Vegetation-environment relationships in grassland communities of central Slovakia

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Abstract

A systematic survey of grassland communities in central Slovakian sub-montane and montane regions (including the Kremnické vrchy Mts., Starohorské vrchy Mts., Veľká Fatra Mts., and Zvolenská kotlina Basin) was performed between 1996 and 2007. The main aim was to identify main environmental gradients in the studied vegetation and to estimate the most important individual variables responsible for the variation of their species composition. Along with the floristic composition, the environmental variables were either recorded in the field (altitude, slope, aspect), calculated (solar radiation, climatic data, and phytochorological affinity), or derived from available maps or GIS digital data layers (type of bedrock, soil parameters). These environmental variables were used as supplementary in the detrended correspondence analysis (DCA) or explanatory in the canonical correspondence analysis (CCA). The affiliation of individual phytosociological relevés to associations was estimated by an electronic expert system for Slovak grassland communities. Altogether, 15 xero-, sub-xero- and mesophilous grassland associations were distinguished. Wet and fen meadows were analysed at the level of alliances. Unconstrained ordination revealed moisture and nutrient gradients as most important for the data set. By means of constrained ordination, the variability of the studied vegetation could be explained by a set of geological, topographic, phytochorological and derived climatic variables, although the percentage of explained variance was rather low and did not exceed 12% for all significant factors combined. Among individual variables, the geological bedrock type, climatic water balance, solar radiation, and slope played the most important role in determining the distribution and variability of individual grassland communities. Affinity to phytochorions determined according to local air temperature gradients was also significant. Soil properties played only a subordinate role in our analyses. The analysis of a more homogeneous subset of the data without wetland relevés gave similar results as the analysis of the complete data set. The differences in results of constrained and unconstrained ordinations are discussed together with the potential reasons for extremely high proportion of unexplained variance revealed by the variation partitioning methods.

Zusammenfassung: Vegetations-Umwelt-Beziehungen in Rasengesellschaften der Zentralslowakei

Wir haben die Rasengesellschaften in den submontanen und montanen Regionen der Zentralslowakei (mit den Mittelgebirgszügen Kremnické vrchy, Starohorské vrchy und Veľká Fatra sowie dem Zvolenská kotlina-Becken) im Zeitraum 1996–2007 systematisch untersucht. Ziel war es, die hauptsächlichen Umweltgradienten und die wesentlichen Variablen zu bestimmen, welche für die Unterschiede in der Artenzusammensetzung verantwortlich sind. Die betrachteten Umweltvariablen wurden entweder gemeinsam mit der Artenzusammensetzung im Gelände erhoben (Höhe, Hangneigung und -exposition), berechnet (Strahlungsgenuss, Klimaparameter, phytochorologische Zugehörigkeit) oder aus verfügbaren GIS-Karten entnommen (Gesteinart, Bodenparameter). Diese Umweltvariablen wurden als passive Variablen in trendbereinigten Korrespondenzanalysen (DCAs) und als erklärende Variablen in kanonischen Korrespondenzanalysen (CCAs) verwendet. Die Zuordnung einzelner Vegetationsaufnahmen zu Assoziationen erfolgte mit Hilfe des Slowakischen Elektronischen Expertensystems für Rasengesellschaften. Insgesamt wurden 15 Assoziationen von Volltrockenrasen, Halbtrockenrasen und mesophilem Grünland unterschieden. Feuchtwiesen und Niedermoorgesellschaften wurden auf der Ebene von Verbänden analysiert. Die DCAs zeigten, dass der Feuchtigkeits- und der Nährstoffgradient die größte Bedeutung für die floristische Differenzierung innerhalb der betrachteten Aufnahmen haben. Nach den CCAs kann die Variabilität in der Artenzusammensetzung durch eine Gruppe von geologischen, topografischen, phytochorologischen und abgeleiteten Klimavariablen erklärt werden, wenngleich der Anteil erklärter Varianz mit maximal 12 % recht niedrig war. Als Einzelvariablen waren Gesteinstyp, klimatische Wasserbilanz, Strahlungsgenuss und Hangneigung am bedeutsamsten. Die Zugehörigkeit zu einem Wuchsgebiet (Phytochorion), welche anhand der regionalen Temperaturgadienten ermittelt wurde, war ebenfalls signifikant. Dagegen spielten Bodeneigenschaften nur eine untergeordnete Rolle. Die Analyse eines reduzierten, homogeneren Datensets ohne die Feuchtgebietsaufnahmen ergab qualitativ ähnliche Ergebnisse wie jene für den Gesamtdatensatz. Abschließend werden die Unterschiede zwischen den Ergebnissen von DCAs und CCAs erläutert und Gründe für den geringen Anteil erklärter Varianz diskutiert.

Keywords: CCA, DCA, derived climatic variable, dry grassland, geology, ordination, mesophilous grassland, soil characteristic, species composition, topography.

Abbreviations: CCA – canonical correspondence analysis, DCA – detrended correspondence analysis, GIS – geographic information system, GPS – global positioning system, IV – indicator value.

1. Introduction

Semi-natural grasslands belong to the most diverse habitats in the agricultural landscape (DIERSCHKE & BRIEMLE 2002, TSCHARNTKE et al. 2005). The variability of their species composition is affected by numerous factors, habitat environmental conditions and human impact being recognised as the most significant (LOSVIK 1993, COUSINS & ERIKSSON 2002, VANDVIK & BIRKS 2002, AUESTAD et al. 2008). Among the environmental factors, soil fertility is considered to be very important (JANSSENS et al. 1998, MYKLESTAD 2004, KLIMEK et al. 2007), together with soil chemistry parameters and soil physical properties. The latter depend largely on bedrock type, which also can determine the distribution and abundance of particular species (KIKUCHI & MIURA 1993, BRATLI & MYHRE 1999). Landscape topography, expressed by elevation, slope, and aspect, belongs to the environmental factors affecting the quantity of incoming solar radiation (PINDER et al. 1997, SEBASTIÁ 2004, BENNIE et al. 2008). Microclimatic conditions are relevant mainly for dry grassland differentiation (BECKER 1998, JANIŠOVÁ 2005, BRUELHEIDE & JANDT 2007). Even macroclimatic factors might have an important effect (SVENNING & SKOV 2007, HLÁSNY & BALÁŽ 2008) e.g. by affecting the large-scale species dispersal or determining water availability during the growing season, thus restricting the distribution of species limited by water supply. Factors related to grassland management determine the vegetation variation especially in semi-natural grasslands (originated and maintained thanks to the permanent human impact), while natural grasslands of saline and montane areas seem to be determined mainly by the microhabitat conditions. The effect of environmental variables can differ significantly for distinct grassland communites (KLIMEK et al. 2007). While in intensive agricultural grasslands the content of basic nutrients seems to be of crucial importance (MYKLESTAD 2004), less productive habitats support vegetation types more dependent on topographic or climatic factors. Different sets of explanatory variables may differ in their relevance depending on the vegetation type or on the region. According to KLIMEK et al. (2007), for example, the mechanisms of individual factors influencing the grassland vegetation are strongly related to the type of grassland management. Also the diversity of the studied vegetation and the size of the regional species pool may affect the role of individual factors in determining the species composition of grassland vegetation (see SCHMIDA & WILSON 1985).

The phytosociological survey of grassland communities in the montane areas surrounding Banská Bystrica detected a high variability of grassland vegetation (RUŽIČKOVÁ 2002, JANIŠOVÁ et al. 2010). Both α- and β-diversity are especially high in these grasslands, concerning mainly the sub-xero- and mesophilous communities, which contain 49 vascular plant species on average and 78 species as maximum in a relevé plot of 16–30 m^2 (JANIŠOVÁ et al. 2010). The varied relief, which makes this region unsuitable for grassland intensification, together with a wide range of available geological and topographic habitat conditions, resulted in development and maintanance of numerous valuable semi-natural grassland types (RUŽIČKOVÁ 2002, JANIŠOVÁ 2007, JANIŠOVÁ et al. 2010). In order to reveal environmental factors that explain the variability of species composition of these grassland communities, we conducted gradient analyses. The forward selection procedure (TER BRAAK & ŠMILAUER 2002) provided an appropriate tool for testing and quantifying the effect of individual environmental factors. For the analyses, we used a subset of our phytosociological data set (analysed syntaxonomically in JANIŠOVÁ et al. 2010) including only relevés with precise geographical location and complete information on the studied environmental conditions. In addition to the directly measured variables, we used selected field-based point data derived from available GIS digital data layers. We were interested whether also simply measurable and easily derivable variables can be used successfully to indicate general patterns in species composition and to explain the major gradients responsible for vegetation variability. The main questions of our study were as follows: (i) what are the main environmental gradients responsible for the variation in species composition of the studied grassland communities? (ii) what individual environmental factors determine the distribution and variability of the studied grassland communities?

