Studies on the floristic composition and quality attributes of Hungarian semi-dry grasslands

Eszter Illyés

Eötvös Loránd University
Biology PhD School
Ecology, Conservation Biology and Systematics Program
Leader of the PhD school: Anna Erdei (PhD, D.Sc., corresponding member of the Hungarian Academy of Sciences)
Leader of the program: János Podani (PhD, D.Sc.)
Supervisor: Sándor Bartha (PhD, Dr. Habil.)

Institute of Ecology and Botany of the Hungarian Academy of Sciences
Vácrátót
2010

Contents

I. Introduction

I.1. Topic of the thesis

My thesis presents studies on semi-dry grasslands of Hungary. Under the scientific term 'semi-dry grasslands' I mean basophilous grasslands characterised by broad-leaved grass species, mostly by *Brachypodium pinnatum*, *Bromus erectus*, *Helictothrichon* spp.. In the stands broad-leaved forbs occur together with drought-tolerant steppe elements. The study object corresponds with the H4 habitat type of the MÉTA survey (Molnár et al. 2008a) and more or less equal to the syntaxonomical entity '*Cirsio-Brachypodion*' (Illyés et al. 2007a, Illyés et al. 2009).

Hungarian semi-dry grasslands bear high esthetic and conservational value both at national and at European level which is reflected by the fact that they are recognised as priority Natural Habitat Types of Community Interest ("Sub-Pannonic steppic grasslands" 6240) and thus many of their stands are protected as a part of the Natura 2000 network. Nevertheless, it is also a fact that so far at national level the knowledge of the actual distribution, floristic patterns and conservation status of semi-dry grasslands was rather limited, and only spatially scattered data were available. Therefore, the main goal of my thesis is to reveal the internal floristic diversity of this habitat type, to document the actual quality (conservation status) of these grasslands and to analyse the factors which determine or affect these two aspects. A comprehensive database was built up from the available vegetation data of Hungarian semi-dry grasslands (literature and unedited sources as well) and up-to date numerical analyses and modelling techniques were used in the thesis.

Hopefully this thesis can serve as a scientific basis for the better understanding of the factors shaping the character of semi-dry grasslands and thus the more effective conservation of them in the future.

I.2. Scientific background

I.2.1 Semi-dry grasslands in the central European and especially in the Hungarian landscape

Grasslands are integral parts of the semi-natural landscape of central Europe and they are of major importance for biodiversity in agricultural landscapes (Wallies De Vries et al.

2002, Klimek et al. 2007). The most species-rich plant communities in the world at small scale (< $10m^2$) are temperate grassland communities (Peet et al. 1983) and they are central object of ecological research and of European nature conservation (Baumann 2006). They are in the focus of nature conservation (e.g. the EU Habitats Directive and Natura2000 network) because of their high species richness and the occurrence of many rare or endangered species (Riecken et al. 1994; Borhidi & Sánta 1999; Chytrý et al. 2001; Stanová & Valachovič 2002). Semi-dry grasslands of central Europe are recognized by the European Community as endangered habitat types, and "Sub-Pannonic steppic grasslands"(6240) as Natural Habitat Types of Community Interest according to Annex I of the Habitats Directive (92/43/EEC).

Permanent grasslands play a major, but not always well recognised or understood role for society (production, employment), the environment, and biodiversity. The grasslands are key habitats for many species: herbs, grazing animals such as deer and rodents, butterflies and reptiles, and many bird species. Dry grasslands contain some specialist species, for example orchids and butterflies, which can survive only in dry well-lit conditions. Grasslands, particularly calcareous grasslands, are important habitats for orchids, and half of the orchid species in France, and between 35 and 42 % in Belgium, the Netherlands and Luxembourg, occur in dry and mesic grasslands. A high proportion of these are either in a highly vulnerable state or close to becoming extinct (European Commission 1999).

Grasslands, especially those visibly rich in species (flowering plants, insects, and raptors) have high recreation value. Grasslands have long been an important feature for landscape painting and the appreciation of the countryside. Grasslands such as steppes are the homes of ancestors to several of the now most widespread crops, garden bulbs, several species and medicinal plants. Permanent grasslands are therefore gradually becoming an important issue of concern in global, European, European Community and national decision-making, although to a widely varying extent (European Commission 1999).

Temperate grasslands occur naturally in the middle latitudes in regions where the seasonal climate favours the dominance of perennial grasses. In Eurasia steppes cover some 250 million ha of rolling plains that extend as a broad belt across the continent from Hungary to Manchuria (Archibald 1995, Fig. 1.). The grasslands of Eurasia form a more or less treeless corridor across the continent in which various regional associations are broadly differentiated according to latitude and altitude. The forest steppe component which corresponds with the tall-grass prairies of North America (Archibald 1995) forms a more or less continous belt in the northern part of the Eurasian steppe region, followed by the real steppe belt and the semi-desert belt southwards. The forest steppe belt reaches its westernmost and northernmost limit in the Carpathian Basin, ranging up to the Vienna Basin and South-Moravia (Borhidi 1961, Zólyomi & Fekete 1994).

Figure 1. Area covered by forest steppe vegetation in Eurasia. Source: WWF.

Mostly secondary steppe or forest steppe meadow-like grasslands occur also elsewhere in Europe with larger extent (especially in south Germany, Switzerland, France, Spain, in the British Isles, Estonia and south-Sweden, Fig. 2.). They are usually called as calcareous grasslands, since in these wetter and more humid parts of Europe dry and semi-dry grasslands usually develop on shallow, rocky soils. Although, they are not the part of the Eurasian forest steppe formation, the species composition, ecology, traditional land use and recent conservation problems of these calcareous grasslands are very similar and comparable those of the dry and semi-dry grasslands of the Carpathian Basin. In the following we make a short digression to the issue of the terms used for the types of dry and semi-dry grasslands. In the Hungarian studies of grasslands, dry grasslands dominated by narrow-leaved grass species on loess or other non-rocky material are often referred to as steppes ('sztyepek'), while the term slope steppes ('lejtősztyepek') is used for closed narrow-leaved communities formed on rocky

Figure 2. Area under permanent grassland (all grassland types) in utilised arable area in Europe in 1995. Source: European Commission, 1999. Agriculture, environment, rural development. Facts and Figures. A Challenge for Agriculture.

soils. Rock grasslands (‘sziklagyepek’) are communities dominated by many drought-tolerant species typical of rocks. Forest steppe meadows or wooded steppe meadows or semi-dry grasslands (‘erdőssztyep-rétek’) are composed of tall-growing grass species and are rich in forbs, while in meadow steppes (‘rétsztyepek’) species of wet habitats are present together with the steppe elements (Zólyomi & Fekete 1994, Illyés & Bölöni 2007). These Hungarian terms more or less correspond to the Russian equivalents (‘stipi’=steppes, ‘ostepnionnie luga’=forest steppe meadows, ‘lugovie stipi’=meadow steppes), however, steppe in general is a broad term in Russian usually used for all types of dry and semi-dry grasslands including rock grasslands, but excluding marshes and meadows (Lavrenko & Karamysheva 1993). The widely used term ‘calcareous grassland’ comprises both rock grasslands and semi-dry grasslands mostly dominated by broad-leaved grasses (Barbaro et al. 2004), however, rock grasslands have much lower significance in western Europe due to their small extent. Consequently, the terms ‘calcareous grassland’ and ‘forest steppe meadow’ indicate something very similar and though these terms are far from being synonyms, the findings of the studies of central and western European calcareous grasslands are highly relevant for the semi-dry grasslands (forest steppe meadows) of the Carpathian Basin (Illyés & Bölöni 2007). Alvar grasslands are special types of semi-dry grasslands occurring in Estonia and south Sweden on shallow soils (Meelis et al. 1999). These grasslands are also similar in their species composition and ecology to other European calcareous grasslands, so the studies regarding alvars are also relevant to the semi-dry grasslands of the Carpathian Basin and Hungary to some extent. Another term often used in the literature is ‘semi-dry grasslands’ which is more or less a synonym to calcareous grasslands, however, it comprises the acidic semi-dry grassland communities as well which are assigned syntaxonomically to the *Koelerio-Phleion phleoides* (Royer 1991, Rodwell et al. 2002). Since in Hungary non-calcareous semi-dry grasslands hardly occur, in my thesis under the term ’semi-dry grasslands’ I mean calcareous semi-dry grasslands, which more or less overlap with the syntaxonomical entity *Cirsio-Brachypodion* in case of Hungary (Illyés et al. 2007a, Illyés et al. 2009).

In semiarid areas of Hungary, semi-dry grasslands are considered to be parts of the Eurasian forest steppe vegetation as remnants of former mosaic landscape of steppes, dry oak forests and shrublands (Zólyomi & Fekete 1994). Although most of the semi-dry grasslands today represent an intermediate stage of secondary succession after deforestation or of regenaration after the abandonment of vineyards or small-size ploughlands, they are characterized by remarkably high species richness (Virágh et al. 2008). Semi-dry grasslands have preserved numerous elements of the former oak woodlands, thus having a great nature conservation value (Fekete et al. 1998, Virágh et al. 2008, Horváth 2009) and being parts of the Hungarian Natura2000 network.

The overall area of grasslands in Europe is hard to estimate since there are no comprehensive studies for this (European Commission 1999). The only available data for Europe as a whole is the Corine Landcover which is not adequate for estimation due to the loose definition of grassland types and the limited possibilities of the recognition of them by remote sensing.

In Hungary the actual semi-natural vegetation of the whole country was surveyed and estimated in the frames of the MÉTA project between 2004 and 2007 (Molnár et al. 2007). The survey was based on the list of semi-natural habitats of Hungary (Bölöni et al. 2007). Calcifrequent semi-dry grasslands correspond to the MÉTA habitat type 'H4 – Bromus erectus-Brachypodium pinnatum xero-mesic grasslands, dry tall herb communities and forest steppe meadows' (Molnár et al. 2008a). According to the MÉTA survey, the actual extension of semi-dry grasslands in Hungary is 12.000 ha, the two-third of that can be found in the Északi-középhegység (8.000 ha). Semi-dry grasslands occur in several places, however with much smaller area (2.700 ha) in the Dunántúli-középhegység, and sporadically in the eastern part of Dunántúli-dombság (700 ha), northern part of Nyugat-Dunántúl (280 ha), and in the western part of Alföld (Mezőföld, 300 ha). Semi-dry grasslands also can be found in small amount in Kisalföld, in the western part of Dunántúli-dombság, and in the northern part of the Duna–Tisza köze (Molnár et al. 2008a).

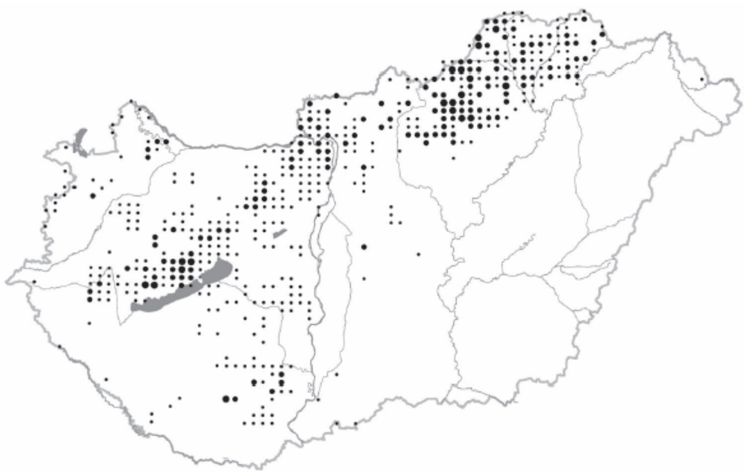


Figure 3. Distribution map of semi-dry grasslands in Hungary. From Molnár et al. 2008a. Small dots indicate small amount of vegetation (0.1 –17 ha), medium dots mean medium amount of vegetation (17.1 –140 ha) and large dots mean large amount of vegetation (more than 140 ha) in the quadrate of approximately 3500 ha.

I.2.2. Study of semi-dry grasslands in central Europe and in Hungary

I.2.2.1. Development of semi-dry grasslands in Central Europe and in Hungary

It is widely accepted that nearly all central European calcareous grasslands developed after Neolithic times from human land use practices, like burning, sheep and cattle grazing, or hay making over the course of thousand years (Pott 1995, Wallis De Vries 2002, Baumann 2006). However, suitable habitats for calcareous grasslands in the natural landscape of central Europe might have existed since the last ice age, but were scarce, small and isolated (Poschlod & Wallis De Vries 2002). Many authors assume that calcareous grasslands may have existed before man settled down (Poschlod & Wallis De Vries 2002). Nevertheless, most of the current semi-dry grasslands of Central Europe are considered to be secondary being developed due to human impact, after cutting the original (mostly dry and semi-dry oak and oak-hornbeam) forests for grazing or hay making (Pott 1995, Willems 2001, Poschlod & Wallis De Vries 2002). However, their history is quite diverse as they originate from different time periods since the Neolithic age and they underwent diverse land use history as well (Poschlod & Wallis De Vries 2002).

The centuries or sometimes thousands of years of traditional management not only stabilised these grassland patches but enabled them to become enriched with light-demanding steppe species while the original species of forests and forest fringes could be maintained as well. In other cases, under favourable environmental conditions and landscape context, species-rich semi-dry grasslands could develop on abandoned fields, orchards or vineyards. Although it seems that nearly all of the calcareous grasslands of north-western Europe have been cultivated (i.e. ploughed) for some time during the 19th century (Wallis De Vries 2002, Dutoit et al. 2003), this is most probably not the case for the Hungarian semi-dry grasslands. At least some small patches of grasslands on the steepest slopes of hills and of narrow valleys on the thick loess bedrock of the Mezőföld areas and on the foothills of the Északi- and Dunántúli-középhegység are thought to be ever free from ploughing (Horváth 2002, Illyés & Bölöni 2007).

I. 2. 2. 2. Composition of semi-dry grasslands

I.2.2.2.1. Phytosociology

Grassland habitats are of major importance to maintain biodiversity in the traditional landscapes of Europe (Wallis De Vries et al. 2002, Klimek et al. 2007). As it was told above, semi-dry grasslands of central Europe are recognised by the European Communities as endangered habitat types. They are labelled with the name and code "Sub-Pannonic steppic grasslands" 6240 as Natural Habitat Types of Community Interest according to Annex I of the Habitats Directive (92/43/EEC). Nevertheless, the 6240 habitat type distinguished so far have only unclear delimitation and were not supported by data at the European level (Demeter 2002). For recognition, effective inventory and monitoring of this habitat type country-level and international studies on habitat diversity are needed (Dúbravková et al. submitted).

