

Classification of the vegetation of mesic meadows and pastures

In this study, the initial large data set included all semi-natural grassland vegetation in the area except for semi-dry and dry grasslands. Then the analysis focused on mesic meadows and pastures. This approach, in combination with the unsupervised classification method, can result in a poor resolution of some plant communities. In contrast, it is possible to display the floristic similarities of particular communities and review their traditional classification in higher-rank vegetation units, which is more difficult if smaller units of vegetation (single alliance) are studied.

Vegetation of extensive pastures was included in cluster A together with meadows at low altitudes. This is consistent with the conclusion of Uhliarová et al. (2007) who transferred *Anthoxantho odorati-Agrostietum tenuis* to the alliance *Arrhenatherion elatioris* instead of its traditional classification in *Cynosurion cristati* (Jurko 1974). Cluster B, which corresponds to *Cynosurion cristati,* includes only the vegetation of intensive pastures and trampled habitats, indicating that not only the type of management but also nutrient availability is an important factor in determining similarities in species composition between pastures and meadows. This result might have important implications for nature conservation. Unlike the *Arrhenatherion* meadows, *Cynosurion* pastures are widely distributed, intensively managed and species-poor grasslands in Western Europe and are not protected within the Natura 2000 system. Because Natura 2000 habitats are often protected nationally, then depending on the phytosociological classification used in a particular country (e.g. Chytrý et al. 2001) many species-rich natural grasslands of *Anthoxantho-Agrostietum* may not be protected, whereas some *Arrhenatherion* meadows of lower conservation importance are protected. This has resulted in even poorer protection of extensively managed pastures in Europe, although they also include grasslands of high conservation interest (Zuidhoff et al. 1995).

Cluster C includes high altitude meadows. Nevertheless, it does not include all of the alliance *Polygono bistortae-Trisetion flavescentis*. On the basis of diagnostic species this alliance can only be included in clusters 11 and 12 (Hegedüšová & Ružičková 2007). As mentioned above, even these clusters include a mixture of montane and mesic meadows. The less clear distinction of meadows of *Polygono-Trisetion* is probably connected with the rare occurrence and patchy distribution of suitable habitats in the West Carpathians. The classification of the North-Carpathian meadows with *Agrostis capillaris* (cluster 9) is somewhat disputable but agrees with the complicated classification history of the association *Gladiolo-Agrostietum*. Originally, it was placed in the alliance *Arrhenatherion elatioris* (Szafer et al. 1923). Marschall (1951) placed this association among mesic montane meadow communities to the alliance *Polygono-Trisetion*. Because of the low representation of diagnostic species of this alliance, Pawłowski et al. (1960) assigned this community back to *Arrhenatherion elatioris* where it remains in the Polish classification system (Matuszkiewicz 2007). Nevertheless, Dierschke (1981) proposed that *Polygono-Trisetion* be divided into three suballiances and the inclusion of *Gladiolo-Agrostietum* in *Alchemillo-Trisetenion* Dierschke 1981, the suballiance including montane meadows in the West Carpathians. The results of the current study support the placing of *Gladiolo-Agrostietum* within *Polygono-Trisetion*, as meadows with *Agrostis capillaris* are floristically different from mesic meadows with *Arrhenatherum elatius*, despite the low frequency of montane floristic elements. More questionable seems to be the position of *Poo-Trisetetum flavescentis*, which is transitional between several types of vegetation including *Cynosurion cristati* and *Violion caninae* Schwickerath 1944.

Relation of the large-scale distribution of meadows to environmental conditions

Although the distribution of the vegetation units studied does not mirror state borders, the results indicate that the differences in the classification systems used in particular countries reflect vegetation diversity of meadows and pastures in the West Carpathians. The Polish mountains have an oceanic climate, with a relatively high rainfall, which might not be favourable for the development of *Anthoxantho-Agrostietum* grasslands. Distribution of this association seems to be concentrated in areas with a temperate or slightly continental climate. It probably occurs also in the adjacent Slovakian East Carpathians (Uhliarová et al. 2007). Extensive pastures in the area of the Romanian Carpathians are currently considered to be *Festuco rubrae-Agrostetum capillaris* Horvat 1951 (Coldea 1991, Sanda et al. 1999), an association that is floristically different from *Anthoxantho-Agrostietum* (Jurko 1969).