2. Materials and methods

2.1. Study area

The study area is located in the wider surroundings of the city of Banská Bystrica, situated on the right side of the Hron River, mainly towards the north and the west of the city (Fig. 1). It is delimited by the following geographical coordinates: latitude from 48° 39 30 to 48° 55′ 00″ N and longitude between 19° 00′ 00″ and 19° 19′ 00″ E. Colline to montane areas of the following orographic units were included: Kremnické vrchy Mts., Starohorské vrchy Mts., Veľká Fatra Mts., and Zvolenská kotlina Basin (Fig. 2a). The altitude of the studied grasslands ranges from 350 to 980 m a.s.l. The study area has a varied geological structure including calcareous (limestones and dolomites), volcanic (andesites), and cristalline (othogneisses) bedrock types as well as quartzites, claystones, and diluvial and colluvial deposits of the Quaternary period. Among the soil types, cambisoils and rendzinas are the most common. In the colline part of the area, the climate is moderately warm (average temperature during the growing season is 12–15 °C, DŽATKO et al. 1989) and moderately wet (evapotranspiration exceeds precipitation during the growing season, Fig. 2b). For Slovakian standards, the montane parts of the study area are cold to very cold (average temperature during the growing season is 10–13 °C, DŽATKO et al. 1989) and wet (precipitation exceeds potential evapotranspiration during the growing season, Fig. 2b).

2.2. Species data and environmental variables

During 1996–2007, phytosociological relevés were sampled according to the principles of the Zurich-Montpellier school (BRAUN-BLANQUET 1964) including all types of semi-natural grassland communities (dry, semi-dry, and mesophilous grasslands as well as wet and fen meadows). Within a larger data set (JANIŠOVÁ et al. 2010), 240 relevés with complete environmental data were selected for the

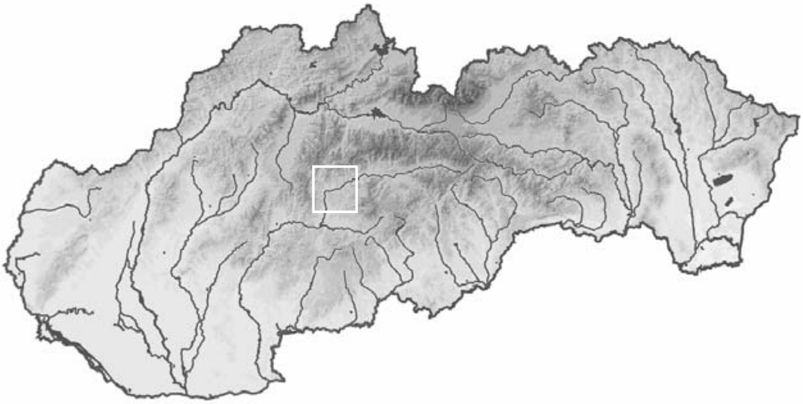

Fig. 1: Location of the study area (white rectangle) in the central part of Slovakia.

Abb. 1: Lage des Untersuchungsgebietes (weißes Rechteck) in der Zentralslowakei.

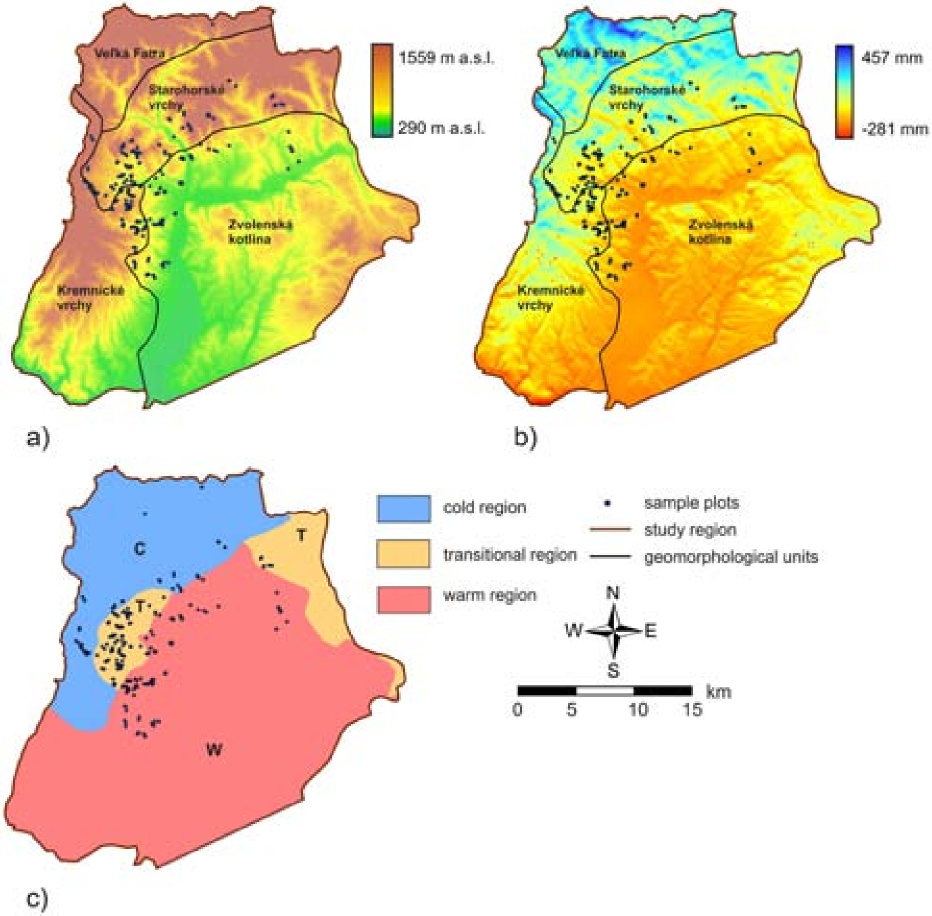

Fig. 2: a) Altitudinal pattern and orographical division of the study area; b) climatic water balance of the study area expressing the difference of precipitation and potential evapotranspiration during the growing season (April–September) calculated from long-term meteorological data between 1951 and 1980 according to HLÁSNY & BALÁŽ (2008); c) phytochorological division of the study area proposed on the basis of grassland vegetation data (TURISOVÁ & HLÁSNY 2010).

Abb. 2: a) Höhenschichten und orographische Gliederung des Unterschuchungsgebietes; b) klimatische Wasserbilanz des Untersuchungsgebietes, ausgedrückt als Differenz zwischen Niederschlag und potenzieller Evapotranspiration während der Vegetationsperiode (April – September) und berechnet anhand der Klimadaten des Zeitraums 1951–1980 (HLÁSNY & BALÁŽ 2008); c) phytochorologische Gliederung des Untersuchungsgebietes auf der Grundlage der Rasengesellschaften (TURISOVÁ & HLÁSNY 2010).

analyses. Plot size varied from 16 to 30 m^2, most of the relevés being sampled on 25 m^2. As non-vascular plants were not recorded in all relevés, we based our analyses on vascular plant records only. Along with the floristic composition, the geographical coordinates and data on altitude, slope, and aspect were recorded in the field. Further environmental variables were calculated (solar radiation, climatic data, and phytochorological affinity) or derived from available maps or GIS digital data layers (soil parameters) for each relevé plot. The GIS layers used were either transformed in a GIS environment from the topographic maps of Slovakia at the scale of 1 : 5,000 into vector data (soil parameters) or produced by means of spatial modeling tools with a resolution of 90 m (climatic data, phytochorological affinity). Solar radiation (heat index) was calculated according to PARKER (1988) as cos (aspect in degrees – 202.5°) x tan (slope in degrees). The information on geological bedrock was based on POLÁK et al. (2003).

The phytochorological affinity followed TURISOVÁ (2009) and TURISOVÁ & HLÁSNY (2010), who estimated the borders of phytochorological regions by ordinary kriging from temperature gradients based on Ellenberg temperature indicator values (ELLENBERG et al. 1992) of the local flora. The data for construction of the phytochorological map were independent from the phytosociological data used in our analyses. They originated from a floristic mapping of semi-natural grassland vegetation by the polygon method (ŠEFFER et al. 2000), which has been performed in Slovakia since 1999. Two main phytochorological regions were recognised in the study area (warm and cold phytochorion) with a transitional zone between them (transitional phytochorion, Fig. 2c). Soil parameters were derived from digitised pedological maps 1 : 5,000. Climatic data were calculated in a GIS environment using long-term measurements (1951–1980) and topographic data (see Table 1 for details). All these environmental variables were used as explanatory in the canonical correspondence analysis (CCA). In the detrended correspondence analysis (DCA), we used unweighted average Ellenberg indicator values for relevés (*continentality IV*, *light IV*, *moisture IV*, *nutrients IV*, *soil reaction IV*, *temperature IV*, ELLENBERG et al. 1992) as passive variables for the identification of main environmental gradients in the studied data set.