The semi-dry grasslands of Central Europe are thus a suitable model for demonstrating the issues related to vegetation classification at an international level. Semi-dry grasslands were one of the first objectives of phytocosiological works (Dutoit 1924, Klika 1931, Soó 1933, Braun-Blanquet 1936), and they still attract many botanists and phytosociologists. In central and western Europe there have been several studies of semi-dry grasslands published continuously since the beginning of phytosociology as a discipline up to now (Klika 1933, Gauckler 1938, Meusel 1939, Wagner 1941, Knapp 1953, Wendelberger 1953, Eijsink et al. 1978, Willems 1982, Mucina & Kolbek 1993), and recently based on the up-to-date numerical analyses of large datasets (Denk 2000, Willner et al. 2004, Chytrý 2007, Janišová 2007). On the contrary, in Hungary the initial enthusiasm stopped soon. It might have been the reason that in the 1950-70-ies Hungarian plant sociological studies were focusing on the primary vegetation and semi-dry grasslands were regarded as of secondary origin (Zólyomi 1958, Soó 1964, 1973). There are only comments in the Hungarian literature on their presence, but detailed syntaxonomical studies, as well as extensive surveys of their range and states are missing. At the same time, the secondary origin of these grasslands was recognized and well accepted by the botanists of the surrounding countries (e.g. Jäger & Mahn 2001), but this fact did not hinder their study nor the acceptance of their botanical value at all.

According to the European phytosociological school, semi-dry grasslands are classified into the class *Festuco-Brometea* Br.-Bl. et Tüxen ex Soó 1947. Within this class most of the central-European calcifrequent semi-dry grasslands are assigned to the orders *Brometalia erecti* Koch 1926, but *Stipetum tirsae* Meusel 1938 is assigned to *Festucetalia valesiacae* Soó 1947 by some authors (e.g. Chytrý 2007), while by others (e.g. Borhidi 2003) to *Brometalia erecti*. Some of the recent national syntheses omit the order level for practical purposes (Chytrý 2007, Janišová 2007) and use the hierarchical levels of classes, alliances and associations only. Most of the European calcifrequent semi-dry grasslands are assigned to two alliances: the grasslands of *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951 contain several continental species and develop on deeper, calcareous soils of the warm and dry areas of Central Europe, while the grasslands of *Bromion erecti* Koch 1926 are distributed in the cooler regions and contain mainly oceanic species. Nevertheless, the ranges and the species composition of these two alliances overlap considerably (Royer 1991). A thrid alliance, *Danthonio-Stipion stenophyllae* Soó 1947, described from Transylvania and containing two *Stipa tirsa* associations was formerly distinguished in Hungary (Soó 1973), however it was never used by Romanian authors (Royer 1991, Sanda 2002), and recently it is regarded as the synonim of *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika (Borhidi & Sánta 1999, Borhidi 2003).

Historically, phytosociological studies of semi-dry grasslands were run independently in different countries, which resulted in a set of national classifications with only limited international compatibility (Klika 1933; Wagner 1941; Oberdorfer 1993; Krausch 1961; Mahn 1965; Eijsink et al. 1978; Mucina & Kolbek 1993; Borhidi 2003). So far, no comparative analysis has been performed that would establish clear links between corresponding semi-dry grassland types of different countries. In the subatlantic north-west, most of these grasslands probably developed as secondary vegetation after the deforestation of mesic forests (Willems 1982, Mucina & Kolbek 1993), while in the subcontinental south-east, particularly in the Carpathian Basin, many of them may be natural components of the forest-steppe landscapes (Zólyomi & Fekete 1994). This implies that a detailed knowledge of community variation within central European semi-dry grasslands may provide the scientific basis for designing management plans that would be more suitable for maintaining the biodiversity of particular landscapes.

In this thesis no comprehensive comparison of the phytosociological scheme of the different Central-European countries for semi-dry grasslands will be presented, since this task would reach far beyond my aims. Nevertheless, a short overview is given of the phytosociological systems of the surrounding countries regarding those semi-dry grassland associations which are presented in the system of more than one country (and thus not supposed to be only a locally occuring vegetation type) and have high relevance for Hungarian semi-dry grasslands. The other reason why we do not undertake the comprehensive comparison is the fact that only in the Czech Republic and in Slovakia have been the grassland associations reviewed recently with the help of numerical techniques (Chytrý 2007, Janisová 2007); however, both of these works aimed at supervising the earlier national systems and none of them intended to create a new one or to extend it to surrounding countries. The list of the relevant associations is presented with short comments. The capital fonts indicate the countries were the unit is the part of the system (Mucina & Kolbek 1993, Sanda 2002, Borhidi 2003, Chytrý 2007, Janisová 2007)

(1) Alliance: *Bromion erecti* Koch 1926 (AU,CZ, HU, SL) - Semi-dry grasslands of suboceanic distribution usually dominated by *Brachypodium pinnatum* and *Bromus erectus*, which lack several Continental and Submediterranean species. They occur mainly in the western part of Central Europe or at higher altitudes (Chytrý 2007, Janisová 2007).

(1a) Ass. *Onobrychido viciifoliae-Brometum erecti* T. Müller 1966 (AU, HU, SL) - *Bromus erectus* dominated species rich stands containing both xerophilous and meadow species (Janisová 2007).

(1b) Ass. *Carlino acaulis-Brometum erecti* Oberdorfer 1957 (AU, CZ, HU) - The stands are mostly dominated by *Brachypodium pinnatum* ocuring in the wetter regions usually on calcareous soils. The stands contain less Continental species (Chytrý 2007).

(1c) Ass. *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 (CZ, SL) - Extremely species rich semi-dry grasslands of the White Carpathians on the border of Czech and Slovak Republics. Stands are composed of species of meadows, dry grasslands, open forests and forest fringes, including species of intermittently wet soils (Chytrý 2007, Janisová 2007).

(2) Alliance: *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951 (AU, CZ, HU, RO, SL) - The stands are species rich and usually dominated by *Brachypodium pinnatum* and *Bromus erectus*, containing several continental species typical of Eastern European meadow steppes. They occur in warm and dry areas of Central Europe on deeper, calcareous soils (Chytrý 2007, Janisová 2007).

(2a) Ass.: *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933 (CZ, SL) - Mostly *Brachypodium pinnatum* dominated stands occuring in warmer regions usually on slopes on calcareous bedrocks. The stands contain xerophilous and calcareous species (Chytrý 2007, Janisová 2007).

(2b) Ass.: *Polygalo majoris-Brachypodietum pinnati* Wagner 1941 (AU, CZ, HU, SL) - Usually *Brachypodium pinnatum* dominated stands containing several continental species developed on moderately deep calcareous soils in lower altitudes (Chytrý 2007, Janisová 2007).

After a considerable time lag, the studies of the composition and evolution of semi-dry grasslands have been revived from the 1990-ies in Hungary; several papers were published. In the following we shortly summarize the findings of the works dealing with phytosociological aspects:

- Schmotzer & Vojtkó (1996, 1997) studied the *Brachypodium pinnatum* dominated grasslands of the Bükk mountains and described part of them as *Polygalo majoris-Brachypodietum pinnati*, other stands could not be assigned to any association due to their transitional character to *Pulsatillo-Festucetum*, *Molinio-Arrhenathalia* and *Quercetalia*. They consider the semi-dry grasslands of the Bükk Mts. to be secondary and derived directly from different type of oak-forests by human land use (Schmotzer & Vojtkó 1996, 1997) and thus they studied the differences in the species composition between the present semi-dry grassland patches and the hypothetised original forest communities. They conclude that the differences in the present species composition of the semi-dry grassland patches can be explained by the differences of the species composition of the original forests the grasslands derived from.
- Semi-dry grasslands of the Aggtelek Karts area were studied in detail by Varga-Sipos & Varga (1996, 1998, Varga 2000, Varga et al. 2000). High species richness, including floristic unicalities, well-developed structure and need of slight management of these grasslands is emphasised in these papers. Varga-Sipos and Varga (1996) proposed a new association *Poo badensi-Caricetum humilis* as well, though the formal description of this association and the holotype relevé is missing.
- Semi-dry grasslands of the western part of the Magyar Középhegység have been hardly studied so far (or at least not published yet). Isépy (1998) suggested – based on his own relevés and on the work of Debreczy (1966) – that the *Xerobrometum*-like *Bromus erectus* dominated grasslands of this part of the country developed on the places of

former white and turkey oak forests should be dealt together and proposed the name *“Lathyro pannonici-Brometum erecti”* based on a synthetic table of 10 relevés.

- Based on the relevés sampled in a loess valley of the Mezőföld region, Bauer et al. 2001 noted that these stands are not identical to any *Brachypodium pinnatum* association described from Hungary. Independently from this work, Horváth (2000, 2002) described a new type of *Brachypodium pinnatum* grassland from the central part the Carpathian Basin (from the loess area of the Mezőföld) extremely rich in Pontic-Pannonian species and proposed a name of *Euphorbio pannonicae-Brachypodietum*. This association is characterised by a dense, multi-layered structure, consists of broad-leaved graminoids and forbs, and is dominated by *Brachypodium pinnatum*. *Festuca rupicola*, *Salvia pratensis* and *Euphorbia pannonica* usually reach high cover in the stands. Species shared with open oak woodlands (*Tanacetum corymbosum*, *Anthericum ramosum*, *Anemone sylvestris*, *Peucedanum cervaria*, *Campanula bononiensis*, *Ranunculus polyanthemos*, *Trifolium alpestre*, etc.) occur frequently in the stands. Recently, Horváth has published the validation of this association with a formal description and a selected holotype (Horváth 2009).
- Recently, Szirmai (2008) has studied the vegetation of the Tardonai Hills in north Hungary taking special attention to secondary semi-dry grasslands developing in abandoned orchards and of different dynamical state.
- A recent study of *Danthonia alpina* grasslands in the Carpathian Basin and its surroundings (Kovács 2008) revealed that *Danthonia alpina* dominated stands most probably belong to several alliances and associations, partly described from central Europe, partly from Romania. This issue definitely needs further studies in the future with the cooperation of Romanian and Hungarian colleagues as well as grassland experts of the Balkan Peninsula and Dobrogea.

Despite the many scattered studies completed in different separate parts of the country, country-level computer-aided phytosociological synthesis for Hungary is still lacking. We consider it as a problem since effective conservation and management planning at the country level need information on the distribution and floristic composition of endangered habitat types. Formalised names, definitions, lists of diagnostic species of the semi-dry grassland types or associations would greatly facilitate biodiversity management. In Hungary, most of the journal publications covering semi-dry grasslands only contain the proposed names of the associations, textural descriptions or synthetic tables, while the original relevés of the described new associations are published in dissertations or are not published at all. In this situation, Hungarian phytosociological syntheses (Soó 1964-80, Borhidi 1996, 2003, Borhidi & Sánta 1999) used to review the associations described in the surrounding countries. Some of them were adopted, some of them were rejected, and the national system was further completed by newly described associations from Hungary, unfortunately, in most cases without detailed descriptions and tables. In the recent work of Borhidi (2003), the following system and associations are listed and described from Hungary, characterized by the dominance of *Brachypodium pinnatum* or *Bromus erectus*.

Order: *Brometalia erecti* Br.-Bl. 1936
- (1) Alliance: *Bromion erecti* Br.-Bl. 1936
  - (1a) Ass. *Onobrychido viciaefoliae-Brometum erecti* Müller 1966
  - (1b) Ass. *Carlino acaulis-Brometum* Oberdorfer 1957
- (2) Alliance: *Cirsio pannonicae-Brachypodion pinnati* Hadač & Klika 1944
  - (2a) Ass. *Polygalo majoris-Brachypodietum pinnati* Wagner 1941
  - (2b) Ass. *Lino tenuifolii-Brachypodietum pinnati* (Dostál 1933) Soó 1971
  - (2c) Ass. *Hypochoerido-Brachypodietum pinnati* Less 1991
  - (2d) Ass. *Carici montanae-Brachypodietum* Soó 1947
  - (2e) Ass. *Poo badensis-Caricetum montanae* V. Sipos & Varga 1996

However, this system, presented in a university textbook, does not contain any critical review of the literature nor any analysis, thus the reasons for some of the syntaxonomical decisions remains unclear. First, according to Soó 1973 the *Bromion erecti* alliance does not reach the interior of the Carpathian Basin, and there is no newer publication which would contradict this statement. Second, besides the 2c and 2e, the other associations are “adopted” from surrounding countries (1a, 2a,: Austria; 1b: Germany; 2b: Slovakia; 2d: Romania – Transylvania). It is a question why these (and not other) associations were placed in the system, however some of them (1a, 1b and 2d) even do not have any published relevés from Hungary. Third, it is unclear what was the reason of including *Hypochoerido-Brachypodietum pinnati* Less 1991 (2c) described from Hungary, which also does not have any published relevés, only an informal textural description (by Z. Varga in Borhidi & Sánta 1999), and excluding other associations with more detailed descriptions such as *Euphorbio pannonicae-Brachypodietum* (Horváth 2000, 2002).

Summing up the recent situation of phytosociology of semi-dry grasslands in Hungary, it can be stated that (1) even the main types and their geographical differentiation, range and differences of the composition is not known well enough; (2) the stands sampled in the field very often cannot be assigned to the associations mentioned in the phytosociological syntheses; (3) the transitional character and the hard identification of these grassland types has been mentioned by several authors (Soó 1964-1980, Varga et al. 2000), implying that at least a part of the semi-dry grasslands of the central Pannonian Basin represent special sub-types within the European semi-dry grasslands.

I.21.2.2.2. Species richness, diversity and the quality of vegetation

Biodiversity indicators are information tools, summarising data on complex environmental issues to indicate the overall status and trends of biodiversity at a local, national or international level (Mitchley & Xofis 2005). Species richness and diversity are among the most widely used biodiversity indicators and are considered to be the most important measures of any biological system in our days. The higher are these numbers, the better is the state of the community, the higher is the value to be conserved. Species richness and diversity have become the "secret words" of ecologists and conservationists which seem to be understood by those as well who are laymen in nature sciences but leaders of our lives; politicians, economists and layers all tend to be familiar with these terms.

Measurements of species richness and diversity are scale-dependent, which means that one has to delimit a particular space to which species richness is related. Only studies taken at the same range of scales can be compared to one another. The semi-dry grasslands of central and northern Europe are good objects for such studies since they are one of the most species-rich communities in Europe (Klimek et al. 2007). The methodology of vegetation studies in central Europe is highly influenced by phytosociology, thus the most often used scale for species richness and diversity studies is 4-16 square meters which corresponds to the quadtat sizes used in phytosociological studies. Sampling units falling into this scale are regarded by Otýpková & Chytrý (2006) as "homogeneous". Field sampling with quadrats of this size-range is relatively easy and fast, since this scale corresponds with the size of the plants as well as the human perception of grassland. Remarkable species richness of semi-dry grasslands at this scale have been documented by many studies (Löbel et al. 2006, Klimek et al. 2007, Löbel & Dengler 2008) from Europe and from Hungary as well (Varga 2000, Illyés et al. 2007a, 2007b, Illyés & Bölöni 2007, Bartha 2007, Kun et al. 2007).