In contrast, the occurrence of montane meadow vegetation at low altitudes in the northern part of the Carpathians is determined by the ecological conditions prevailing there and specific management practices. The presence of montane meadow elements in *Gladiolo-Agrostietum* is nevertheless low, probably because of the scarce occurrence of mountain ranges with well developed subalpine and alpine zones (only the Pilsko and Babia Góra peaks and the High Tatra Mts). The existence of this specific plant community is acknowledged only in the Polish classification, although corresponding habitats occur in adjacent areas in Northern Slovakia. Outside the study area, *Gladiolo-Agrostietum* is recorded in the Beskid Niski Mts, where it is however poor in many characteristic species (Dubiel et al. 1999). Gradual changes in the species composition of mesic montane meadows along a longitudinal geographical gradient led to different vegetation units being described in the Polish East Carpathians (Pawłowski & Walas 1949, Denisiuk & Korzeniak 1999). Further large-scale studies are nevertheless needed to reveal the exact distribution of *Gladiolo-Agrostietum* and *Anthoxantho-Agrostietum,* and analogous types of vegetation occurring in the Carpathians and the Balkans.

See http://www.preslia.cz for Electronic Appendix 1.

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Souhrn

Fytocenologický výzkum luční vegetace v Západních Karpatech probíhal v jednotlivých zemích (Česká Republika, Polsko, Slovensko) spíše nezávisle, a rozšíření některých vegetačních jednotek je tak vymezeno státní hranicí. Cílem této jednotné studie vegetace mezofilních luk a pastvin (*Arrhenatheretalia elatioris*) je zjistit, zda různá pojetí používaná v klasifikačních systémech jednotlivých zemí odráží diverzitu této vegetace v oblasti. Z důvodu nejednotnosti klasifikačních systémů nebylo možné pro klasifikaci použít pouze snímky zařazené jejich původními autory do řádu *Arrhenatheretalia elatioris*. Nejprve jsme proto vytvořili datový soubor zahrnující veškerou vegetaci kosených luk a pastvin v oblasti: *Arrhenatheretalia elatioris*, *Molinietalia* a *Nardetalia strictae*. Soubor jsme klasifikovali shlukovou analýzou. Na úrovni tří shluků jsme vybrali shluk odpovídající vegetaci řádu *Arrhenatheretalia elatioris*, který byl podroben shlukové analýze o stejných parametrech. Pro ekologickou interpretaci klasifikace jsme použili nadmořskou výšku, Ellenbergovy indikační hodnoty a geologické podloží. Výsledky klasifikace jsme porovnali s autorským zařazením snímků do vegetačních jednotek. Klasifikací byla rozlišena většina společenstev mezofilních luk a pastvin známých z oblasti Západních Karpat a naznačena jejich vzájemná podobnost. Extenzivní pastviny, řazené do asociace *Anthoxantho odorati-Agrostietum tenuis* jsou floristicky podobnější mezofilním ovsíkovým loukám svazu *Arrhenatherion elatioris* než intenzivněji využívaným pastvinám svazu *Cynosurion cristati*, kam byly tradičně řazeny. Tento výsledek může být důležitý z hlediska ochrany biotopů, například v rámci soustavy Natura 2000, kdy je klasifikace vegetace na úrovni svazu v tomto případě brána jako hlavní argument pro označení biotopu jako evropsky významného. Louky vyšších poloh byly rozlišeny do čtyř společenstev včetně eutrofních luk s *Agrostis capillaris* (asociace *Gladiolo imbricati-Agrostietum capillaris*), považovaných za nejrozšířenější luční společenstvo v polských Karpatech, avšak nevyskytující se v okolních zemích. Horské louky, klasifikované do svazu *Polygono bistortae-Trisetion flavescentis*, nebyly jasně odlišeny od luk vyskytujících se ve vyšších polohách, ale bez výskytu horských prvků, zřejmě z důvodu vzácného a ostrůvkovitého výskytu vhodných stanovišť. Výsledky studie naznačují, že rozdíly v klasifikačních systémech jednotlivých zemí odrážejí diverzitu luční a pastvinné vegetace podmíněnou ekologickými faktory. Louky asociace *Gladiolo imbricati-Agrostietum capillaris* se vyskytují převážně v severní části území, kde převažuje oceanické klima. V této oblasti naopak téměř chybí asociace *Anthoxantho odorati-Agrostietum tenuis.*

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