The relevés were classified to associations by the expert system formulated for the Slovak grassland vegetation (JANIŠOVÁ 2007) either according to association definitions or (in case of relevés not matching any association definition) according to the Frequency-Positive Fidelity Index (FPFI; TICHÝ 2005). Individual relevés and their assignment to associations are published in JANIŠOVÁ et al. (2010; in this volume). Altogether, fifteen associations of dry, semi-dry and mesophilous grasslands were distinguished in the study area. Wetland relevés were classified at the level of alliances; wet meadows of the *Calthion palustris*, *Glycerio-Sparganion*, and *Phragmition* and fen meadows of the *Caricion davallianae* were distinguished. The syntaxonomic overview of the recorded grassland communities is shown in Table 2.

2.3. Data analyses

Cover estimates of species were square-root transformed. CANOCO 5 for Windows (TER BRAAK & ŠMILAUER 2002) was used for running both indirect and direct gradient analyses. DCA was run *a priori* in order to choose between linear and unimodal ordination methods (LEPŠ & ŠMILAUER 2003). Resulting gradient lengths (6.5 for the first axis in the complete data set and 4.2 in the reduced data set) clearly indicated that the unimodal method (CCA) was more appropriate. CCA was used to evaluate the independent (marginal), conditional, and pure effects of individual variables. The pure effect of individual variables was set as percentage variance explained by individual variable after all variables that were individually significant were eliminated by using them as covariables (TER BRAAK & PRENTICE 1988). Forward selection was used for ranking environmental variables in order of importance using a Monte Carlo permutation test (9999 runs of unrestricted permutations) for statistical testing of their effects (TER BRAAK 2002). A set of partial CCAs was carried out to quantify the independent variance accounted for by individual variables (BOCKARD et al. 1992, ØKLAND 1999). All nominal dummy variables representing a single environmental factor (e.g. geological bedrock type, phytochorological affinity) were included at once after the first of them had passed the forward selection as significant.

2.4. Nomenclature

Plant species nomenclature follows MARHOLD & HINDÁK (1998). Nomenclature of syntaxa follows JANIŠOVÁ (2007) for dry, semi-dry, and mesophilous grassland communities and VALACHOVIČ (2001) for the wetland communities.

3. Results

3.1. Grassland types and environmental gradients

According to the results of the DCA (eigenvalues: I. axis 0.691, II. axis 0.333; length of gradient of the main ordination axis: 6.5, Fig. 3), our data set consists of a big and rather homogeneous group of meso- to xerophilous grassland relevés and of two smaller groups of wetland relevés. Ellenberg indicator values used as passive supplementary variables confirmed our hypothesis that the main environmental gradient in our data set can be interpreted as moisture gradient (*post hoc* correlation of the first ordination axis with *moisture IV* was −0.98). The second most important environmental gradient represented by the second ordination axis is correlated mainly with the Ellenberg indicator values for nutrients (*post*

Table 1: Environmental variables used in the canonical correspondence analyses (CCAs)

Tab. 1: Umweltvariablen, die in den kanonischen Korrespondenzanalysen (CCAs) verwendet wurden

Variable type/variable	Variable characteristics
Topographic	
Altitude (m)	Elevation measured by a GPS or derived from the topographic maps 1 : 50,000.
Slope (degrees)	Inclination of microrelief estimated directly at the relevé plot.
Macro_slope	Inclination of macrorelief derived from digitised topographic maps. Average slope values of six categories.
Basic climatic	
Temperature_year	Mean annual air temperatures calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Temperature_July	Mean July air temperatures calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Growing season_narrow	Number of days with air temperatures over 5 ºC calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Growing season_broad	Number of days with air temperatures over 0º C calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Precipitation_year	Annual precipitation totals calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Precipitation_July	July precipitation totals calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Precipitation_growing season	Precipitation totals during the growing season (April–September) calculated in a GIS environment using long-term measurements (1951–1980) and topographic data.
Climatic region "A"	Moderately warm and moderately wet climate region according to Džatko et al. (1989)
Climatic region "B"	Moderately cold and moderately wet climate region according to Džatko et al. (1989)
Climatic region "C"	Cold and wet climate region according to Džatko et al. (1989)
Climatic region "D"	Very cold and wet climate region according to Džatko et al. (1989)
Derived climatic	
Solar radiation	Potential direct solar irradiation (heat index) calculated from the slope and aspect data according to Parker (1988).
Climatic water balance	Difference between precipitation and evapotranspiration used as indicator of landscape humidity during the growing season (April–September). Modelled in a GIS environment using the FAO Penman-Monteith equation (Hlásny & Baláž 2008).
Phytochorological	
Cold phytochorion	Main cold phytochorological region of the West Carpathian flora. Binary variable.
Warm phytochorion	Main warm phytochorological region of the West Carpathian flora. Binary variable.
Transitional phytochorion	Transitional zone with mixed influence of both cold and warm phytochorological regions. Binary variable.
Geological	
Dolomites, *Limestones*, *Andesites*, *Quartzites*, *Claystones*, *Quaternary sediments*, *Orthogneisses*	Bedrock type derived from geological maps 1 : 25,000 and 1 : 50,000. Binary variables.
Pedological	
Disturbed soils on slopes, *Fluvisols*, *Gleysols*, *Cambisols*, *Rendzinas*	Main pedological unit derived from digitised pedological maps 1 : 5,000. Binary variables.
Soil depth	Soil depth categories (shallow, moderately deep, deep) derived from digitised pedological maps 1 : 5,000 and expressed in ordinal scale.
Soil texture	Soil types derived from the proportion of different grain sizes of mineral particles in a soil. Three binary variables (light, moderately heavy, and heavy soils) derived from digitised pedological maps 1 : 5,000.
Soil gravel proportion	Categories of soil/gravel proportion (without gravel, low, moderate, high) derived from digitised pedological maps 1 : 5,000.

Table 2: Classification scheme of the studied grassland communities and indication of grassland types: X – xerophilous grasslands, SX – sub-xerophilous grasslands, M – mesophilous grasslands, W – wet meadows, F – fen meadows.

Tab. 2: Klassifikation der untersuchten Rasengesellschaften mit Zugehörigkeit zu fünf Haupttypen: X – Volltrockenrasen, SX – Halbtrockenrasen, M – mesophiles Grünland, W – Feuchtgrünland, F – Niedermoorgesellschaften.

Syntaxon	Grassland type
Class *Festuco-Brometea* Br.-Bl. & Tx. ex Soó 1947	
Order *Festucetalia valesiacae* Br.-Bl. & Tx. ex Br.-Bl. 1949	
Alliance *Festucion valesiacae* Klika 1931	
Association *Festuco rupicolae-Caricetum humilis* Klika 1939	X
Order *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968	
Alliance *Diantho lumnitzeri-Seslerion* (Soó 1971) Chytrý & Mucina in Mucina et al. 1993	
Association *Festuco pallentis-Seslerietum calcariae* Futák 1947 corr. Janišová 2007	X
Alliance *Bromo pannonici-Festucion pallentis* Zólyomi 1966	
Association *Orthantho luteae-Caricetum humilis* Kliment & Bernátová 2000	X
Order *Brometalia erecti* Koch 1926 em. Br.-Bl. 1936	
Alliance *Cirsio-Brachypodion pinnati* Hadač & Klika ex Klika 1951	
Association *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933	SX
Association *Carici albae-Brometum monocladi* Ujházy et al. 2007	SX
Alliance *Bromion erecti* Koch 1926	
Association *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939	SX
Association *Onobrychido viciifoliae-Brometum erecti* T. Müller 1966	SX
Class *Molinio-Arrhenatheretea* Tx. 1937	
Order *Arrhenatheretalia* Tx. 1931	
Alliance *Cynosurion cristati* Tx. 1947	
Association *Lolio perennis-Cynosuretum cristati* Tx. 1947	M
Alliance *Arrhenatherion elatioris* Luquet 1926	
Association *Pastinaco sativae-Arrhenatheretum elatioris* Passarge 1964	M
Association *Poo-Trisetetum flavescentis* Knapp ex Oberdorfer 1957	M
Association *Anthoxantho odorati-Agrostietum tenuis* Sillinger 1933	M
Association *Ranunculo bulbosi-Arrhenatheretum elatioris* Ellmauer in Mucina et al. 1993	M
Association *Lilio bulbiferi-Arrhenatheretum elatioris* Ružičková 2002	M
Order *Poo alpinae-Trisetetalia* Ellmauer & Mucina 1993	
Alliance *Polygono bistortae-Trisetion flavescentis* Br.-Bl. & Tx. ex Marshall 1947	
Association *Campanulo glomeratae-Geranietum sylvatici* Ružičková 2002	M
Order *Molinietalia* Koch 1926	
Alliance *Calthion palustris* Tx. 1937	W
Class *Nardetea strictae* Rivas Goday & Borja Carbonell 1961	
Order *Nardetalia strictae* Oberd. ex Preising 1949	
Alliance *Nardo strictae-Agrostion tenuis* Sillinger 1933	
Association *Violo sudeticae-Agrostietum capillaris* Ujházy in Janišová 2007	M
Class *Phragmito-Magnocaricetea* Klika in Klika & Novák 1941	
Order *Phragmitetalia* Koch 1926	
Alliance *Phragmition communis* Koch 1926	W
Order *Nasturtio-Glycerietalia* Pignatti 1953	
Alliance *Glycerio-Sparganion* Br.-Bl. & Sissingh in Boer 1942	W
Class *Scheuchzerio-Caricetea fuscae* Tx. 1937	
Order *Caricetalia davallianae* Br.-Bl. 1949	
Alliance *Caricion davallianae* Klika 1934	F