However, the range of a few square meters may be useful to reflect relatively well the overall composition of a grassland, it does not tell much about the finer structure of it, about the way how the coexistence of numerous plant species is realised in a particular stand. For answering these kinds of questions we have to look at the grasslands at another scale. Fine-scale compositional studies have long traditions in Hungary. With a use of a high number of micro-quadrats from 5x5 up to 20x20 cm size, the fine-scale coalition structure of semi-dry grasslands can be revealed. Dynamical processes, degradation, regeneration and overall "well-being" of semi-dry grasslands can be detected this way. For the analysis of small scale data information theory methods of Juhász-Nagy are used (Juhász-Nagy 1976, 1993, Juhász-Nagy and Podani 1983). Small-scale studies of semi-dry grasslands revealed that the stands in good conservation status are spatially well-organized with complex multispecies coalition structure (Virágh & Bartha 2003). Studies with permanent plots proved that *Brachypodium pinnatum* and *Bromus erectus* dominated semi-dry grasslands in the central Pannonian basin are in a relatively stable state with slow vegetation changes for decades at the level of a vegetation patch or stand, despite the frequent and swift species turnover which occurs at the finer scale of the individuals (Virágh & Bartha 1998, 2003, Virágh et al. 2000). It was also proven that grazing alters the composition of *Brachypodium pinnatum* dominated semi-dry grasslands at the stand level considerably while the fine-scale patterns and coalition structure remain relatively stable (Horváth 2000, 2002).

One of the hot topics of recently published studies focusing on grasslands is to determine the factors which affect species richness and diversity. This is not a trivial question and we have to admit that the results highly depend on the factors involved in the analysis. Factors which are missed out from the analysis are either thought to be less important by the researcher or simply the researches does not have data on them. However, these missed out factors might turn to be the most important ones affecting species richness of grasslands in other studies.

So far we know that the actual species richness as well as the compositional and structural characteristics of semi-dry grasslands depend on several different factors, such as site history, recent and former land use, landscape context on different scales, size of the site, topographical parameters (slope, exposition), climate, soil characteristics, threatening factors, etc. (Pärtel et al. 1996, Wellstein et al. 2007), although the reported importance of the individual factors is varies from situation to situation and from publication to publication.

Phytodiversity in general has been shown to be determined by the overall productivity and the land-use history of the study systems (Milchunas & Laurenroth 1993), while local and regional species pools determine the species richness of a particular stand (Pärtel et al. 1996, Horváth 2002).

Studies on the relative importance of environmental conditions and management already have come to contradictory results. Some of the results show that the most important factors affecting species richness are soil properties, namely the pH of the soil (Sebastiá 2004, Löbel et al. 2006, Janssens et al. 1998). Others found that management regime explained the highest amount of variation in species richness (Klimek et al. 2007). However, in the same study, the effect of soil quality had significant effect on species richness as well. Landscape effects are also proven to influence plant species richness (Söderström et al. 2001, Löbel et al. 2006). Studies of historical landscape structure revealed that in many cases the actual species richness of a particular stand can be explained only by the historical configuration (connectivity, former patch sizes) of semi-dry grassland patches (Eriksson et al. 2002, Cousins 2006, Helm et al. 2006, Cousins et al. 2007). The reason of the contradictory results is most probably that different authors tested different sets of affecting factors and thus the results are not comparable. Moreover, only a very limited set of mainly subjectively chosen factors have been used in most of the cases and thus perhaps the most important factors were not tested at all.

Several papers have been published recently to show which factors affect biodiversity. In these papers biodiversity is measured exclusively as total species richness of a particular area (Dumotier et al. 2002, Dauber et al. 2003, Heikkinen et al. 2004, Devictor & Jiguet 2007) or species number and diversity of valuable species (Paltto et al. 2006) in different patches within different landscape contexts. Though species richness and proportion of valuable species are relatively easy to assess and have been widely-used indicators of biodiversity (understood as qualitative measures for the patch or landscape), species richness reflects only a very limited part of the whole habitat quality (Jeanneret et al. 2003, Bartha et al. 2004). Identification of the environmental, management, historical and spatial factors affecting the species composition of a stand or a habitat type – i.e. the level of the community as a whole – is another approach (e.g. Vandvik & Birks 2002, Klimek et al. 2007, Wellstein et al. 2007, Batáry et al. 2008). Nevertheless, in these cases the quality of the vegetation stand cannot be determined (there is no exact quality value of species composition), thus the role of factors explaining habitat quality cannot be revealed.

However, there is a different approach for assessing the quality of a vegetation stand. In Hungary, the 'naturalness based habitat quality' as a measure to determine habitat quality is widely used and accepted (Fekete et al. 1997, Molnár et al. 2007, Molnár et al. 2008b). It is a qualitative measure for a whole community or a habitat patch. Determining the overall quality of a particular habitat patch or habitat type is not an easy task; there is no absolute standard measure, since naturalness – similarly to human health – is not quantifiable as a whole. Nevertheless, there are thoroughly field-tested empirical methods available besides the one used in Hungary (Dierschke 1984, Németh & Seregélyes 1989, Parkes et al. 2003, Molnár et al. 2007), which make it possible to measure habitat quality.

In the landscape scale survey of the (semi-)natural vegetation of Hungary (the MÉTA project) we have developed a consistent method for determining the quality of a particular habitat patch called 'naturalness based habitat quality' (see Molnár et al. 2007). For defining the naturalness based habitat quality the following aspects were taken into consideration: proportion of specialist plant species, proportion of weedy and disturbance tolerant species and structure of the stand (Molnár et al. 2007), which is in accordance with the conventions used in some other European countries (Dierschke 1984, Bastian 1996, Ružičková et al. 1996, Grabherr et al. 1998, Mägi & Lutsar 2001). In the MÉTA project a four grade scale measure was used with values 2, 3, 4, and 5; where 2 means habitat patch with totally destroyed vegetation, only weeds and very general species are present, bad structure, even the habitat type is hard to identify; and 5 means patches in near-natural state, specialist and rare species present, the structure of vegetation is good. During the MÉTA survey the vegetation was mapped in 35 ha hexagonal grid, making a list of occurring habitat types in the grid cells. For each habitat type one naturalness based habitat quality value must have been given. Combined values such as 5r4 (or 4r2) were allowed meaning that 10 percent of the area of the habitat type has value 5 (4) and 90 percent of it has value 4 (2) (For more details, see Molnár et al. 2007.)

The measure 'naturalness-based habitat quality' (shortly referred to as naturalness) is realitvely quick to assess on the field and though it is burdened with an amount of subjectivity, it gives a good on-spot estimation of the conservation status of the particular stand. It has an advantage that data are available for the whole of the country and for all vegetation types and thus enables country-level analyses of the factors effecting naturalness of different habitat types.

I. **2. 2. 3. Conservation and management**

I.2.2.3.1. Threats to European and Hungarian semi-dry grasslands

Habitat loss is the primary environmental cause of biodiversity decline at local, regional and global scales also in case of grasslands (Dirzo & Raven 2003). It is recognised as a serious threat to high numbers of rare and declining plant species in Europe (Söderström et al. 2001). Over the past century, grasslands and other semi-natural plant communities in temperate Europe have suffered dramatic decline in their area due to land-use changes, and thereby once widespread vegetation types became highly vulnerable (Louto et al. 2003). In particular, calcareous grasslands decreased dramatically in area all over Europe. For example, in England the Agricultural Act of 1947 caused drastic agricultural development and thus long established grasslands were converted to arable fields to maximize cereal production (Baumann 2006).

Intensification and abandonment of traditional agricultural practices have drastically altered farmland landscapes in Europe and thus semi-natural grasslands became increasingly fragmented (Söderström et al. 2001). The situation of semi-dry grasslands in Hungary is the same as in other parts of Europe; most of the stands are fragmented and are threatened by different factors such as shrub encroachment or low intensity management (Illyés & Bölöni 2007, Illyés et al. 2007b, Virágh et al. 2006, 2008, Molnár et al. 2008b). Proportion of patches smaller than 5 ha of Hungarian semi-dry grasslands is strikingly high, it reaches 80% according to the MÉTA database (Fig 3.).

In the literature I found only sporadical data on the main threats which actually jeopardize European semi-dry grasslands. Fragmentation, habitat loss and change or abandonment of the traditional land use practice are the most widely mentioned factors (Dirzo & Raven 2003, Baumann 2006, Helm et al. 2006, Klimek et al. 2007); however, there are no available data on the frequency of these threats yor on the proportion or of the area they affect. During the MÉTA survey of (semi-)natural vegetation of Hungary (Molnár et al. 2007) threats on the particular habitat types were documented as well. According to this survey main threats of Hungarian semi-dry grasslands are summarized in Fig. 4. In a survey of the semi-dry grasslands of the Északi- Középhegység (Illyés et al. 2007b) we gained very similar patterns to what is shown on Fig. 4.

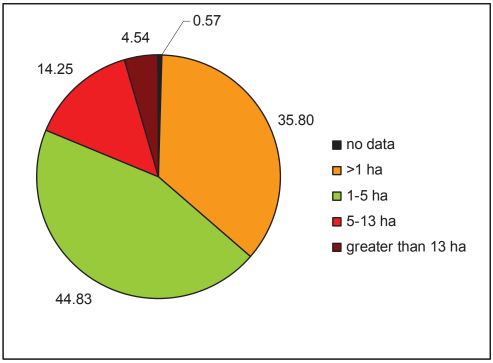


Figure 3. Distribution of patch-size categories semi-dry grasslands according to the MÉTA database of (semi-)natural vegetation of Hungary (for details of the survey see Molnár et al. 2007).

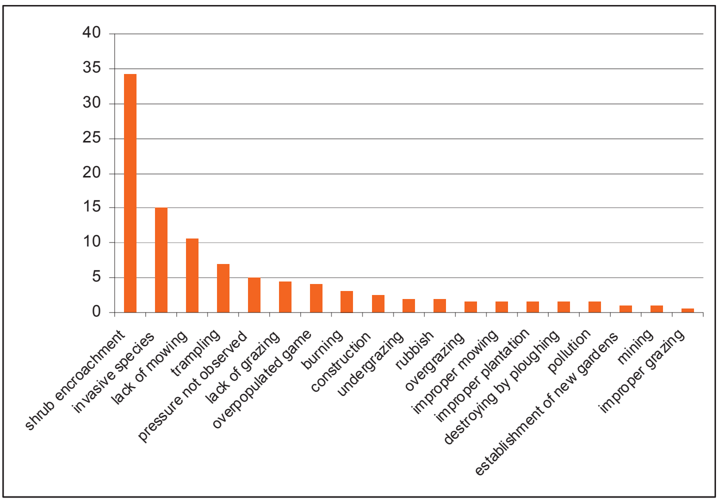


Figure 4. Factors threatening semi-dry grasslands according to the MÉTA database of (semi-)natural vegetation of Hungary. Data are compiled from Molnár et al. 2008b.

Burning generates much debate burdened with high subjectivity in case of Hungarian semi-dry grasslands. In Hungary it is a kind of tradition that if a grassland or fallow land is not used because of lack of capacity and/or willingness, local people burn it irregularly or even every year. Burning is considered to be highly dangerous for the diversity of grasslands. In spite of the fact that burning as a management is thought to be rather frequently used, the occurence of it as an actual threatening factor is low both in the data of the MÉTA survey (Molnár et al. 2008b) and the survey of the semi-dry grasslands of the Északi-Középhegység (Illyés et al. 2007b). The reason for this is most probably the difficult identification of early-spring buring in a semi-dry grasslands. However, it is also a fact that the real effects of burning to semi-dry grasslands are hard to estimate accurately. There are stands documented to be burnt regularly which are very rich in species and represent high conservational values, and at the same time, there are strikingly species poor stands supposedly again because of burning. Most probably, burning that can be detected is only one factor among the many others (e.g. historical land use, time of abandonment, surrounding landscape) which shape the conservation status of a semi-dry grassland stand and more detailed analyis of those many acting factors would be needed in order to reveal the real effect of burning.

I.2.2.3.1. Historical management of semi-dry grasslands

In historic dimensions, traditionally managed grasslands have been extensively used by mowing and grazing and have hardly received artificial fertiliser (Klimek et al. 2007). Maintenance of permanent grasslands was formerly done through haymaking and grazing in integrated labour-intensive systems. Maintenance at present tends to be either through grass cutting or grazing, and the intensity of cutting and grazing (over- or under-cutting or grazing) is a major issue for continuation of specific grassland types. Cattle farming with full or partial stabling and concentration of cattle geographically have caused considerable problems for the continuation of many grazing schemes for nature protection. Decrease or disappearance of old grazing regimes (mountain dairy meadows) and of transhumance (annual migrations of grazing flock) has led to the abandonment and disappearance of large grasslands (European Comission 1999). It happened at different times in different landscapes, however, severe decline occured mainly in the 20th century due to the abandonment of grazing and traditional farming systems. For example, in the Northern Franconian Albs around 95% of semi-dry grasslands disappeared between 1860 and 1993; while in Hanila, the largest alvar site in

Estonia, 70% of open grasslands disappeared from 1951 to 1994-96 due to absence of grazing (Baumann 2006). Many authors argue that the grasses *Bromus erectus* and *Brachypodium pinnatum* started to spread after the abandonment of grazing (Bobbink & Willems 1987, Hurst & John 1999, Willems 2001).

Traditional management of Hungarian semi-dry grasslands was probably similar to the ones in western Europe, however, transhumance shepharding was most probably ceased much earlier than in the montainous parts of Europe, where it lasted even till the 1960-ies in some regions (Poschlod & Wallis De Vries 2002). The reason for this was most probably the fragmentation and isolation of grasslands which led to the establishment of numerous smaller herds to graze in the vicinity of the village. Very roughly the collapse of the traditional farming system started around the 1960-ies in Hungary when the collectivisation was initialized. Many of the former pastures became abandoned, while others became overused due to to the concentrated livestock. The number of sheep reached a peek around the middle 80-ies with 3000 thousand individuals and started to decrease heavily only in the middle 90-ies to 1000 thousand (Hungarian Central Statistical Office). Many small-sized vineyards and orchards were abandoned at the same time since the owners had no energy to cultivate them besides the full-time work in the kolhoz. In these former orchards and vineyards species-rich semi-dry grasslands developed in many places; while, simultanously the original grasslands might have dissapeared due to the spread of trees and shrubs (Illyés & Bölöni 2007, Illyés et al. 2007b).

I.2.2.3.1. Management for conservation purposes

Conservation of semi-dry grasslands is a priority issue at European level because of their high species richness and the occurrence of many rare or endangered species (Riecken et al. 1994; Borhidi & Sánta 1999; Chytrý et al. 2001; Stanová & Valachovič 2002). This is also reflected by the fact that semi-dry grasslands are priority habitats in the EU Habitats Directive and Natura 2000 network.

In western Europe the management of grasslands for conservation purposes started long ago (Baumann 2006). Most probably the first and still running conservation management was established in the south Netherlands over 30 years now in order to halt the spreading of the agressive *Brachypodium pinnatum* (Willems 2001). Different kinds of mowing regimes were introduced and tested in order to find the best solution for decreasing the cover *Brachypodium* *pinnatum* and maintaining or even increasing the number of species (Bobbink & Willems 1987, Willems 2001). Since the sites are too small and isolated, grazing is recently not feasible in south Netherlands, however, that was the traditional management of the area (Willems 2001). In other places grazing, mowing or the combination of these two are used for the maintenance of semi-dry grasslands (e.g. Hurst & John 1999, Dutoit et al. 2003, Barbaro et al. 2004, Mitchley & Xofis 2005, Klimek et al. 2007). In western Europe it was recognized decades ago that for effective conservation of semi-dry grasslands planned management is needed, the aim of which is exclusively the maintenance of the state of the grassland and not economical benefit (Dutoit et al. 2003, Barbaro et al. 2004, Mitchley & Xofis 2005, Klimek et al. 2007).

Conservational management of semi-dry grasslands in Hungary according to my knowledge is sporadical and affects only very small areas. In most cases the management is run by the supervisorship of the particular National Park (the whole territory of Hungary, even the non-protected ones is assigned to one of the national park authorities). Yet the recent management regimes or techiques might be rather effective from practical point of view, a severe problem is that nearly all of them lack scientific basis, monitoring and in many cases even documentation. In most cases these management activities are linked to the management of some rare and protected species, while the effects on the grassland community have only secondary importance. Another problem is that it is very hard to get even a very small bit of information on these managements.

To sum it up, I know about only a few conservational management plans in semi-dry grasslands in Hungary, although, Iq searched for them actively on different formal and informal forums in the last 6 years. I omit the listing and evaluation of the few managed sites here, since it is not a focal point of my thesis. Notwithstanding, in my opinion urgent management actions are needed for the conservation of semi-dry grasslans, thus nearly 90% of them is threatened by at least one factor (Illyés & Bölöni 2007, Seregélyes et al. 2008).

I.3. Aims of the study

The focus of my thesis is the semi-dry grasslands of Hungary. These grasslands hold high aesthetic and conservational value and they used to play a key role in the traditional farming system. In Hungary so far there is no comprehensive syntaxonomical study of semi-dry grasslands, which is a problem in my point of view, since for the long-term conservation of these habitats high quality data are needed. To make it understand that the conservation of these grasslands is not only a desire of some vegetation scientists but an obligation, hereby I draw the attention to the fact that semi-dry grasslands are priority habitats of the Bern Convention and are parts of the Natura 2000 network; thus it is a European level duty of Hungary not only to keep these habitats in their current state but in special areas even to improve their quality. There are many scattered data on the floristic composition of semi-dry grasslands (Schmotzer & Vojtkó 1996, 1997, Horváth 1998, Isépy 1998, Vojtkó 1998, Varga et al. 2000, Virágh et al. 2001, Szirmai 2008) and fortunately thanks to the MÉTA project (Molnár et al. 2007) the distribution and main attributes of this habitat type on country level are roughly known (Molnár et al. 2008a, 2008b). We know surprisingly lot about the fine-scale processes of Hungarian semi-dry grasslands thanks to the decade-long studies of Klára Virágh, Sándor Bartha, András Horváth and Imelda Somodi (Virágh & Bartha 1998, 2003, Horváth 2002, Virágh et al. 2006, Virágh et al. 2008). Nevertheless, I have a feeling that for conservation practice we need a bit different knowledge, a rather generalised rough sketch but at country-scale on the floristic patterns and factors which determine the actual state of Hungarian semi-dry grasslands. Floristic patterns must be revealed at country-scale in order to see the internal diversity of the habitat type. I hope that in conservation practice in the future the sub-types revealed by the floristic analysis will serve as bases for a kind of stratification which will ensure that representatives of all subtypes are protected on the adequate level. An analysis of the acting factors and their effects is needed to understand the current patterns of naturalness, diversity and other quality attributes of semi-dry grasslands. In the future this knowledge is hoped to be used for conservation planning, i.e. at the first place for prioritizing the conservation efforts to areas which are now in the best state and will stay in this state according to the predicted effects, or the other way round, for choosing the sites which need intermediate intervention (conservational management) in order to keep them in the current good state. To sum it up, I think that revealing the floristic patterns is a first step and understanding the factors affecting species richness, diversity and naturalness of semi-dry grasslands is the next one to establish scientific bases of conservation and management of semi-dry grasslands. Thus, these two types of analyses I performed, both on two spatial scales. However, so far I did not contact the colleagues of State Nature Conservation unfortunately, in the future I will and I hope that my thesis can serve as a basis for better conservation of Hungarian semi-dry grasslands in the long run.

In the first part of my thesis I present a cluster analysis with validation on the variation of floristic composition of central European semi-dry grasslands. Semi-dry grasslands are integral parts of central-European landscape and they hold considerable part of biodiversity in the semi-natural landscapes. The semi-dry grasslands of central Europe are a suitable model for demonstrating the issues related to vegetation classification at an international level. They are the focus of nature conservation (e.g. the EU Habitats Directive and Natura 2000 network) because of their high species richness and the occurrence of many rare or endangered species (Riecken et al. 1994; Borhidi & Sánta 1999; Chytrý et al. 2001; Stanová & Valachovič 2002). Historically, they were investigated independently in different countries, which resulted in a set of national classifications with only limited international compatibility (Klika 1933; Wagner 1941; Oberdorfer 1993; Krausch 1961; Mahn 1965; Eijsink et al. 1978; Mucina & Kolbek 1993; Borhidi 2003). So far, no comparative analysis has been performed that would establish clear links between corresponding semi-dry grassland types of different countries, although it would be inevitable also for effective conservation practice. Therefore, in the frames of an international cooperation we compiled a relevé database of semi-dry grasslands of Hungary, Czech Republic, Slovak Republic, east-Austria, Germany and Romanian Transylvania. We analysed the relevé data with recently elaborated numerical techniques. In the thesis I describe the main types of semi-dry grasslands revealed by our analysis and show their relations to associations mentioned in the relevant literature.

In the second part of the thesis I present a more detailed cluster analysis with validation of the Hungarian semi-dry grasslands based on a large relevé dataset compiled by various sources including published and unpublished material and partly newly sampled on the field. Despite the many scattered previous studies completed in separate parts of the country in Hungarian semi-dry grasslands, country-level computer-aided synthesis had not been available. I consider it as a problem since effective conservation and management planning at the country level needs information on the distribution and floristic composition of endangered habitat types. For this analysis I used the same numerical technique as for the previous international analysis, since it appeared to be an effective tool. I describe the clusters and according to the results of the analysis I propose a new syntaxonomical system for the Hungarian semi-dry grasslands.

The third part of the thesis is a study on the factors affecting the quality of Hungarian semi-dry grasslands on landscape scale. Effective conservation of (semi-)natural grasslands requires not only knowledge of where the vegetation occurs, but also upon its naturalness, the actual quality of a habitat or vegetation patch, and the factors that affect it (Németh and Seregélyes 1989, Parkes et al. 2003, Raatikainen et al. 2007). For this analysis I used data from the MÉTA database of (semi-)natural vegetation of Hungary (Molnár et al. 2007). I used a hypothesis generating and testing method and linear modelling. Since previous studies revealed that both local or patch variables (e.g. size of a patch, vegetation cover in the patch), and landscape or matrix variables (e.g. proportion of different habitat types in the surroundings) influence the quality of habitats (Wagner et al. 2000, Dauber et al. 2003, Mitchell et al. 2006, Vandvik & Birks 2002, Campagne et al. 2006, Barbaro et al. 2007, Raatikainen et al. 2007), I analysed the effects at both scales.

In the fourth part of the thesis I present a study on the factors affecting the quality of Hungarian semi-dry grasslands on stand level. The reason for running this new analysis is the fact that although the MÉTA data have an advantage of country-level coverage, the resolution of the data are rather coarse and many important characteristics of semi-dry grassland stands were not feasible to document in the frame of the MÉTA survey. For estimating quality on stand level I chose the following indicators: species richness, diversity, cover of dominant grasses, and presence of valuable species and proportion of rough physiognomical forms (graminoids, forbs, shrubs and trees). These data were derived from newly sampled vegetation relevés. I calculated correlation between the quality indicators to reveal positive and negative relations among them. I tested the effect on the quality of a grassland patch of several factors including soil properties, local and regional landscape neighbourhood, former and recent land use and threats. There is very little known on the factors affecting species richness of Hungarian semi-dry grasslands. So far there are no published studies on the significant effects on different factors on species richness and diversity of Hungarian semi-dry grasslands. Therefore I think an analysis trying to take into consideration many kinds of factor types which have been ever shown to be important determinants of species richness and focusing on the Hungarian semi-dry grasslands would give some new information on this topic.

In the conclusions I summarize my results from conservation point of view and I give some suggestions for the conservation practice and management of semi-dry grasslands.

I.4. Questions

A.1. What major vegetation types of central European semi-dry grasslands can be revealed by a large-scale numerical analysis?

A.2. Is there a difference in geographical range and climatic attributes of this major vegetation types (clusters)?

A.3. How the major types gained by the analysis (clusters) can be related to associations described in the literature?

A.4. Where the Hungarian semi-dry grasslands are positioned within the central-European semi-dry grasslands?

B.1. What major vegetation types of Hungarian semi-dry grasslands can be revealed by a country-scale analysis?

B.2. How the major types gained by the analysis (clusters) can be related to associations described in the literature?

B.3. Does the present syntaxonomical system satisfactorily reflect the floristic patterns of Hungarian semi-dry grasslands revealed by a numerical analysis based on high amount of data?

C.1. What factors affect the naturalness- based quality of Hungarian semi-dry grasslands on landscape level?

C.2. What is the overall relative importance of patch and matrix attributes in the naturalness of Hungarian semi-dry grasslands on landscape level?

D.1. What factors affect the species richness, diversity and other quality attributes of Hungarian semi-dry grasslands on stand level?

D.2. What are the relations among the quality attributes of Hungarian semi-dry grasslands?

D.3. What is the relative importance of the factors affecting the quality attributes of semi-dry grasslands on stand level?

D.4. Is it possible to predict the quality of a semi-dry grassland patch?

II. Material and Methods

II.1. Field sampling, data collection

II. 1. 1. Variation in species composition of Central European *Brachypodium pinnatum* and *Bromus erectus* dominated semi-dry grasslands

The analysis was designed and partly performed during a three-month-long grant at the Masaryk University in Brno, Czech Republic given by the Hungarian Scholarship

Committee (MÖB), under the supervisorship of Milan Chytrý (Department of Botany and Zoology, Masaryk University, Brno). In this study I cooperated with Zoltán Botta-Dukát (Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót), Monika Janisová and Iveta Skodová (Institute of Botany, Slovak Academy of Sciences, Bratislava), Wolfgang Willner (VINCA – Vienna Institute for Nature Conservation and Analyses, Vienna) Ute Jandt (Institute of Geobotany and Botanical Garden, Halle) and Ondrej Hájek (Department of Botany and Zoology, Masaryk University, Brno). The study was published in JVS in 2007 (Illyés et al. 2007a).

II.1.1.1. Vegetation data

We collected 13 412 relevés of semi-dry grasslands from a geographic and macro climatic gradient running from central Germany through the Czech Republic, Austria, Slovakia and Hungary to north-western Romania and built a TURBOVEG database (Hennekens & Schaminée 2001) of them. The German relevés were from the database compiled by Jandt (1999), the Czech and Slovak relevés from the respective Czech and Slovak national phytosociological databases (Chytrý & Rafajová 2003; Valachovič 1999). The Hungarian relevés were partly collected from the literature (Kun 1996, Szerényi 1997, Varga et al. 2000, Szabó 2001, Virágh et al. 2001, Honti 2004) and unpublished sources and partly newly recorded by E. Illyés; presently they are stored in the Hungarian national phytosociological database (Coeno-Dat, Lájer et al. 2008). The Austrian and Romanian relevés were mostly taken from local literature (Wagner 1941, Soó 1949, Ciurchea 1964, Ratiu et al. 1969, Ioan 1970, Schneider-Binder 1971, Täuber & Weber 1976, Eijsink et al. 1978, Şuteu 1979, Ruprecht et al. 2003, Willner et al. 2004). We only selected relevés from plots 4 m^2 and 100 m^2. Please consult Appendix 1. on the availability of the vegetation data for furher analysis. Headers of the used relevés and Turboveg backup file of the relevés newly sampled by E. Illyés are placed on the CD attached to the thesis.

A particular problem was the formal delimitation of the study object: semi-dry grassland vegetation. We could not base our relevé selection on syntaxonomical categories, because classification schemes of these grasslands are rather arbitrary and differ between countries (e.g. Mucina & Kolbek 1993; Oberdorfer 1993; Borhidi 2003; Chytrý 2007). Therefore we only selected relevés in which at least one of the grasses *Brachypodium pinnatum* and *Bromus erectus* occurred with a cover > 25% and which were assigned to the phytosociological class of dry grasslands, *Festuco-Brometea*. This selection yielded 2926 relevés. *Brachypodium pinnatum* and *Bromus erectus* are frequently dominant in Central European semi-dry grasslands, so their dominance could be used as an operational criterion for the inclusion of relevés in our data set.

Bryophyte and lichen records were excluded since they were missing in many relevés; generally, cryptogams are not very common in these grasslands. Taxonomically difficult species were merged into aggregated species (e.g. *Brachypodium pinnatum* and *B. rupestre* were merged into *B. pinnatum*). For the analysis we replaced the cover estimates contained in the original data by presences/absences, because our validation method uses this data type for the calculation.

II.1.1.2. Climatic and geographic data

Climatic data such as mean annual temperature, July temperature, January temperature and mean annual precipitation for relevé locations were derived from the WORLDCLIM database (http://www.worldclim.org/bioclim.htm) by Ondrej Hájek. As the relevés were located on a NW-SE transect, we also defined geographic position as a potential explanatory variable for vegetation patterns.

II. 1. 2. Variation in species composition of Hungarian semi-dry grasslands

The results of the analysis of the Central European semi-dry grasslands revealed that there is a unique type of semi-dry grassland restricted in range to the Pannonian region (Illyés et al. 2007a). Therefore I found it important to run a separate analysis of the Hungarian semi-dry grasslands to reveal the variation in species composition of the Hungarian grasslands and into the position of this unique Pannonian type of grassland in the ‘space of other semi-dry grasslands’ of the country.

I cooperated in this analysis with Norbert Bauer (National History Museum, Budapest) and Zoltán Botta-Dukát. The design of the analysis is very similar to the analysis of Central-European dry grasslands. The study is published in Preslia (Illyés et al. 2009).