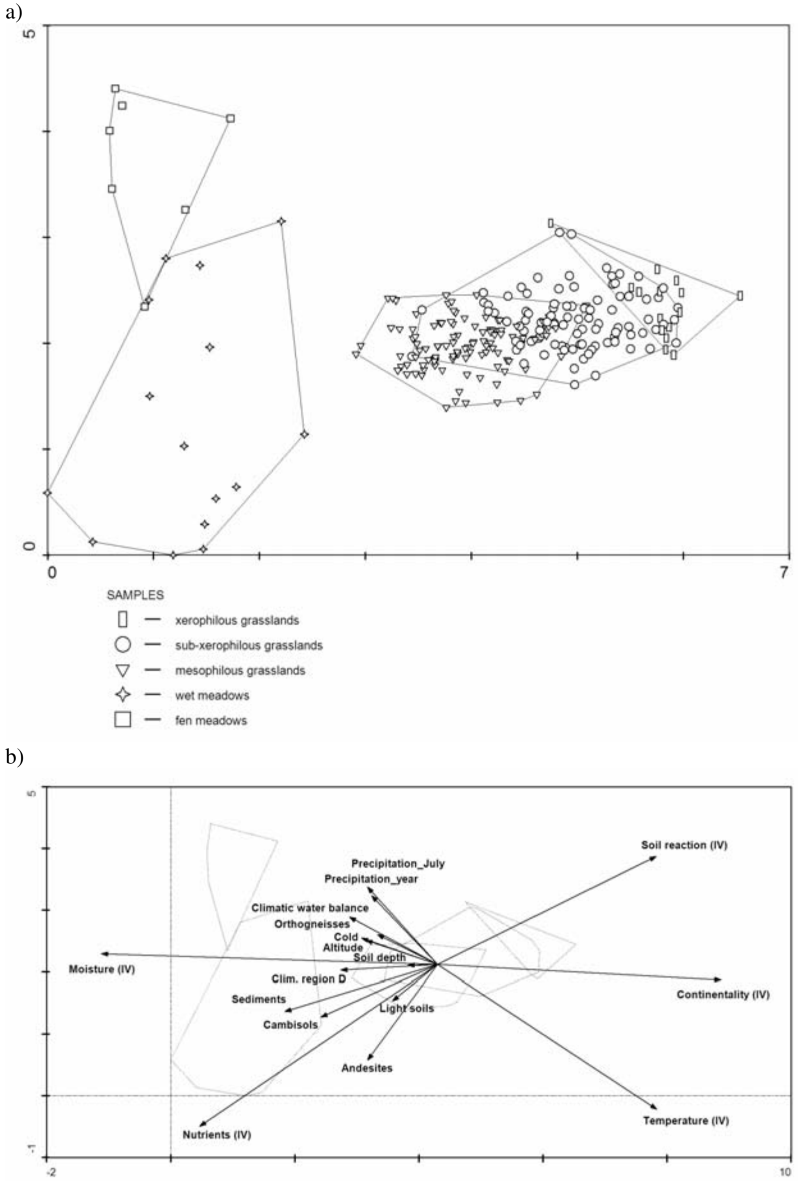

Fig. 3: DCA of the complete data set (eigenvalues: I. axis 0.691, II. axis 0.333; length of gradient of the main ordination axis is 6.5). Relevé positions (a) and supplementary environmental variables with the highest correlation to the ordination axes (b). Wet and fen meadow communities are conspicuously separated from other grassland types along the first ordination axis, which can be interpreted as a moisture gradient (*post-hoc* correlation with *moisture IV* was –0.98). The second axis represents the nutritional status of habitats (*post-hoc* correlation with *nutrients IV* was –0.48).

Abb. 3: DCA des Gesamtdatensatzes (Eigenwerte: I. Achse 0,691; II. Achse 0,333; Gradientlänge der I. Achse 6,5). Dargestellt ist die Lage der Aufnahmen (a) und jene der Umweltvariablen mit der höchsten Korrelation zu den Ordinationsachsen (b). Feuchtwiesen- und Niedermoorgesellschaften sind von den übrigen Rasengesellschaften entlang der I. Achse getrennt, womit sich diese als Feuchtegradient interpretieren lässt (*post hoc*-Korrelation mit dem Ellenberg-Zeigerwert für Bodenfeuchte war –0,98). Die II. Achse repräsentiert die Nährstoffverfügbarkeit (*post hoc*-Korrelation mit dem Ellenberg-Zeigerwert für Stickstoff war –0,48).

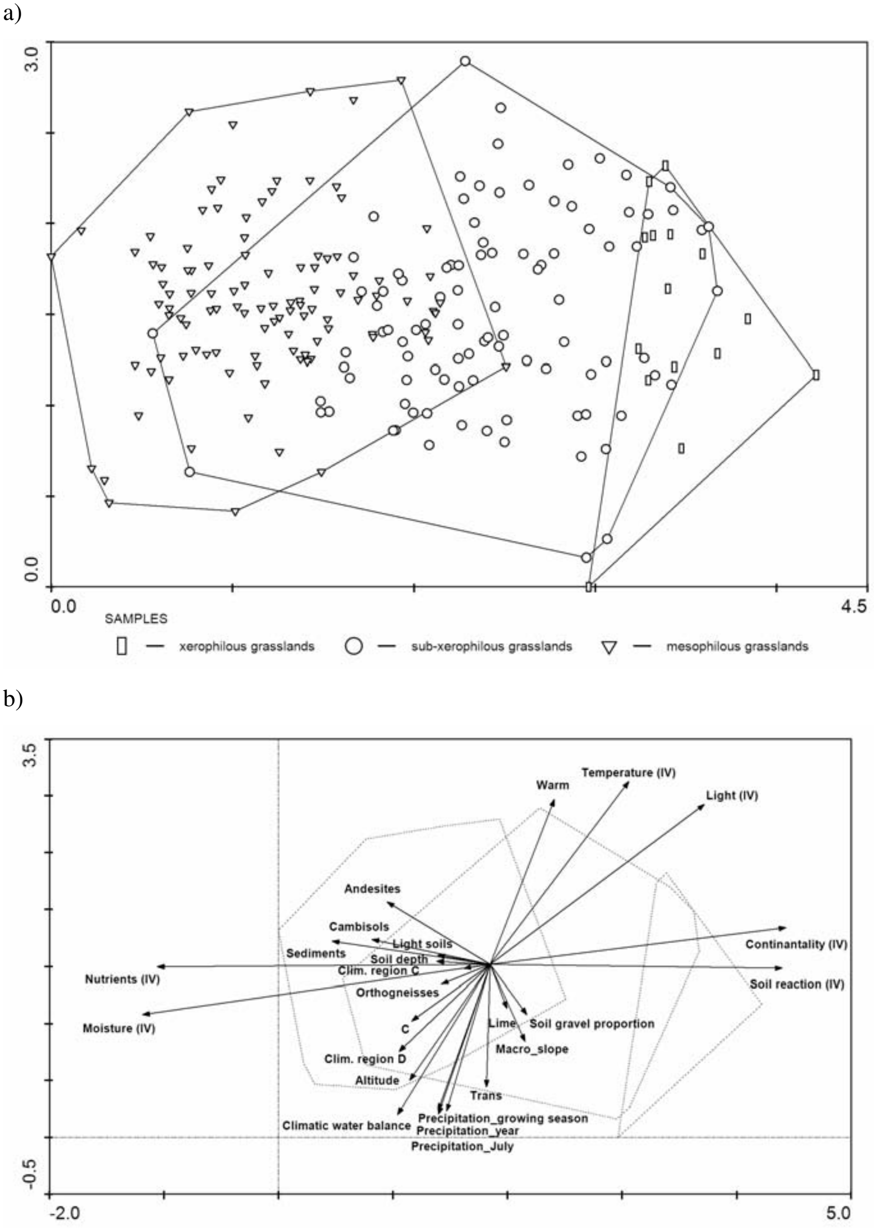

Fig. 4: DCA of the reduced data set (eigenvalues: I. axis 0.438, II. axis 0.226; length of gradient of the main ordination axis is 4.2). Relevé positions (a) and supplementary environmental variables with the highest correlation to the ordination axes (b). The first ordination axis has the highest correlation with *moisture IV* (–0.94) and *nutrients IV* (–0.90). The second axis correlates mostly with *temperature IV* (0.59) and *warm phytochorion* (0.53).