II.1.2.1. Vegetation data

We compiled a database with 722 relevés of semi-dry grasslands from Hungary. This database is an extension of the one used for Hungary in Illyés et al. (2007a). We tried to collect all the relevés made in Hungarian semi-dry grasslands till 2006, so we asked colleagues for their hardcopies, personal databases, reports, dissertations and so on (Kun 1996, Szerényi 1997, Varga et al. 2000, Szabó 2001, Virágh et al. 2001, Honti 2004). The database was extended by new data mainly from the Északi- and Dunántúli-Középhegység mountains to gain better representativity of semi-dry grasslands. The new localities to be sampled were chosen with the help of the MÉTA database (Molnár et al. 2007, Molnár et al. 2008a), which contains actual data on the vegetation of Hungary for 86 habitat types. Calcifrequent semi-dry grasslands correspond to habitat type 'H4 – Bromus erectus-Brachypodium pinnatum xero-mesic grasslands, dry tall herb communities and forest steppe meadows' (Molnár et al. 2008a). The dataset compiled is thought to be representative for the country according to the distribution map of the 'H4' habitat type (Molnár et al. 2008a). The relevés were partly collected from the literature and from various unpublished sources, partly made in the field by E. Illyés and N. Bauer; and now they are stored in the Hungarian national phytosociological database (COENODATREF, Lájer et al. 2008). Nearly all of the sampling sites are personally known by one of the authors in Illyés et al. (2009), even if the particular relevé was taken by another person, as well as the purpose of taking that particular relevé, which ensures that the relevés are thoroughly chosen for the present analyis. We have to emphasize these points since we have been doing the first country-scale analysis of a rather complicated vegetation type, and there were no precedents to adjust to, consequently we had to rely on our expert judgment and knowledge of the literature. We used relevés from plots ≥ 4 m^2 and ≤ 100 m^2, which is an acceptable plot size range in these kind of studies (Otýpkova & Chytrý 2006). A particular problem was the formal delimitation of the study object, which we insisted to make in this vague situation. We could not base our relevé selection on associations, nor on characteristic species lists, because consensus classification scheme of these grasslands is still not available for Hungary.

Therefore we applied subjectively chosen but formalized and consistent selection criteria for filtering our original database, and selected only those relevés, in which at least one of the grasses *Brachypodium pinnatum*, *Bromus erectus*, *Danthonia alpina*, *Avenula pubescens*, and *A. adsurgens* occurred with a cover > 10%, since these grass species are known to be characteristic and reach higher cover in semi-dry grasslands in Hungary. (We did not include any *Molinio-Arrhenatheretea* Tüxen 1937 relevés in the analysis, where *Avenula* species could reach high cover as well.) This approach was already applied successfully in Illyés et al. (2007a). This selection resulted in a data set of 699 relevés.

For taxonomically problematic species, subspecies and species hardly determinable on the field species aggregates were used. Here we note that we aggregated *Festuca rupicola* into *Festuca valesiaca* agg., since these two taxons are not distinguished unambigously by many botanists. Bryophyte and lichen records were excluded since they were missing in most of the relevés; generally, cryptogams do not seem to reach high cover nor to have good distinctive power in these grasslands in the study area, and they are hardly ever recorded in Hungarian semi-dry grasslands. The nomenclature of plants follows Simon (2000), chorological data are from Horváth et al. (1995).

In the original relevés Braun-Blanquet's cover-abundance scale and percentage cover were used, which were replaced by presences/absences, because our validation method uses this data type for the calculation. All relevés were georeferenced by latitude and longitude.

Please consult Appendix 1. on the availability of the vegetation data for furher analysis. Headers of the used relevés and Turboveg backup file of the relevés newly sampled by E. Illyés are placed on the CD attached to the thesis.

II. 1. 3. Analysis of the factors affecting the naturalness based quality of semi-dry grasslands in Hungary on landscape level

This analysis was performed by using the MÉTA database. The records in the database were collected by more than 200 mappers during the MÉTA project, about 86 habitat types all over the country. The MÉTA database contains the raw data of the survey, and is owned by the Institute of Ecology and Botany. The data are available for further analysis if a request form is filled in and submitted to the peering committee. In the request form the aim and methods of the planned analysis have to be declared and the amount and type of the data needed have to be specified.

I was one of the mappers in the MÉTA survey and I contributed to the design of the MÉTA method as well as to the further analyses from the beginning. In this study I cooperated with Zoltán Botta-Dukát and Zsolt Molnár. This study is a part of a paper published in Acta Botanica (Illyés et al. 2008).

For this analysis we derived the data from the MÉTA database (Molnár et al. 2007). The MÉTA is the GIS database of Hungarian Habitats, containing information of the (semi-) natural habitat types of Hungary. The data for the MÉTA database has been surveyed between 2002 and 2007 by a grid-based, landscape-ecology-oriented, satellite-image supported, field vegetation mapping method. This method uses a hexagon grid with cells of 35 hectares. In the hexagons, habitat types are listed, then the area, naturalness-based habitat quality, spatial pattern in the hexagon, effect of the neighbourhood, connectedness, and threats are recorded for each habitat type. Other attributes are recorded in the hexagons: potential natural vegetation, area occupied by invasive plant species, area of old fields, land use of grasslands, and landscape health status (naturalness and regeneration potential of the landscape in general).

In the MÉTA method the (semi-)natural vegetation of Hungary is mapped in prescribed categories of 86 habitat types (Bölöni et al. 2007). All the habitat types have a definition, and a description which tells the main characteristics of the habitat such as range, landscape context, species composition, structure. We choose the habitat 'H4 – *Bromus erectus*-*Brachypodium pinnatum* xero-mesic grasslands, dry tall herb communities and forest steppe meadows' (Molnár et al. 2008a) (habitat code: H4, Natura 2000 code: 6210 and partly 6250; typical species of the habitat type are: *Brachypodium pinnatum*, *Bromus erectus*, *Festuca rupicola*, *Peucedanum* spp., *Salvia pratensis*, *Stachys officinalis*) as a model habitat. This habitat type is more or less corresponds to the syntaxonomical categories *Brometalia erecti* and *Cirsio*-*Brachypodion* and represent the semi-dry grassland types of the forest steppe region, mainly occurring in the foothills in small, rather fragmented patches. These formerly grazed primary and secondary forest steppe meadows are mostly abandoned today, which causes severe deterioration of their composition and structure.

For the analysis all cells of the MÉTA database – 35 hectare hexagons (see Molnár et al. 2007, Horváth & Polgár 2008) – were selected wherever the model habitat was present (4593 hexagons for H4) using the SQL interface created by Horváth and his colleagues and described in Horváth & Polgár 2008 in detail.

We selected every other attribute from the database for these hexagons as well (see Molnár et al. 2007), and we created a matrix from it containing the geographical position of the cell, the area of the model habitat (H4) in the cell, the proportional area of the model habitat to total cover of semi-natural habitat types in the cell, neighbourhood, connectedness, pattern, threats, presence / absence and area (proportional to the area of semi-natural vegetation in the cell) of all other habitat types (see Bölöni et al. 2007), land-use in the cell, total cover of semi-natural habitat types, number of habitat types in the cell and total area covered by old fields and invasive alien species in the cell. This matrix served as input data for the modelling.

The following predictor (independent) variables were involved in the analysis (predictor variables are defined and explained in detail in Molnár et al. 2007):

a) patch variables: area of the model habitat (H4) in the cell, the proportional area of the model habitat to total cover of semi-natural habitat types in the cell, neighbourhood (positive or negative effect of neighbouring habitats), connectedness (isolated, in question, non-isolated), pattern inside the hexagon (1-2 patches, 3 or more patches, diffuse pattern), and threats (see Molnár et al. 2007 and Molnár et al. 2008b for details) relevant to the model habitats (e.g. undergrazing, trampling)

b) matrix variables: presence / absence and area (proportional to the area of semi-natural vegetation in the cell of all other habitat types (see Bölöni et al. 2007), land-use (grazing, mowing) in the cell, total cover of semi-natural habitat types, number of habitat types in the cell and total area covered by old fields and invasive alien species in the cell.

Rare habitat types and threats – occurring in less than 2.5% of the dataset selected for the analysis of the H4 habitat – were omitted from the further analysis. The original levels of some predicting variables were merged in order to gain better predicting power and to eliminate the cases present with low frequency (for example bad method of grazing and lack of grazing was merged).

II.1.4. Factors explaining the species richness, the diversity and other compositional and structural characteristics of semi-dry grasslands in Hungary on stand level

This analysis was performed on a database which is a subset of the database we used for a previous analysis for revealing the patterns of floristic composition of semi-dry grasslands in Hungary (see II.1.2). The analysis was designed and the methods were selected by me and Zoltán Botta-Dukát. Eszter Kovács and Bálint Czúcz (Institute of Ecology and Botany of the HAS) gave help in the preparation of the environmental data. Soil samples were analysed in the Research Institute for Soil Science and Agricultural Chemistry of the HAS with the kind help of Tibor Tóth. The analysis was performed by me. We are planning to publish a paper on this part of the thesis.

II.1.4.1. Field sampling

Although the data derived from the MÉTA database (Molnár et al. 2007) has an advantage of the full coverage of the country, the resolution of the data are too coarse to understand the factors shaping the quality of grasslands at stand level. With the frames of the MÉTA survey there was no possibility to collect data on many structural and environmental factors which are supposed to affect the quality of a semi-dry grassland stand. Therefore we designed a new data collection and a new analysis which is highly similar to the MÉTA approach in its principles, but provides data at stand level which can be used to test what environmental and structural attributes play key role in the present quality of Hungarian semi-dry grassland patches.

The vegetation data used for this analysis is a subset of the database we used for a previous analysis for revealing the patterns of floristic composition of semi-dry grasslands in Hungary (see II.1.2). The 110 relevés used in this analysis were exclusively taken by E. Illyés in the summer of 2005, 2006 and 2007. The Turboveg backup file placed on the CD attached to the thesis contains the relevés. In plots of 4 by 4 meters in semi-dry grasslands throughout the country, cover of each vascular plant, cover of bare ground, cryptogams and litter were recorded. We intended to sample wide geographic range of semi-dry grasslads in Hungary, therefore we usually took only one sample of one dominant grass species in one locality. If there were patches dominated by different species, we took samples from each patch. These vegetation data were supplemented by several other types of data partly recorded in the field, partly derived from other sources in order to build a database suitable for the modelling of factors affecting species richness and diversity of Hungarian semi-dry grassland. In the following we describe all the attributes used for the analysis.

For the description of the structural characteristics of the stands, minimum and maximum height of the forb layer, deepness of litter layer were recorded for each sample measured by tape. Denseness of the vegetation was recorded by a subjective measure with values 1, 2, and 3 characterizing the overall density of the stand. Density is irrespective to the species which make the stand dense, however it correlates somewhat to the species composition, since there are particular species which have dense foliage (e.g. *Geranium sanguineum*, *Peucedanum cervaria*) and species which have thin foliage (e.g. *Linum austriacum*, *Echium rubrum*). Dense stands can be very species poor on the other hand. Value 3 was given to those stands which had a very diverse vertical structure, with multitude of vertical overlaps of the cover of species; these stands look like as meadows. Value 1 was given to stands which were less diverse vertically, where there are nearly no overlaps among the leaves of the individuals; these stands look like as very dry sites even if their water conditions are balanced.

Besides the above mentioned parameters regarding the characteristics of the vegetation of the stand, several other attributes were collected which reflect the position of the stand in the landscape. Local geographical factors like the size of the patch, elevation above see level, slope and exposition were also recorded.

Effects of the surrounding landscape to the species richness has been shown in several studies (Söderström et al. 2001, Devictor & Jiguet 2007). In order to test the influence of these kinds of factors in Hungarian semi-dry grasslands, we used landscape characteristics at two spatial scales in the modelling. In the field we recorded attributes on the landscape characteristics at local scale, the wider scale landscape characteristics were derived from the MÉTA databases (see below). The local-scale landscape characteristics used for this analysis highly correspond with the data collected in the MÉTA survey (Molnár et al. 2007), however, we needed a new data collection since the resolution of the MÉTA mapping (a grid of 35ha cells) was much coarser than what we needed for this analysis. The following landscape characteristics were recorded in the field:

- neighbouring vegetation types and their effects (positive, negative and neutral) to the patch. (For example a neighbouring non-native black locust plantation had negative effect on the grassland patch). In the analysis we finally used only the number of positive, negative and the total number of neighbours as indicator of the habitat diversity of the surrounding landscape.

- potential dispersal possibilities. These indicate whether the species of the grassland patch have any possibility to spread over as individual species or the patch as a community have any possibility to extend or to spread to the adjacent different types of patches of the landscape (yes or no). Several species of semi-dry grasslands can spread rather quickly for example to adjoining abandoned plough lands or orchards, while nearly none of them can spread into an actively used and hoed vineyard. We assume that if there are possibilities in the close surrounding for grassland species or grassland patch to spread than the landscape pattern is supportive to the grassland patch and contributes to its long-run maintenance. Species richness and diversity is thought to be positively affected by the supportive landscape.

Most of the semi-dry grasslands of Central Europe and Hungary have been developed due to human impacts, after cutting the original (mostly dry and semi-dry oak and oak-hornbeam) forests for grazing or hay making (Pott 1995). Thus for the long-term existence of semi-dry grasslands and for the maintenance of the species richness of them slight management or recurring disturbance is needed. Without management or other disturbance the semi-dry grasslands most probably will loose their species richness and diverse structure because the dominant grasses will overgrow the stands, litter accumulates which hinders seedlings to establish. Therefore we also documented any natural or human processes which could help the maintenance of the species richness and diversity of the grassland (e.g. activity of ants which periodically creates open surfaces and consequently helps smaller plants to establish) as well as any type of land use (grazing, cutting, burning).

According to the MÉTA survey, 90% of the Hungarian semi-dry grasslands are threatened by at least one factor (Illyés et al. 2007b). Invasion of shrubs and alien species are the more widespread threats for Hungarian and for European semi-dry grasslands (Bobbink & Willems 1987, Mitchley & Xofis 2005, Illyés et al. 2007b). These factors undoubtedly affect the species richness and diversity of the grassland as well. Therefore we documented those factors on the field which profoundly had negative effects on the semi-dry grassland patch.

Soil characteristics were proven to affect species richness and composition of grasslands (Sebastiá 2004, Löbel et al. 2006). There were no data on this aspect so far from Hungary, so we decided to collect soil samples and test the effects of soil characteristics. In each grassland patch we collected a soil sample (few relevés share one soil sample) of app. 50 cm^3 from the upper 10 cm of the soil. For each relevé one soil sample was taken from the upper 5-10 cm of the soil by a small spade. For the further analysis we prepared the soil samples by cleaning from dead plant material, rubbing and homogenising.

We analysed the samples in the laboratory of the Research Institute for Soil Science and Agricultural Chemistry of the HAS with the kind help of Tibor Tóth and recorded the following characteristics: weight proportion of stone in the sample, humus and carbonate content, conductivity, pH, proportion of grain in grain classes (>0,25 mm; 0,25-0,05 mm; 0,05-0,02; 0,02-0,01 mm; 0,01-0,005 mm; 0,005-0,002 mm; <0,002 mm - m/m%).

The total humus content of the soil was determined by the method of Turin. (The organic material of the soil is oxidised by potassium-bicromate in the solution of sulphuric acid. The humus content of the soil is gained by the multiplication by the factor 1.724 of the measured organic carbon content). The total carbonate content is determined by the method of Schleibler. (The soil is shaked with diluted hydrochloric acid and the amount of the issuing carbon-dioxide gas is measured).

The mechanical composition (proportion of grain in grain classes) was determined by the depositon technique. Suspension dispelled to elementary particles is made from the prepared fine-grained soil. The soil suspension is strirred up and then let to deposit. Then from certain depths, samples are taken from the suspension. When the the particles have been weight, the amount of particles in different grain sizes (sand, loam, clay) can be calculated if the density of the particles is known. For the dispellion of the soil, sodium pirophosphate is used; organic material is decomposed by H_2O_2, inorganic material by hydrochloric acid. Granules larger than 2 mm are measured by dry sieving.

The pH was measured in the 1:2.5 ratio suspension of soil and distilled water. The suspension is left for 12 hours with a lid on it, then the pH is measured potentiometrically.

The whole input data matrix of the analysis is placed on the CD attached to the thesis (model_matrix.xls).

II.1.4.2. Additional attributes

II.1.4.2.1. Derived vegetation characteristics

Since we were interested in measures of the semi-dry grasslands which are important both from ecological and from conservation aspect, we decided to use synthetic measures which describe the whole stand and can be understood a measure of quality. We used the relevé records as basis data for the calculation of further derived vegetation characteristics as number of species, Shannon diversity and evenness for each plot. We calculated evenness by the following formula: Shannon diversity divided by the logarithm of the number of species. We choose to use these synthetic measures since these are the most often used and thus widely accepted measures for expressing a kind of quality in ecology and both in conservation practice.

From conservation point of view besides the species richness the presence and cover of valuable species is also important. From the 341 species recorded in the 110 samples 110 species were identified as “valuable species”. These 110 species include species protected by law and species which are considered to be valuable elements Hungarian of semi-dry grasslands. Since there is no available published and well-accepted list on valuable species, the label “valuable species” was given by expert judgement based on field experience. (See the list of valuable species on the CD attached to the thesis.) In the compilation of this list Cs.

Molnár, J. Bölöni and S. Bartha gave kind help. For the analysis we calculated the number and the cover of valuable species for each plot.

Perennial grasses and dicotyledons form the matrix of semi-dry calcareous grassland vegetation (Rodwell 1992). Therefore it is a common place that perennial grasses have important effects on the species richness and diversity of grasslands. Dominant species of Hungarian semi-dry grasslands – *Brachypodium pinnatum Bromus erectus* and *Helitotrichon praeusta* – differ from one other both in their growing characteristics and in ecological demands. *Brachypodium pinnatum* is a more mesic and shade-tolerant, rhizomatous species which usually forms dense and tall stands. *Bromus erectus* is a tussock-forming species which tolerates better the dry and sandy soils and forms more open stands. *Helitotrichon praeusta* is a species which occurs rather sporadically but sometimes with high cover. Its stiff and pointed leaves and tussocks make the structure of the stand very diverse. Soil and landscape characteristics as well as historical landcover types and recent management are possible to affect the cover of dominant species. Therefore we used the cover the main grassland species (*Brachypodium pinnatum*, *Bromus erectus*, and *Helictotrichon praeusta*) in each plot as a response variable. We performed arc sin transformation of the original percentage cover data in order to gain normal distribution of cover data which was the condition of the chosen method.

Moreover, *Brachypodium pinnatum* in some cases is an aggressively spreading graminoid and is reported from Western Europe to threaten the species diversity of semi-dry grasslands by overgrowing the stands rapidly. Cover of *Brachypodium pinnatum* was proven to effect species richness negatively (Bobbink & Willems 1987, Hurst & John 1999). This aspect was never studied in Hungary before neither the effects of different dominant species on species richness and diversity.

In semi-dry grassland of high conservation value the proportions of graminoids and forbs are more or less balanced, none of them overdominates the other. Scattered shrubs or a few tree individuals enhance the diversity and species richness of the grasslands, while too high cover of shrubs and trees provides unfavourable conditions for light-demanding grassland species. Proportion of graminoids, forbs, trees and shrubs in semi-dry grasslands is thought to be affected by closer and wider landscape context as well as by historical and recent land use (Pykälä et al. 2005). We used a physiognomical grouping with the following categories: graminoids (grasses and sedges), forbs (all vascular plant besides graminoids), shrubs and trees (seedlings were regarded as trees) for this analysis. The cover of graminoids, shrubs and trees are compared to the ratio of forbs.

II.1.4.2.2. Historical landcover

Former land use and landcover categories are proven to affect the actual species richness and diversity of grasslands (Eriksson et al. 2002, Cousins et al. 2007) Series of geo-referred historical military maps (1st survey in the 1790-ies, 2nd survey in the 1840-ies, 3rd survey in the 1880-ies) covering the whole area of Hungary were used to determine the former landcover type (forest, pasture, mown meadow, arable field, vineyard and orchard) of the patches. To be able to do this, the sampling points were localised on the previously geo-referred historical military maps. This task was kindly performed by E. Kovács (Institute of Ecology and Botany, HAS.) The former land use type was identified by visual observation. Although there is a considerable subjectivity in this method, since all of the data were gained by E. Illyés, all data are burdened by the same bias. We used rough categories for the analysis of the maps. The used former landcover types are summarized in Table 1.

Table 1. Landcover categories used for the interpretation of the historical maps.

	1st Military Survey	2nd Military Survey	3rd Military Survey
Forest	x	x	x
Wooded pasture		x	
Pasture	x	x	x
Meadow	x		
Ploughland	x	x	x
Vineyard	x	x	x

II.1.4.2.3. Wider landscape context

For the information on the wider landscape context, we derived data from the database of Landscape Ecological Vegetation Mapping Project of Hungary (MÉTA) (for details see Molnár et al. 2007 and Horváth & Polgár 2008). For the characterisation of the surroundings of each sample plot we calculated the estimated area in hectares of *Bromus erectus* and *Brachypodium pinnatum* dominated semi-dry grasslands (habitat code: H4), the area of dry grasslands (H2, H3a, H5a, H5b), the area of dry forests (L1, L2a, L2b, L4a, L4b, LY2, M1, M2), the area of wet meadows and marshes (B1a, B2, B3, B4, B5, B6, D1, D2, D34) and the area of all kinds of forests and shrublands in the 35 hectares cells of the MÉTA database (see Molnár et al. 2007 for explanation) around the sample plot. In this query K. Oláh (Institute of Ecology and Botany of the HAS) gave kind help.

II.1.4.2.4. Climatic data

We used the climatic data of the WORLDCLIM open-access database (http://www.worldclim.org/bioclim.htm). This database contains several types of climatic data for the entire world with a resolution of 1 by 1 km. In most cases the data represent the 1950-2000 time period. The climatic data were derived from the database according to the coordinates of the sites, and joined to each of the relevés. We thank the kind help of B. Czúcz (Institute of Ecology and Botany of the HAS) in this process. The used climatic data are presented in Table 2.

Table 2. Climatic data derived from the WORLDCLIM database for the analysis.

BIO1 = Annual Mean Temperature
BIO4 = Temperature Seasonality (standard deviation *100)
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of Driest Quarter
BIO10 = Mean Temperature of Warmest Quarter
BIO11 = Mean Temperature of Coldest Quarter
BIO12 = Annual Precipitation
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO15 = Precipitation Seasonality (Coefficient of Variation)
BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter
BIO18 = Precipitation of Warmest Quarter
BIO19 = Precipitation of Coldest Quarter

The whole input data matrix of the analysis is placed on the CD attached to the thesis (model_matrix.xls).

II. 2. Data analysis

II. 2. 1. Variation in species composition of Central European and Hungarian *Brachypodium pinnatum* and *Bromus erectus* dominated semi-dry grasslands

Since the design of the analysis was the same in the Central European and the Hungarian studies, I present the steps of the analyses together in this chapter. The way of the analysis was mostly designed by Zoltán Botta-Dukát, Milan Chytrý and Eszter Illyés. Both analyses were performed by me with the help of Milan and Zoltán.

II.2.1.1. Data stratification, training and test dataset and outlier analysis

Large phytosociological data sets compiled from heterogeneous sources often contain many relevés from some small areas where sampling was more intensive than elsewhere. In order to prevent such local oversampling affecting the analysis, we tried to increase the representativeness of our data set by geographically stratified resampling (Knollová et al. 2005). We randomly selected a maximum of five relevés in the Central European analysis (further referred as **A1**) and ten relevés in the Hungarian analysis (further referred as **A2**) from each cell of a geographic grid of 6' latitude and 10' longitude. Then we randomly split the resampled data set into two subsets of equal size, hereafter called TRAINING and TEST, with the aim of using the TRAINING dataset to create the classification and the TEST dataset for validating the individual clusters resulting from this classification. After the split we had 442 relevés in each of the data sets in **A1** and 300 and 301 relevés in the TRAINING and TEST datasets of **A2**.

To remove the undue effect of relevés with outlying species composition, we performed separate outlier analyses for the TRAINING and TEST data sets, using the PC-ORD 4 program (McCune & Mefford 1999) with the Sørensen coefficient. After outlier exclusion, TRAINING and TEST data sets of **A1** contained 422 relevés each, including 114 and 123 relevés from Germany, 179 and 190 from the Czech Republic, 52 and 49 from Slovakia, 49 and 36 from Hungary, 18 and 15 from Austria and 10 and 9 from Romania, respectively (Fig. 5.). After outlier exclusion in **A2**, TRAINING data set contained 287 relevés and in the TEST data set there were 290 relevés.

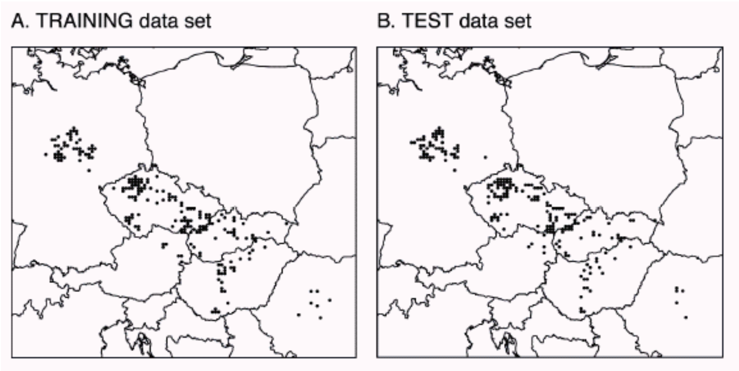


Fig. 5. Geographic distribution of the relevés in the TRAINING and TEST data sets. Each point represents 1-12 relevés.

II.2.1.2. Ordination and cluster analysis

Large vegetation databases may contain a high proportion of noise, i.e. random variation, which can cause artefacts in the numerical classification processes, in particular in agglomerative methods because these methods join pair of objects with the highest similarity (lowest dissimilarity) in each step , and do not consider the structure of the whole (dis)similarity matrix (Lambert & Williams 1966; Hill et al. 1975; Pielou 1977: 316; Gauch 1982a: 208). Noise can be reduced by using the coordinates of the relevés along the ecologically meaningful axes of the principal coordinates analysis (PCoA; Legendre & Legendre 1998) instead of the raw data as input for the classification (Gauch 1982b; Botta-Dukát et al. 2005). Therefore we performed PCoA in the R software (www.r-project.org) with the VEGAN package by J. Oksanen (http://cc.oulu.fi/~jarioksa) using presence/absence data with Sørrensen dissimilarity (Legendre & Legendre 1998). Theoretically the possible number of ordination axes equals the number of relevés or number of species minus 1, whichever is smaller; but usually only the higher axes contain interpretable ecological information. To determine the PCoA axes that contain interpretable ecological information, we compared the percentage eigenvalues with random expectations based on the broken-stick model (Legendre & Legendre 1998: 410). The number of significant axes was 59 in the TRAINING and 63 in the TEST data set in **A1**, and the significant axes explained 64% and 69% of the total variation in these data sets, respectively. The number of significant axes was 46 in the TRAINING and 44 in the TEST data set of **A2**. We used the positions of relevés along the significant axes of PCoA as inputs for the classifications. Euclidean distance and Ward's algorithm of minimum increment of sum of squares (Legendre & Legendre 1998) were used for dendrogram construction in the PC-ORD 4 program.

II.2.1.3. Validation of classification

The method of the validation of clusters by the constancy of species was suggested by Zoltán Botta-Dukát. Here I present the logic of the validation briefly. The method is published in Botta-Dukát (2008a) in detail.

The set of relevés used in any analysis is a sample from the statistical population of all possible relevés that satisfy pre-selected criteria defining this population: in **A1** it was certain plot size, dominance of some species and species composition corresponding to the class *Festuco-Brometea*; in **A2** it was certain plot size, certain level of abundance of some species and species composition thought to correspond to the orders *Cirsio-Brachypodion* and *Brometum erecti*.

Numerical classification methods explore the structure of the sample, but the aim is to explore the structure of the whole statistical population. Some clusters resulting from numerical classification may be artefacts in the sense that they reflect the structure of the sample but not of the statistical population. This means that the same classification method applied to other samples from the same population would not reveal such clusters. This problem can be overcome by applying the following validation procedure. The set of relevés is randomly split into two subsets of equal size (in our case called TRAINING and TEST) and the same classification procedure is independently applied to each of them (Duda et al. 2001). On each level of the classification hierarchy groups occurring in the corresponding TRAINING and TEST classifications are compared based on the relative frequency of species. The *Z*-statistic (Zar 1999) is used to compare the relative frequencies of each species:

$$Z = \frac{|q_1 - q_2|}{\sqrt{\frac{Q(1-Q)}{n_1} + \frac{Q(1-Q)}{n_2}}} \tag{1}$$

where q_1 and q_2 are relative frequencies (constancies) in the corresponding groups of TRAINING and TEST data sets, n_1 and n_2 are group sizes, i.e. numbers of relevés assigned to the groups, and

$$Q = \frac{n_1 q_1 + n_2 q_2}{n_1 + n_2} \quad . \tag{2}$$

Z approximately follows the standard normal distribution, thus the corresponding Type I error probability (p) can be calculated easily. Then these p values are combined by the Fisher's omnibus test (Sokal & Rohlf 1995):

$$\chi^2 = -2\sum \ln p_i \tag{3}$$

where p_i is the Type I error probability for species i. First χ^2 is calculated for the whole TRAINING and TEST data sets, and then cluster pairs with χ^2 lower than this value are considered as similar (Botta-Dukát 2008a). A cluster of the TRAINING data set is regarded to be valid, if there is one and only one similar cluster in the TEST data set. If there is no such cluster in the TEST data set, the cluster is characteristic only for the sample, but not for the whole population. If there is more than one similar cluster in the TEST data set, i.e. the differences between them are arbitrary, the cluster cannot be validated unambiguously.