Abb. 4: DCA des Teildatensatzes ohne die Feuchtgebietsaufnahmen (Eigenwerte: I. Achse 0,438; II. Achse 0,26; Gradientlänge der I. Achse 4,2). Dargestellt ist die Lage der Aufnahmen (a) und jene der Umweltvariablen mit der höchsten Korrelation zu den Ordinationsachsen (b). Die erste Achse hat die höchste Korrelation mit den Ellenberg-Zeigerwerten für Bodenfeuchte (–0.94) und Stickstoff (–0.90). Die zweite Achse korreliert v. a. mit dem Ellenberg-Zeigerwert für Temperatur (0,59) und dem warmen Phytochorion (0,53).

hoc correlation with *nutrient IV* was −0.48). A clear separation of two wetland types along this axis is obvious, fen meadows of the *Caricion davallianae* occuring on nutrient-poor habitats in the upper part of the ordination graph, and wet meadows of the *Calthion palustris* inhabiting sites rich in nutrients in the lower part of the graph. According to the DCA of the reduced data set (eigenvalues: I. axis 0.438, II. axis 0.226; length of gradient of the main ordination axis: 4.2, Fig. 4), the first ordination axis had the highest correlation with *moisture IV* (−0.94) and *nutrients IV* (−0.90). The second axis was correlated mostly with *temperature IV* (0.59) and *warm phytochorion* (0.53).

3.2. Canonical correspondence analysis of the complete data set

In the CCA of the complete data set (eigenvalues: I. axis 0.282, II. axis 0.131, Fig. 5) the following variables explained the highest proportion of the individual data variation (Table 3): *quaternary sediments* (1.34%), *slope* (1.26%) and *climatic water balance* (1.19%), followed by a set of basic climatic variables expressing attributes of air temperature, precipitation, or length of the growing season. In general, geological, topographic, climatic, derived climatic, and phytochorological variables explained more variance than pedological variables. Among pedological variables, the main pedological soil type explained the highest proportion of the variance, namely *cambisols* (1.15%) and *rendzinas* (0.80%).

In the forward selection, bedrock types were included in the first step, explaining altogether 5.31% of the data variation (Table 3). Phytochorological affinity was indicated as the second most important factor (the three phytochorions explained 1.47% of data variation), followed by *slope* (0.79%) and *solar radiation* (0.76%). All these variables were significant at $p < 0.001$ and together explained 8.3% of compositional variance. Among the variables passing the forward selection, only *slope* and *solar radiation* had a significant pure effect of 0.5% and 0.7%, respectively (Table 3). The position of the main grassland types in relation to four environmental factors passing the forward selection is shown in Fig. 5. Concerning the geological bedrock type, a clear preference of quaternary sediments, andesites, and orthogneisses is obvious in wet meadows, while fen meadows occur mostly on limestones and quaternary sediments. The concentration of xerophilous grasslands in the sun-exposed sites of the warm phytochorion is reflected in their position in the left part of the graph. Sub-xerophilous grasslands are also distributed mainly on calcareous bedrock of the warm and transitional phytochorions preferring steeper slopes. Both of them are missing on the bedrock formed by andesites, quaternary sediments, and orthogneisses, thus they are not present in the right-most part of the ordination graph. On the other hand, mesophilous grasslands do not show clear preferences and are rather evenly distributed in the ordination space.

3.3. Canonical correspondence analysis of the subset of xerophilous to mesophilous grasslands

After omitting all wetland relevés (wet and fen meadows), the data subset consisted of more homogeneous relevés of xero-, sub-xero-, and mesophilous grasslands. The results of the CCA of the reduced data set (eigenvalues: I. axis 0.229, II. axis 0.151) are shown in Fig. 6. The percentage of explained variance in the studied subset was higher than in the former analysis of the complete data set for all analysed variables (Table 4). *Climatic water balance* and all basic climatic variables showed the highest values of explained variance as the only constraining variables. Other variables with sizeable values were *altitude*, *dolomites*, *warm phytochorion* and *quaternary sediments*. Similar to the former analysis, pedological variables were least important in explaining the data variability not only individually, but also in the forward selection. After inclusion of *climatic water balance* (explaining 1.63% of data variation) in the forward selection, geological bedrock type appeared to be the most important factor (together explaining 5.99% of data variation). The third most important factor was *solar radiation* (1.04%), followed by *slope* (0.82%), *precipitation_July* (0.75%), and phytochorological affinity (the three dummy variables together explained 1.30% of the variance).

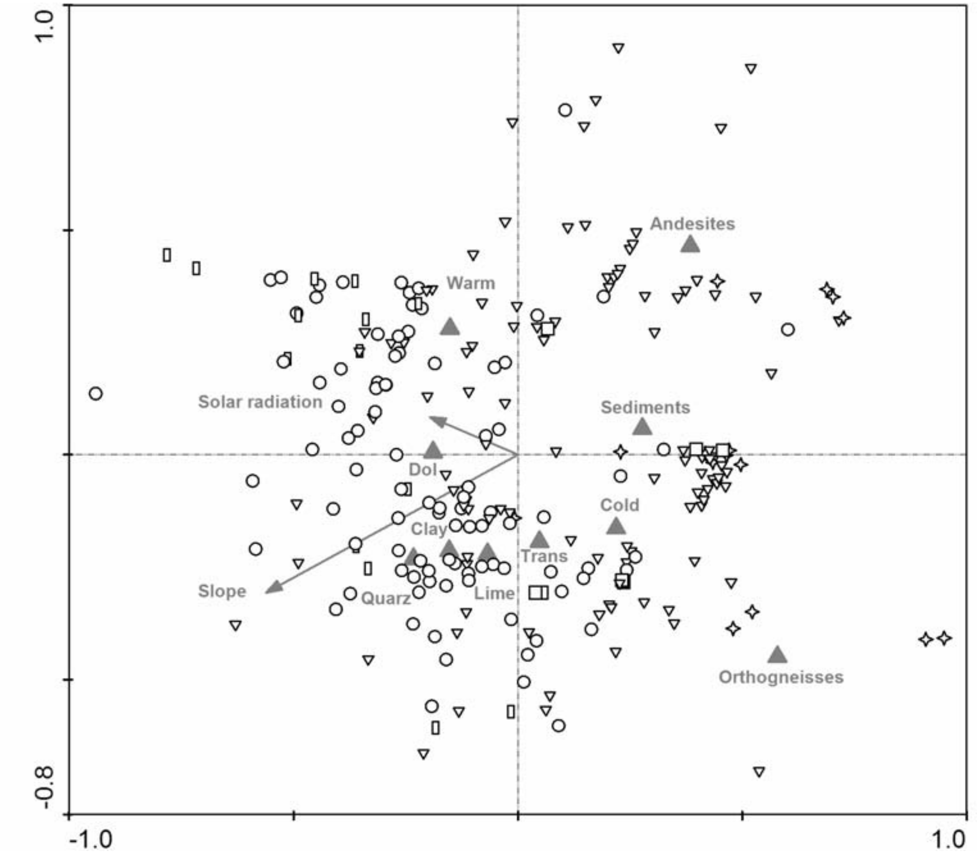

Fig. 5: CCA of the complete data set (eigenvalues: I. axis 0.282, II. axis 0.131). Relevé positions of five main grassland types (explanation of symbols according to Fig. 3a) in relation to four groups of environmental factors passing the forward selection at $p < 0.001$ are depicted. The two main axes display 3.7% of the variance in the species abundances and 44.3% of the variance in the species-environment relation. The significant environmental factors represent 8.3% of the data variation. The order of inclusion of individual variables in the forward selection is shown in Table 3. Quantitative environmental variables (*slope* and *solar radiation*) are indicated by arrows. Nominal environmental variables (geological bedrock type and phytochorological affinity) are indicated by triangles. Abbreviated names of environmental variables: *Clay* – Claystones, *Cold* – Cold phytochorion, *Dol* – Dolomites, *Lime* – Limestones, *Quarz* – Quartzites, *Sediments* – Quaternary sediments, *Trans* – Transitional phytochorion, *Warm* – Warm phytochorion.