The number of valid clusters depends on the total number of clusters in the partition. It is low in partitions with few clusters, because the clusters are too large and heterogeneous. As the number of clusters increases, the number of valid clusters also increases, but when the total number of clusters becomes too high, the valid clusters are divided into smaller clusters rather arbitrarily and the number of valid clusters decreases again. This means that we have to search for valid clusters over a wider range of partitions with different numbers of clusters to find the partition with maximum number of valid clusters. In our data sets we tested partitions with 2-12 clusters.

II.2.1.4. Determination of diagnostic species

After the valid clusters were determined by the validation procedure, fidelity of species occurrence to the TRAINING data set (**A1**) or to the joint valid cluster pairs of the TRAINING and TEST data sets (**A2**) was calculated in order to determine diagnostic species of each cluster (Chytrý et al. 2002). This calculation was done for the partition that already contained all the valid clusters but at the same time contained the smallest number of non-valid clusters, in **A1** at the level 11 and in **A2** at level of 10 clusters. Diagnostic species at this level were determined by calculating the fidelity of each species to each cluster with the JUICE program (Tichý 2002), using the phi coefficient applied to clusters of equalized size (Tichý & Chytrý 2006). Numerical values of the phi coefficient do not inform about statistical significance of species concentration in the relevés of particular clusters, but it can be easily obtained from simultaneous calculation of the Fisher's exact test in the JUICE program (Tichý 2002). In our case, we set the threshold phi value for species to be considered diagnostic to 0.3, but we did not consider those species whose fidelity was not significant at $\alpha = 0.01$. The value of $\Phi = 0.3$ was selected because it yielded neither too long nor too short lists of diagnostic species for individual clusters.

II.2.1.5. Comparison of geographic position and climatic variables for the valid clusters of Central European semi-dry grasslands

For better understanding of environmental factors which cause the changes in species composition along the gradient, we compared the range of the grassland types defined by the valid clusters and the climatic variables along the ranges of the types.

Instead of the usual way of identifying location by simply using longitude and latitude, we defined a single geographic variable running in along of the major gradient in geographic locations. This was defined as the position of relevés on the first PCA axis (CANOCO 4.5 program; ter Braak & Šmilauer 2002) where the longitudes and latitudes of relevés were used as input data. Medians of the climatic variables were calculated for the merged valid clusters of TRAINING and TEST data sets and differences were tested by Kruskal-Wallis non-parametric ANOVA and subsequently by Dunn's *post-hoc* test (Zar 1999).

II. 2. 2. Analysis of the factors affecting the naturalness based quality of semi-dry grasslands in Hungary at landscape level

For conservation practice in general such attributes are needed which describe the quality of a stand simply but effectively, since the designation and management efforts need to be prioritised due to the limited amount of money available for conservation and due to other needs of business, policy and society (e.g. developments, constructions, recreation). Therefore, effective conservation of (semi-)natural grasslands requires, not only knowledge of where the vegetation occurs, which factors and to what extent explain its compositional characteristics, but also upon naturalness of vegetation, the actual quality of a habitat or vegetation patch (Németh & Seregélyes 1989, Parkes et al. 2003, Raatikainen et al. 2007). Quality of landscapes or habitats is often assessed through biodiversity (number of species or diversity indices such as Shannon index) or through the presence or abundance of a particular species or species group, since these measures are relatively easy to get. However, other attributes, like the synthetic value of naturalness can be used effectively for assessing quality for conservation purposes. The MÉTA database of (semi-)natural vegetation of Hungary contains data on the naturalness of all vegetation types of Hungary (Molnár et al. 2007) and thus enables queries and analyses both for scientific and for practical purposes (Illyés et al. 2008). We aimed to specify those factors which affect the naturalness of vegetation at landscape scale by modelling techniques.

In the MÉTA project a four grade scale measure was used with values 2, 3, 4, and 5; where 2 means habitat patch with totally destroyed vegetation, only weeds and very general species are present, bad structure, even the habitat type is hard to identify; and 5 means patches in near-natural state, specialist and rare species present, the structure of vegetation is good. During the MÉTA survey the vegetation was mapped in 35 ha hexagonal grid, making a list of occurring habitat types in the grid cells. To each habitat type, one naturalness-based habitat quality value was assigned. Combined values such as 5r4 (or 4r2) were allowed meaning that 10% of the area of the habitat type has value 5 (4) and 90% of it has value 4 (2). (For more details see Molnár et al. 2007.)

The original naturalness-based quality values given for the model habitat in each hexagon were simplified to bad and good quality, the 5, 5r4 and 4 values were regarded as good quality, the other values are as bad quality; see Molnár et al. (2007) and Bölöni et al. (2008) for more details. This binary form of naturalness-based habitat quality was the response (dependent) variable. The ease of using binarised form of naturalness-based quality value is that there is no similar modelling method for variables on ordinal scale and in case of categorical variables the interpretation of regression models is much more problematic.

Since we did not have a priori hypotheses about the effects of studied predictors, we followed a procedure proposed by Hallgren et al. (1999): the dataset was split into two equal parts randomly in order to gain two separate datasets. The TRAINING dataset was used to generate hypotheses, which were then validated with the TESTING dataset (Hallgren et al. 1999). The analysis was performed in the R statistical environment (R Development Core Team 2007).

Since the dependent variable (i.e. naturalness) was binary, generalised linear models with binomial distribution and logit link were used (Dobson 1990, Hastie & Pregibon 1992). The models were evaluated by likelihood-ratio tests. We performed preliminary analyses to test the effects of some disturbing factors. The effect of the surveyor was highly significant (this bias was reported by Honnay et al. 2003 as well), despite the fact that we have already performed a thorough standardization during the survey phase of the project for the naturalness based habitat quality. Consequently, the surveyor was involved in all models as a co-variable. Following the suggestion of Borcard et al. (1992), the third-order polynomials of centred geographic position were also incorporated into all models, because we were interested in spatially unstructured relationships. In the case of the predictor variable 'proportion of another habitat in the cell', the effect of the presence of the same habitat type in the cell was partialled out, as well, in order to separate the effect of the proportion of the habitat from its presence.

For generating hypotheses, all of the possible predicting variables were tested separately in the TRAINING dataset, and each significant effect was regarded as a hypothesis and tested in the subsequent analysis of the TESTING dataset. In the case of categorical predictors (e.g. pattern) the post-hoc tests were completed using the 'glht' function in the 'multcomp' package of R (Hothorn et al. 2007). Since the number of tested hypotheses was high, following the applied hypothesis generating procedure, the Benjamini-Hochberg correction (Verhoeven et al. 2005) was used to create a false discovery rate of 5%. Due to the large sample sizes, relatively small effects could prove to be statistically significant.

Therefore, to avoid interpreting such effects, Nagelkerke's R^2 (Nagelkerke 1991) was calculated, and predictors with a value lower than 0.01 (i.e. 1%) were disregarded.

To be able to compare the overall effects of matrix and patch variables, Nagelkerke's R^2 was calculated for models built with all significant patch and matrix variables and all significant variables together. The value of Nagelkerke R^2 can be lower than the sum of all R^2 calculated for individual factors due to the correlation among the factors.

II. 2. 4. Factors explaining species richness, diversity and other compositional and structural characteristics of semi-dry grasslands in Hungary at stand level

We used a modelling approach to determine the factors which affect species richness, diversity and composition. We designed the modelling together with Z. Botta-Dukát (Institute of Ecology and Botany of the HAS). Fist we determined the dependent (response) and independent (predictor or explanatory) variables (Table 3. and Table 4.). (The whole input data matrix of the analysis is placed on the CD attached to the thesis (model_matrix.xls)).

Table 3. The dependent (response) variables used for the modelling

	Response (dependent) variables
Species richness and diversity	number of species in the plot
	Shannon diversity
	Evenness
Dominant grasses	cover of *Brachypodium pinnatum*
	cover of *Bromus erectus*
	cover of *Helictotrichon praeusta*
Valuable species	proportion in the species number
	proportion in cover
Structural species group	cover of trees
	cover of graminoids
	cover of shrubs

Before the analyses, the original cover data of dominant grasses given in percentages were transformed by arc sin transformation in order to normalise the distribution of the input data, which is necessary for general linearised models. The cover of trees, graminoids and shrubs is expressed in every plot as the proportion of the forbs in the same plot in order to gain independence of cover of the elements of the structural species group within the plot. Percentage cover data of the structural species group was also arc sin transformed in order to normalise the distribution of the input data.

Since we did not have a priori hypotheses about the correlation patterns among the response variables and the effect of studied predictors, we followed a procedure proposed by Hallgren et al. (1999) in this analysis as well: the dataset was split into two equal parts randomly in order to gain two separate datasets. The TRAINING dataset was used to generate hypotheses, which were then validated with the TESTING dataset (Hallgren et al. 1999).

First we run a Spearman-correlation test for the pairs of response variables in the TRAINING dataset and validated the hypotheses in the TEST dataset. Those correlations were accepted as significant where the correlation was significant in both datasets. The analysis was run in the R statistical environment (R Development Core Team 2007).

Then we tested the effect of geographical position for each response variable in the whole data set following the suggestion of Borcard et al. (1992), by using the third-order polynomials of centred geographic position. In case of those independent variables where the effect of geography appeared to be significant, the geographic positions were incorporated into the subsequently built models run on the TRAINING and on the TEST dataset, because we were interested in spatially unstructured relationships.

Linear models with normal distribution were used, since the distribution of the residuals for each model and for each independent variable was checked by QQ-plots and more or less followed normal distribution. Significant effects revealed in the TRAINING dataset were validated and tested on the TEST dataset. An effect was regarded as significant if the p value was smaller than 0.05 in both datasets and the direction of the effect was the same. Due to the large sample sizes, relatively small effects could prove to be statistically significant. Therefore, to avoid interpreting such effects, R^2 was calculated for all models, and predictors with a value lower than 0.01 (i.e. 1%) were ignored. In cases where the geographical position was revealed to be significant, variation partitioning was performed to separate the effects of the geographical position and the particular independent variable by calculating the R^2 for the single model with geography, for the single model with the factor and for the combined models. Factors which had a significant effect but the R^2 of their single model was < 0.05 (i.e. 5%) were not interpreted.

Table 4. The independent (explanatory, predictor variables)

Independent variables		
Patch attributes	Soil parameters	weight of stone pieces (m/m%)
		carbonate content (%)
		humus content (%)
		conductivity
		pH
		>0.25 mm particles (m/m%)
		0.25-0.05 mm particles (m/m%)
		0.05-0.02 mm particles (m/m%)
		0.02-0.01 mm particles (m/m%)
		0.01-0.005 mm particles (m/m%)
		0.005-0.002 mm particles (m/m%)
		<0.002 mm particles (m/m%)
	Local geographical attributes	size of the grassland patch
		exposition
		slope angle
		elevation
	Structural attributes	minimum height of the stand (cm)
		maximum height of the stand (cm)
		deepness of the litter layer (cm)
		cover of litter
		denseness
	Local neighbourhood	number of neighbouring habitat types with positive effects
		number of neighbouring habitat types with negative effects
		total number of neighbouring habitat types
	Dispersal attributes	potential dispersal of the grassland species
		potential dispersal of the grassland patch
	Land use and Threatening factors	Grazing or mowing of the stand (yes/no)
		shrub encroachment
		too low intensity of land use
		spead of invasive alien species
		disturbance by animals

		presence of any preserving factors
Landscape attributes	Climatic data	BIO1 = Annual Mean Temperature
		BIO4 = Temperature Seasonality (standard deviation *100)
		BIO8 = Mean Temperature of Wettest Quarter
		BIO9 = Mean Temperature of Driest Quarter
		BIO10 = Mean Temperature of Warmest Quarter
		BIO11 = Mean Temperature of Coldest Quarter
		BIO12 = Annual Precipitation
		BIO13 = Precipitation of Wettest Month
		BIO14 = Precipitation of Driest Month
		BIO15 = Precipitation Seasonality (Coefficient of Variation)
		BIO16 = Precipitation of Wettest Quarter
		BIO17 = Precipitation of Driest Quarter
		BIO18 = Precipitation of Warmest Quarter
		BIO19 = Precipitation of Coldest Quarter
	Land use history	land cover type at the time of the 1st Military Survey
		land cover type at the time of the 2nd Military Survey
		land cover type at the time of the 3rd Military Survey
	Landscape neighbourhood	area of the fallow lands
		area covered by invasive alien species
		area of the semi-dry grasslands (H4)
		total area of (semi)natural habitat types
		Number of habitat types
		summed area of (semi-)dry grasslands
		summed area of dry forests
		summed area of wet grasslands and marshes
		summed area of forests and shrublands

III. Results

III. 1. Variation in species composition of Central European Brachypodium pinnatum and Bromus erectus dominated semi-dry grasslands

III.1.1. Classification and validation results

The hierarchical level of the dendrogram with the highest number of valid clusters was the one with 11 clusters, of which six were valid. In the TRAINING data set the valid clusters contained altogether 204 relevés (48.3% of the data set), while the remaining 218 relevés (51.2%) belonged to non-valid clusters. In the TEST data set the corresponding figures were 215 (50.9%) and 207 (49.1%). Usually the valid clusters had more diagnostic species than had the non-valid clusters (Table 6.) and narrower geographic ranges (Fig. 8.), though some valid clusters had a large range in one of the TRAINING or TEST data sets but a small one in the other. Dendrogram topographies of the TRAINING and TEST data sets (Fig. 6) reveal that the same pairs of valid clusters form smaller groups (A-B, C-D and E-F) in both data sets. The higher level, i.e. the linkage of the cluster pairs, is different in the two dendrograms, which explains why the higher-level clusters were not confirmed as valid.

In order to visualise the spatial relations of clusters, we plotted the diagrams of the PCoA analysis run prior to the clustering process (Fig. 7.). The positions of the valid clusters in the ordination space support the findings based on the dendrogram structure: the pairs of smaller groups (A-B, C-D and E-F) are closed to each other or even overlap along the first two axes.

III.1.2. Description and interpretation of the classification

There are remarkable differences among the valid clusters in all climatic variables (Table 5.). Clusters A and B (subatlantic *Brachypodium pinnatum* and *Bromus grasslands*) are the most oceanic ones according to geographic position, precipitation and temperature.