Abb. 5: CCA des Gesamtdatensatzes (Eigenwerte: I. Achse 0,282, II. Achse 0,131). Die Lage der Aufnahmen der fünf Haupttypen von Rasengesellschaften (Symbole wie in Abb. 3a) in Relation zu den vier Gruppen von Umweltvariablen, welche in der Vorwärtsselektion für $p < 0.001$ ausgewählt wurden, sind dargestellt. Die beiden Hauptachsen erklären 3,7 % der Varianz in der Artenzusammensetzung and 44,3 % der insgesamt erklärten Arten-Umwelt-Beziehung. Die signifikanten Umweltfaktoren stehen für 8,3 % der Varianz. Die Reihenfolge der Aufnahme von Variablen in der Vorwärtsselektion kann Tab. 3 entnommen werden. Quantitative Umweltvariablen (Hangneigung und Strahlungsgenuss) sind durch Pfeile symbolisiert, nominale Umweltvariablen (Gesteinstyp und phytochorologische Zugehörigkeit) mit Dreiecken. *Clay* – Tonsteine, *Cold* – kaltes Phytochorion, *Dol* – Dolomit, *Lime* – Kalk, *Quarz* – Quarzite, *Sediments* – quartäre Sedimente, *Trans* – Übergangs-Phytochorion, *Warm* – warmes Phytochorion.

Table 3: Overview of the results of the CCA for the complete data set of 240 relevés.
Cover estimates were square-root transformed and environmental variables ordered by their marginal effects. Marginal effect – percentage variance explained by individual variable when used as the only constraining variable. Conditional effect – additional variance explained by the variable when included in the stepwise selection (only variables significant at $p < 0.001$ are shown). Pure effect – percentage variance explained by the variable after all variables that are individually significant were used as covariables. Variance explained is shown as % of total inertia. Significance was tested by running 9999 unrestricted Monte Carlo random permutations. Legend: ^{ns} not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Tab. 3: Übersicht der CCA-Ergebnise für den Gesamtdatensatz von 240 Aufnahmen.
Die Deckungsangaben wurden wurzeltransformiert und die Umweltvariablen sind gemäß ihrer marginalen Effekte angeordnet. Als marginaler Effekt wird der Anteil erklärter Varianz bezeichnet, wenn eine Variable als einzige *constraining variable* genutzt wird, während der konditionelle Effekt die anteilige erklärte Varianz in einer schrittweisen Regression ist (nur Variablen mit $p < 0.001$ sind dargestellt). Reiner Effekt = Anteil erklärter Varianz durch eine Variable, wenn alle anderen einzel signifikanten Variablen als Covariablen genutzt werden. Die erklärte Varianz ist als Prozentsatz der *total inertia* dargestellt. Signifikanzen wurden mit 9999 unbegrenzten Monte-Carlo-Permutationen getestet. Legende: ^{ns} nicht signifikant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Environmental variable	**Marginal effects**	**Conditional effects (selection order)**	**Pure effects**
Quaternary sediments	1.34 ***	1.34 (1)/5.31 all bedrock types	0.50 $^{n.s.}$
Slope	1.26 ***	0.79 (3)	0.73 **
Climatic water balance	1.19 ***		0.47 $^{n.s.}$
Temperature_July	1.19 ***		0.39 $^{n.s.}$
Growing season_broad	1.18 ***		0.36 $^{n.s.}$
Warm phytochorion	1.18 ***	0.95 (2)/1.47 all phytochorions	< 0.10$^{n.s}$
Precipitation_growing season	1.17 ***		0.39 $^{n.s.}$
Temperature_year	1.16 ***		0.70 **
Precipitation_July	1.16 ***		0.42 $^{n.s.}$
Precipitation_year	1.16 ***		0.39 $^{n.s.}$
Cambisols	1.15 ***		0.42 $^{n.s.}$
Growing season_narrow	1.14 ***		0.72 **
Dolomites	1.14 ***	(1)/5.31 all bedrock types	0.44 $^{n.s.}$
Altitude	1.11 ***		0.30 $^{n.s.}$
Climatic region "D"	1.08 ***		0.47 $^{n.s.}$
Andesites	0.92 **	(1)/5.31 all bedrock types	0.52 $^{n.s.}$
Climatic region "A"	0.88 **		0.32 $^{n.s}$
Orthogneisses	0.82 $^{n.s.}$	(1)/5.31 all bedrock types	
Cold phytochorion	0.80 ***	(2)/1.47 all phytochorions	< 0.10$^{n.s}$
Rendzinas	0.80 ***		0.33 $^{n.s.}$
Transitional phytochorion	0.75 ***	(2)/1.47 all phytochorions	< 0.10$^{n.s}$
Solar radiation	0.72 **	0.76 (4)	0.70 **
Climatic region "B"	0.68 **		0.46 $^{n.s.}$
Macro_slope	0.66 **		0.38 $^{n.s.}$
Limestones	0.63 *	(1)/5.31 all bedrock types	0.45 $^{n.s.}$
Heavy soils	0.59 *		0.37 $^{n.s.}$
Light soils	0.58 *		0.40 $^{n.s.}$
Claystones	0.55 $^{n.s.}$	(1)/5.31 all bedrock types	
Soil depth	0.55 $^{n.s.}$		
Disturbed soils on slopes	0.52 $^{n.s.}$		
Quartzites	0.48 $^{n.s.}$	(1)/5.31 all bedrock types	
Climatic region "C"	0.45 $^{n.s.}$		
Soil gravel proportion	0.44 $^{n.s.}$		
Moderately heavy soils	0.42 $^{n.s.}$		
Fluvisols	0.32 $^{n.s.}$		
Explained variance by significant variables		8.3	

Table 4: Overview of the results of the CCA for the complete data set of 218 relevés (wetland and wet meadow relevés omitted). For details, see legend of Table 3.

Tab. 4: Übersicht der CCA-Ergebnise für den Teildatensatz von 218 Aufnahmen (ohne Feuchtwiesen- und Niedermoorgesellschaften). Details der Darstellung sind in der Überschrift von Tab. 3 erklärt.

Environmental variable	**Marginal effects**	**Conditional effects (selection order)**	**Pure effects**
Climatic water balance	1.63 ***	1.63 (1)	0.53 *
Precipitation_year	1.60 ***		0.48 $^{n.s.}$
Precipitation_growing season	1.60 ***		0.48 $^{n.s.}$
Temperature_July	1.59 ***		0.55 *
Growing season_broad	1.59 ***		0.41 $^{n.s.}$
Temperature_year	1.58 ***		0.83 **
Precipitation_July	1.58 ***	0.75 (5)	0.53 *
Growing season_narrow	1.55 ***		0.89 ***
Altitude	1.50 ***		0.42 $^{n.s.}$
Dolomites	1.46 ***	(2)/5.99 all bedrock types	0.56 *
Warm phytochorion	1.44 ***	0.71 (6)/ 1.30 all phytochorions	< 0.10$^{n.s}$
Quaternary sediments	1.41 ***	1.38 (2)/5.99 all bedrock types	0.46 $^{n.s.}$
Cambisols	1.32 ***		< 0.10$^{n.s}$
Climatic region “D”	1.25 ***		< 0.10$^{n.s}$
Slope	1.24 ***	0.82 (4)	0.73 ***
Climatic region “A”	1.18 ***		< 0.10$^{n.s}$
Andesites	1.16 ***	(2)/5.99 all bedrock types	0.60 *
Solar radiation	1.07 ***	1.04 (3)	0.85 ***
Cold phytochorion	1.02 ***	(6)/ 1.30 all phytochorions	< 0.10$^{n.s}$
Transitional phytochorion	0.92 ***	(6)/ 1.30 all phytochorions	< 0.10$^{n.s}$
Rendzinas	0.92 ***		< 0.10$^{n.s}$
Climatic region “B”	0.90 ***		< 0.10$^{n.s}$
Macro_slope	0.90 ***		0.60 **
Orthogneisses	0.88 $^{n.s.}$	(2)/5.99 all bedrock types	
Limestones	0.87 ***	(2)/5.99 all bedrock types	0.59 **
Heavy soils	0.87 ***		< 0.10$^{n.s}$
Soil depth	0.73 **		0.64 **
Disturbed soils on slopes	0.71 *		< 0.10$^{n.s}$
Light soils	0.70 **		< 0.10$^{n.s}$
Claystones	0.69 *	(2)/5.99 all bedrock types	0.50 $^{n.s.}$
Quartzites	0.65 *	(2)/5.99 all bedrock types	0.42 $^{n.s.}$
Soil gravel proportion	0.59 $^{n.s.}$		
Climatic region “C”	0.56 $^{n.s.}$		
Moderately heavy soils	0.52 $^{n.s.}$		
Fluvisols	0.45 $^{n.s.}$		
Explained variance by significant variables		11.53	

These six significant factors combined explained 11.53% of the compositional variance, and all except the last of them (phytochorological affinity) showed significant pure effects (Table 4).

The position of the main grassland associations is shown in Fig. 6. Although several associations show clear preferences for certain environmental conditions indicated by the measured variables, some associations seem to be indifferent to them. The xerophilous vegetation occupies the right-most border of the ordination graph, indicating habitats with high solar radiation and steeper slopes. Communities of the *Cirsio-Brachypodion pinnati* are separated along the second ordination axis. The stands of the *Scabioso ochroleucae-Brachypodietum pinnati* occur mainly in the warm phytochorion in habitats exposed to intensive solar radiation. On the other hand, the stands of the *Carici albae-Brometum monocladi* occur mainly in the transitional phytochorion with higher precipitation and on very steep slopes, often in contact with the stands of *Lilio bulbiferi-Arrhenatheretum elatioris*. The two associations of the *Bromion erecti* alliance overlap in their occurrence to a high extent. Still, stands of *Brachypodio pinnati-Molinietum arundinaceae* occur more frequently in the transitional phytochorion, occupying various bedrock types, while stands of the *Onobrychido viciifoliae-Brometum erecti* are more common in drier habitats of the warm phytochorion. Among the mesophilous grasslands, the *Poo-Trisetetum flavescentis* shows the highest level of con-

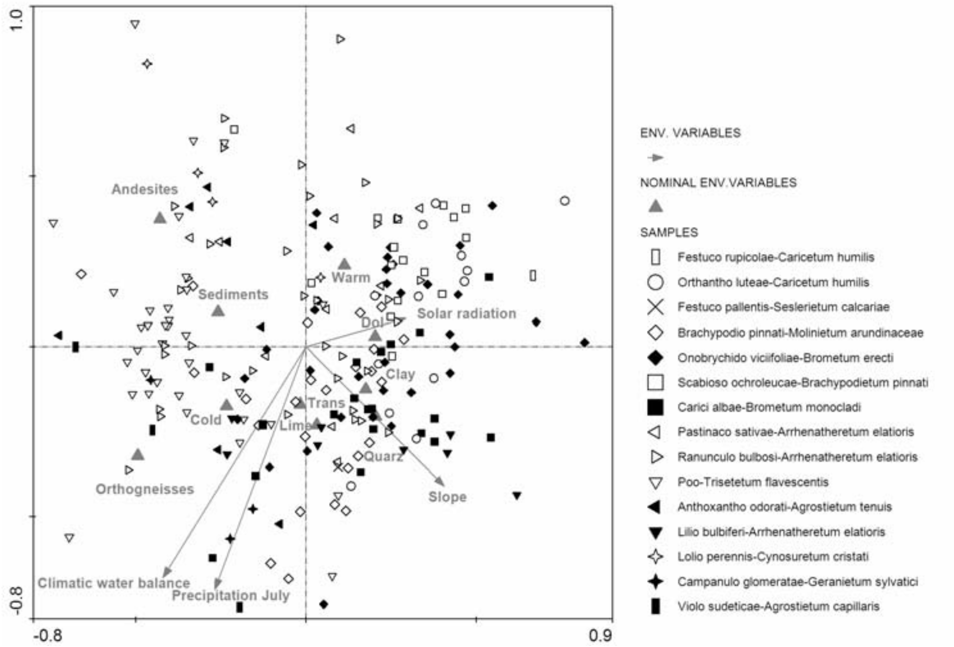

Fig. 6: CCA of the reduced data set (eigenvalues: I. axis 0.229, II. axis 0.151). Relevé positions in relation to six groups of environmental factors passing the forward selection at $p < 0.001$ are depicted. The two main axes display 4.8% of the variance in the species abundances and 42% of the variance in the species-environment relation. The significant environmental factors represent 11.53% of the data variation. The order of inclusion of individual variables in the forward selection is shown in Table 4. Abbreviated names of environmental variables are according to Fig. 5.

Abb. 6: CCA des Teildatensatzes ohne die Feuchtgebiete (Eigenwerte: I. Achse 0,229, II. Achse 0,151). Die Lage der Aufnahmen in Relation zu den sechs Gruppen von Umweltvariablen, welche in der Vorwärtsselektion für $p < 0.001$ ausgewählt wurden, sind dargestellt. Die beiden Hauptachsen erklären 4,8 % der Varianz in der Artenzusammensetzung and 42 % der insgesamt erklärten Arten-Umwelt-Beziehung. Die signifikanten Umweltfaktoren stehen für 11,53 % der Varianz. Die Reihenfolge der Aufnahme von Variablen in der Vorwärtsselektion kann Tab. 4 entnommen werden. Details der Darstellung sind in der Legende von Abb. 5 erklärt.

centration in habitats defined by the measured environmental factors. It is concentrated in the cold phytochorion over andesites and quaternary sediments. Pasture communities of the *Lolio perennis-Cynosuretum cristati* occur on gentle slopes in the warm phytochorion mainly on andesites and quaternary sediments. The stands of the *Ranunculo bulbosi-Arrhenatheretum elatioris* prefer drier habitats of both the warm and transitional phytochorion irrespective of the geological bedrock type. The associations *Pastinaco sativae-Arrhenatheretum elatioris* and *Anthoxantho odorati-Agrostietum tenuis* do not show clear preferences for any of the conditions defined by the measured variables; their relevés are spread widely over the ordination graph. The montane grassland associations *Campanulo glomeratae-Geranietum sylvatici* and *Violo sudeticae-Agrostietum capillaris* occur in the cold phytochorion in regions with high precipitation and positive values of *Climatic water balance*. The preferences of some associations could not be evaluated due to the low number of their relevés in our analysis (e.g. *Festuco rupicolae-Caricetum humilis*, *Festuco pallentis-Seslerietum calcariae*).

Omitting the wetland communities from the second analysis did not change the results of the forward selection dramatically. All environmental variables included in the analysis of the complete data set (Table 3, Fig. 4a) were confirmed as significant in the reduced data set (Table 4, Fig. 5). The order of inclusion of individual variables differed: in the heterogeneous complete data set , the geological bedrock type *quaternary sediments* was included first, while in the more homogeneous data set of xero-, sub-xero- and mesophilous grasslands only, the *climatic water balance* was the variable explaining the largest proportion of compositional variance.

4. Discussion

4.1. Main environmental gradients and factors with the highest explanation power

The results of the DCA show that floristic differences between the studied grassland communities are much more pronounced than suggested by the results of the CCA: eigenvalues are much lower in the CCA, and the patterns are very different suggesting that the floristic relations are not accurately captured by the constrained ordinations. This was the reason why we decided to interpret the main environmental gradients predominantly on base of the unconstrained ordination by relating environmental variables in the *post hoc* correlation analysis. In both DCAs (performed on the complete and the reduced data sets), *moisture IV* showed the highest correlation with the first ordination axes. However, none of the measured variables showing correlation with the first ordination axis and *moisture IV* was powerful enough to explain this main environmental gradient. None of the best correlated factors – *soil depth*, *climatic region D*, *altitude*, and *cold phytochorion* – had a significant pure effect (Fig. 3, Tables 3, 4). Among the variables supposingly related to water regime of habitats – *climatic water balance*, *slope*, *solar radiation*, and precipitation totals – only *slope* and *solar radiation* had significant pure effects in both DCAs, and *precipitation_July* had a significant pure effect in the analysis of the reduced data set. *Climatic water balance*, *solar radation*, and *slope* were selected as constraining variables in the forward selection of the reduced data set (Table 4). This suggests that the main environmental gradient interpreted so precisely by *moisture IV* is related more to the habitat conditions at the microscale (reflected by *slope* and *solar radiation*) than to the larger-scale topographic and climatic variables. The second axis in the complete data set can be interpreted as nutrient status of habitats (Fig. 3) based on the high correlation of the second ordination axis with *nutrients IV*. Among our directly measured and derived variables it is most positively correlated with several pedological and geological factors (*light soils*, *cambisols*, *andesites*, *quaternary sediments*). These factors showed significant marginal effects; nevertheless, their pure effects were not significant. With the highest marginal effect, the variable *quaternary sediments* was selected as the first restricting variable in the forward selection of the complete data set (Table 4).

These disparities in the results of constrained and unconstrained ordinations might raise the question whether the variables indicated as most important by the forward selection method have any biological effect at all, or if they are just correlated with a number of biologically important variables. According to our opinion and field experience, the factors indicated as most important by the forward selection really do play a crucial role in the determination of the vegetation species composition. The role of bedrock is obvious in the study area as reflected in the development of several well-distinguished associations confined to calcareous bedrock types (cf. Janišová et al. 2010). In a similar way, certain associations are bound in their distribution to volcanic rocks (andesites) and quaternary sediments (see e.g. the difference in distribution of wet and fen meadows in Janišová et al. 2010). The most common bedrock types – quaternary sediments, andesites, dolomites, and limestones – had also significant effect upon the variation in species composition when used as the only constraining variables (Table 3). The effects of *slope* and *solar radiation* are biologically well interpretable and widely recognised (Parker 1988, McCune & Keon 2002, McCune 2007). *Climatic water balance* indicated as the most important variable in the reduced data set represents a complex indicator of landscape humidity during the growing season calculated from precipitation, air temperature, and topographic data (Hlásny & Baláž 2008). The most surprising result was that the affinity to phytochorological regions with its relatively simple and homogeneous pattern (Fig. 2c) explained such a high fraction of the variance. Its classes are based on Ellenberg indicator values for temperature, so they should theoretically be directly related to topographic features. The correlation of phytochorological variables with altitude were 0.55, 0.16, and 0.60 (cold, transitional, and warm phytochorion, respectively), thus only certain aspects of these variables can be explained by regional topography. One possible explanation is that the phytochorological variables reflect a really important consequence of local flora distribution resulted from combined climatic and historical effects.

Among the different groups of variables (topographic, basic climatic, derived climatic, geological, pedological, and phytochorological), derived climatic, geological, and phytochorological variables explained the highest proportion of the data variation in CCAs. The inclusion of additional factors in our analyses would possibly change the relative explanation power of individual factor groups. In our study, we selected simply measurable and easily derivable variables. We did not record data on soil chemical properties and grassland management as they require time- and cost-consuming procedures (questionnaires for landowners, soil laboratory analyses). Our conclusions should therefore be regarded against the background of the limited set of predictor variables used.

4.2. Topographic and spatial variables

The only topographic variable having a significant pure effect was *slope*. Some authors suggest that purely spatial components might reflect historical processes like large-scale dispersal limitation as seen in European-scale patterns in tree species composition and richness (Svenning & Skov 2005). Although dispersal is a spatial process, most grassland species are not long-lived in the seed bank, and their dispersal among grasslands is limited in fragmented landscapes (Bakker & Berendse 1999, Eriksson et al. 2002). Thus in many studies, large-scale spatial trends are not strong predictors of grassland variability (e.g. Klimek et al. 2007).

4.3. Pedological, geological, and management variables

Pedological variables describing soil properties played only a subordinate role in the determination of the vegetation composition if compared with climatic, geological, and topographic factors. Although some pedological variables showed a significant effect as only constraining variables (*cambisols*, *rendzinas*, *heavy soils*, Tables 3 and 4), none of them passed the forward selection. This could be caused by a high correlation with other measured variables, in particular the geological bedrock types and slope. Thus, even though many publications confirmed a strong effect of soil characteristics upon vegetation composition (e.g. Cousins & Eriksson 2002, Auestad et al. 2008), in our study, the effect of soil properties can rather be interpreted as secondary (they are a consequence of geological and topographic factors rather than factors primarily affecting the species composition). Another possible explanation for the low ability of pedological variables to explain the variability of species composition is their low resolution. Our pedological data were obtained from the GIS digital maps scaled 1 : 5,000. It is possible that this scale was too small for the purpose of our analyses and that the directly measured soil characteristics would give better results.

Soil chemistry and management are generally considered to be the most important factors affecting species composition and diversity in grassland ecosystems, while the first-mentioned factor is often considered to be an effect of the second one (MYKLESTAD 2004). Parameters of soil chemistry (especially the content of nitrogen and phosphorus) can serve as strong predictors in data sets including both intensive and slightly managed grasslands (VANDVIK & BIRKS 2002, MYKLESTAD 2004, KLIMEK et al. 2007). However, in the data set of species-rich xero- and mesophilous grasslands of low productivity, even the directly measured soil chemistry parameters explain only part of the species data variation (e.g. MICHÁLKOVÁ et al. 2007, ŠKODOVÁ 2007). Also for our data set, we would expect the explanatory power of basic soil nutrients to be rather limited as the studied grasslands were not subjected to intensive management and fertilisation in the past. More probably, a stronger effect of Ca and Mg could be expected, caused by different bedrock types in the study area, especially since the effect of geological bedrock was confirmed to be one of the most significant effects in our analyses.

4.4. Proportion of explained variance

The amount of unexplained variance in both data sets (the complete and the reduced) was unusually high, i.e., the measured variables explained only a small proportion of the variance in species composition, both individually and combined (8.30% and 11.53% for the complete and the reduced data set, respectively). Such a large fraction of unexplained variance may be interpreted as evidence for the existence of (i) important, but non-measured deterministic factors or (ii) large fractions of random compositional variance in the data (VANDVIK & BIRKS 2002).

(i) It is possible that the simply measured and easily derivable variables analysed in our contribution did not include the main factors affecting the studied vegetation. We did not study the effect of soil fertility and management factors, which are considered to be very important in grassland ecosystems especially with regard to grassland species richness (MYKLESTAD & SÆTERSDAL 2004, KLIMEK et al. 2007). Although we did not directly study the soil chemistry parameters, we tested numerous pedological factors including soil types, soil depth, soil texture, and soil gravel proportion. All of them explained very little variance in species composition. The inclusion of additional soil chemistry parameters would probably at least slightly increase the explained variance. Similarly, the analysis of the combined effects of more environmental variables could help to explain the residual variation.

(ii) There appears to be a high degree of randomness in the grassland vegetation. Grasslands represent semi-natural vegetation with a rather short evolutionary history (in the study area, the age of most grassland plots does not exceed 200 years). In contrast to climax forest communities, grassland vegetation seems to be less dependent on macro- and meso-environmental factors and more dependent on direct human influence. In reaction to changing management practices, the species composition of grasslands is characterised by pronounced spatial and temporal dynamics. The state of equilibrium in species composition can hardly be developed within such a short period, especially while the human impact fluctuates in its quality, frequency, and intensity (dependent on e.g. economic situation of the landowners, availability of technical tools, remoteness of the grassland plots from the village, etc.). Some historical management practices can hardly be traced today, and thus the use of historical records and maps would be necessary to explain their effect on the present species composition (MAURER et. al 2006). Also, the effect of stochastic factors such as weather fluctuations, droughts, or wet periods is probably more pronounced in open grassland communities than in closed forests. All these facts might substantially contribute to the non-attributable variance in the grassland species composition.

As it was demonstrated by ØKLAND (1999), large fractions of the total inertia may arise from purely statistical reasons, and thus a large amount of unexplained variance, especially in species composition data, is a common finding in ordination models. According to TER BRAAK & VERDONSCHOT (1995), the low percentage of explained inertia is an inherent feature of ecological data with a strong presence/absence aspect. In species-rich grasslands with a high α- and β-diversity, even a comprehensive set of environmental factors can explain only small proportion of their variability. This assumption is supported by SCHMIDA & WILSON (1985), who defined the so-called “mass effect” to explain the substantial noise in species-rich data caused by the occurrence of numerous rare and accessory species, which occur outside their habitats in places where they cannot maintain themselves on a longer timescale. This could also be the case for our data originating from a region with a large species pool. Some authors showed that the relative amount of explained variation captured by statistically significant variables was much higher for species richness than for species composition data (KLIMEK et al. 2007). They explain it by the fact that the mechanisms controlling species composition in managed grasslands are more complex than those controlling species richness. This statement is supported by OZINGA et al. (2005), who suggest that the explanation of species composition requires specific knowledge of the nature of the species.

As a consequence, some authors state that the fraction of explained variance should not be overinterpreted and that the comparison between relative contributions and potential importance of the different explanatory variables should give equally valuable results as the comparison between precisely explained and unexplained fractions (VANDVIK & BIRKS 2002). Although the variance partitioning approach (BOCKARD et al. 1992) is a powerful tool to clarify the complex variance-covariance structure within the data and to identify potentially important factors, its results cannot be used to determine causal relationships or to identify superfluous or missing explanatory variables.

Acknowledgement

We would like to thank E. Illyés, J. Dengler and an anonymous reviewer for valuable comments to the manuscript, A. Huckauf for improving our English, and J. Dengler for translating the abstract as well as figure and table legends into German. This contribution was financially supported by grant SK 0115 through the EEA Financial Mechanism and the Norwegian Financial Mechanism and by the state budget of the Slovak Republic, by the Slovak Research and Development Agency (APVT-51-015804), the Science Grant Agency of the Ministry of Education of the Slovak Republic, the Slovak Academy of Sciences (VEGA 2/0181/09), and the Floristisch-soziologische Arbeitsgemeinschaft (language editing).

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Co-ordinating editor: Jürgen Dengler
Manuscript received: 24.11.2009; accepted: 25.04.2010