Clusters C (semidry grasslands on wetter soils with wider distribution), D (species-rich meadows, mainly found in the White Carpathians) and E (open subcontinental dry grasslands) have a transitional character, while cluster F (*Brachypodium grasslands* of the inner Carpathian Basin) are confined to the driest and warmest areas. The first axis of the ordination plot reflects well this geographical and climatic gradient. This pattern shows that species composition of semidry grasslands changes considerably along the NW-SE gradient across Central Europe (Willems 1982). In areas characterized by suboceanic climate in central Germany and the middle altitudes of the Czech Republic and Slovakia these grasslands contain subatlantic species such as *Cirsium acaule*, *Gentianella germanica* agg., *Potentilla neumanniana* and *Thymus pulegioides*. By contrast, in the drier parts of the study area, semi-dry grasslands contain several species of continental distribution, which are also typical of dry oak forests, e.g. *Centaurea triumfettii*, *Galium glaucum*, *Geranium sanguineum*, *Inula ensifolia*, *I. hirta*, *Peucedanum cervaria*, *Tanacetum corymbosum* and *Thesium linophyllon*, or continental steppe species such as *Chamaecytisus austriacus*, *Linum flavum* and *Stipa capillata*.

This provides the basis for the traditional phytosociological division of the alliances *Bromion erecti* (subatlantic group) and *Cirsio-Brachypodion pinnati* (subcontinental group) (Krausch 1961; Mahn 1965; Royer 1991; Mucina & Kolbek 1993; Chytrý 2007). Our classification seems to confirm this separation, with clusters A and B belonging to the former and E and F to the latter alliance. Clusters C and D represent transitional vegetation types between these two alliances, C being confined to specific habitats (wetter soils) and D representing a locally specific vegetation type. The ordination plot supports this concept well: the two alliances are separated on the 1st axis. Clusters C and D are in the middle position along the 1st axis, but they are also separated on the 2nd axis from the other clusters, showing the special environmental demands the communities belonging to these clusters.

The artificially defined 25% cover limit of *Brachypodium pinnatum* or *Bromus erectus* in the relevés selected for this analysis makes it impossible to interpret our valid clusters directly in terms of the traditional phytosociological syntaxa, because syntaxa also include stands with similar species composition but lower cover of these grasses. Still, when compared with the Central European phytosociological literature, the valid clusters can be linked to the traditional associations. The species composition, geographic range, climatic features and syntaxonomy of the valid clusters can be summarized as follows:

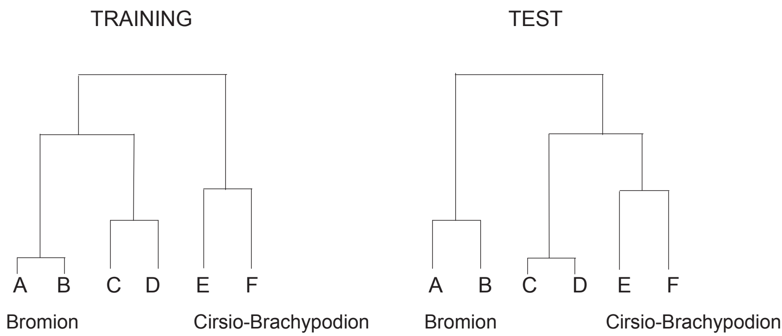


Fig. 6. Topology of dendrograms based on the TRAINING and TEST data sets. Only valid clusters are shown

Clusters A and B: These grasslands, mostly dominated by *Brachypodium pinnatum*, are found in areas with relatively cool summers and high precipitation, especially in central Germany and the submontane areas of the western Czech Republic (Table 6., Fig. 7. and Fig. 8.). The diagnostic species, e.g. *Anthyllis vulneraria, Carex flacca, Linum catharticum, Potentilla neumanniana*, *Ranunculus bulbosus* and *Scabiosa columbaria* are indicators of calcareous soils, which are usually medium deep rendzinas or pararendzinas over limestone or other calcareous bedrocks. At the same time, the occurrence of species adapted to low-pH soils (e.g. *Festuca ovina* and *Calluna vulgaris*) indicates leaching of carbonates, typical of areas with higher rainfall. These grasslands are of secondary origin, developed after the clearing of *Fagus* or *Quercus*-*Carpinus* forests and subsequent grazing by sheep and/or goats (Oberdorfer 1993). Cluster A represents managed or recently abandoned stands, while Cluster B represents successional stages after abandonment, as indicated by the occurrence of shrubs, e.g. *Crataegus* spp., *Cornus sanguinea*, *Rosa* spp. and *Prunus spinosa*. This vegetation corresponds to the association *Carlino acaulis*-*Brometum erecti* Oberdorfer 1957, which is also frequently called *Gentiano*-*Koelerietum pyramidatae* Knapp ex Bornkamm 1960.

Cluster C: These semi-dry grasslands are usually found on the footslopes, often in a contact zone between semi-dry grasslands and intermittently wet *Molinion* meadows. The specific topographic position and the good water-holding capacity of soils make such habitats wetter than other types of *Brachypodium* and *Bromus* grasslands, but the areas of distribution of this vegetation are macroclimatically rather dry (Table 6.). The dominant species is usually *Bromus erectus* and diagnostic species are indicators of mesic or intermittently wet soils

Table 5. Comparison of geographic position (relative scores on the NW-SE axes) and climatic variables for the valid clusters of the TRAINING and TEST data sets. Values are medians. Clusters in columns with the same letter do not differ significantly (Dunn's test; $P < 0.05$).

	cluster A	Cluster B	cluster C	cluster D	cluster E	cluster F
Geographic position NW-SE	-1.19^{a}	-1.33^{a}	0.14^{bc}	0.78^{cd}	-0.17^{b}	1.22^{d}
Mean January temperature (°C)	-0.9^{c}	-0.6^{d}	-1.5^{bc}	-3.3^{a}	-2.2^{b}	-1.6^{b}
Mean July temperature (°C)	16.5^{a}	16.4^{a}	18.3^{cd}	17.4^{b}	17.6^{bc}	20.7^{d}
Mean annual temperature (°C)	8.0^{a}	8.1^{a}	8.8^{b}	7.8^{a}	7.1^{a}	10.5^{b}
Difference between Jan-Jul temperature (°C)	17.30^{b}	17.00^{a}	20.15^{cd}	20.60^{d}	19.75^{c}	22.30^{e}
Precipitation (mm)	719^{b}	742^{b}	569^{a}	723^{b}	537^{a}	560^{a}

(*Equisetum arvense*, *Glechoma hederacea, Potentilla reptans*, *Pastinaca sativa* and *Ranunculus acris*). This cluster has a broad geographic range (Fig. 7. and Fig. 8.) from central Germany through the Czech Republic and Slovakia to southern Hungary. This vegetation has been traditionally assigned to several associations, within which it was often considered as a transitional type to other associations. Studnička (1980) described this vegetation as the *Potentillo reptantis-Caricetum flaccae* association. Although this type is well delimited in the current data set, it tends to be neglected in the local phytosociological literature.

Cluster D: Most relevés of this cluster are from the White Carpathians, a mountain range on the border between the Czech Republic and Slovakia. This area is very close to the dry areas with Pannonian steppic flora in the southeastern Czech Republic (southern Moravia) and western Slovakia, but at the same time it receives higher precipitation (650-850 mm/year) than other dry grasslands of Central Europe (Table 6.). Some sites from other parts of the Czech Republic and Slovakia also belong to this cluster (Fig. 7.). The relevés in our data sets are dominated by *Bromus* or *Brachypodium*, but grasslands of similar species composition can also be dominated by *Molinia arundinacea* or *Carex montana*. These grasslands combine species of mesic meadows, steppes and oligotrophic submontane grasslands. If regularly cut,

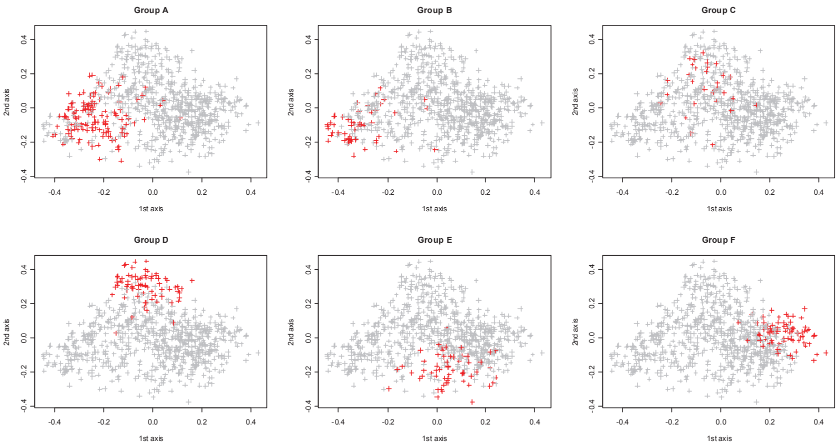


Fig. 7. Spatial position of the valid clusters A-F along the first two axes in the PcoA plot. Presence-absence data with Sørrensen dissimilarity were used.

Table 6. Synoptic table of the 11 clusters of the TRAINING data set with percentage frequency (constancy) of species. Within blocks of diagnostic species, species are ranked by decreasing fidelity, measured by the phi coefficient for relevé groups of equalized size (*: $\Phi > 0.3$; **: $\Phi > 0.5$). Species with non-significant occurrence concentration in the given cluster were not included in the groups of diagnostic species, even if they had $\Phi > 0.3$ (Fisher's exact test, $P < 0.01$).

Group No.	**A**	**B**	**nv**	**C**	**D**	**nv**	**nv**	**nv**	**E**	**nv**	**F**
No. of relevés	61	30	49	18	28	71	20	46	25	32	42
A. *Brachypodium* dominated atlantic grasslands of central Germany and the Czech Republic											
Koeleria pyramidata agg.	89 *	53	22	28	14	13	15	--	28	19	2
Pinus sylvestris	23 *	--	--	--	--	8	--	--	--	--	--
Hieracium pilosella	61 *	37	16	--	7	4	15	20	28	22	--
Campanula rotundifolia agg.	56 *	10	20	6	4	13	--	17	16	31	17
Melilotus alba	8 *	--	--	--	--	--	--	--	--	--	--
Ranunculus bulbosus	38 *	13	16	6	25	6	5	4	--	6	--
Ononis repens	13 *	3	2	--	--	1	--	--	--	--	--
Anthyllis vulneraria	49 *	33	22	--	29	7	--	22	12	31	--
Linum catharticum	85 *	70	47	61	64	24	20	26	52	69	14
Carex ornithopoda	8 *	3	--	--	--	--	--	--	--	--	--
Polygala chamaebuxus	5 *	--	--	--	--	--	--	--	--	--	--
Avenochloa pratensis	36 *	7	2	--	--	4	25	17	20	34	5
Calluna vulgaris	7 *	--	--	--	--	--	--	2	--	--	--
B. *Bromus* and *Brachypodium* dominated atlantic grasslands invaded by shrubs											
Medicago lupulina	39	70 *	31	17	25	4	5	4	--	9	--
Gymnadenia conopsea	15	33 *	--	--	14	--	--	--	4	3	2
Rosa canina agg.	25	57 *	27	--	18	24	5	4	4	16	5
Prunus spinosa agg.	10	47 *	16	--	7	14	5	4	8	16	10
Rosa rubiginosa agg.	3	20 *	--	--	--	--	5	4	--	--	--
Gentianella germanica agg.	18	27 *	--	6	--	--	--	--	4	--	--
Frangula alnus	--	17 *	--	6	--	1	--	--	--	--	--
Fraxinus excelsior	5	17 *	--	6	--	--	--	2	--	3	--
Crataegus species	8	50 *	29	6	14	17	15	17	8	9	31
Cornus sanguinea	21	33 *	8	17	--	11	5	--	--	9	2
Non-valid group 1											
Polygala vulgaris	3	--	18 *	--	11	1	--	4	--	3	--
Galium pusillum agg.	20	13	22 *	--	--	3	--	--	--	9	--
Corylus avellana	8	--	14 *	--	4	7	--	--	--	--	--
Potentilla recta	--	--	6 *	--	--	1	--	--	--	--	--

C. Semi-dry grasslands on wetter soils dominated by *Bromus erectus*											
Equisetum arvense	--	3	2	33 *	4	3	--	--	--	--	--
Potentilla reptans	2	3	8	44 *	4	10	10	--	--	--	--
Tetragonolobus maritimus	2	--	--	39 *	--	1	--	--	20	3	--
Cirsium tuberosum	--	--	--	17 *	--	--	--	--	--	--	--
Glechoma hederacea agg.	--	3	2	22 *	4	--	5	--	--	--	--
Succisa pratensis	--	--	--	11 *	--	--	--	--	--	--	--
Silaum silaus	--	--	--	11 *	--	--	--	--	--	--	--
Senecio erucifolius	2	7	--	17 *	--	--	--	--	--	--	--
Rubus caesius	--	7	2	17 *	--	1	--	--	--	--	--
Carex hirta	--	--	4	17 *	4	--	--	2	--	--	2
Pastinaca sativa	2	10	2	22 *	--	1	10	--	--	3	--
Agrostis gigantea	2	--	--	17 *	--	3	--	4	4	3	--
D. Mostly *Bromus* dominated grasslands of the White Carpathians											
Campanula patula	--	--	8	6	61 **	3	--	--	--	--	--
Luzula campestris agg.	7	--	20	11	79 **	4	--	11	--	--	5
Cruciata glabra	--	--	27	--	68 **	4	--	--	--	6	2
Anthoxanthum odoratum	11	3	27	6	79 **	6	--	7	--	3	5
Carex pallescens	--	--	--	--	39 **	--	5	--	--	--	--
Rumex acetosa	7	--	12	11	64 **	6	--	4	--	--	17
Trifolium pratense	21	7	16	22	75 **	4	--	4	4	9	2
Trifolium repens	7	--	14	11	50 **	--	--	--	--	3	--
Alchemilla vulgaris agg.	7	--	22	6	50 *	1	--	--	--	--	--
Cerastium holosteoides	7	7	6	11	46 *	--	--	--	--	--	--
Ajuga reptans	--	--	--	--	25 *	--	--	--	--	--	--
Primula veris	21	3	18	22	75 *	8	15	2	8	12	5
Viola canina	2	--	8	--	32 *	--	--	--	--	--	--
Crepis biennis	5	--	4	6	36 *	1	--	--	--	--	--
Prunus domestica	--	3	2	--	29 *	1	--	--	--	--	--
Danthonia decumbens	2	--	10	--	36 *	--	--	2	4	--	--
Leucanthemum vulgare agg.	23	50	51	33	89 *	7	--	11	8	16	7
Carex montana	10	--	14	--	46 *	3	--	--	4	3	10
Festuca pratensis agg.	11	--	10	--	54 *	1	20	2	--	3	17
Centaurea phrygia agg.	--	--	4	--	25 *	1	--	--	--	--	--
Trisetum flavescens	13	27	18	6	68 *	14	35	--	--	9	--
Cynosurus cristatus	2	--	4	6	29 *	--	--	--	--	--	--
Vicia cracca agg.	16	3	35	28	71 *	17	15	4	--	3	17
Trifolium montanum	3	--	29	6	79 *	10	10	22	12	41	43
Veronica officinalis	--	--	12	--	29 *	1	--	--	--	--	--

Hypericum maculatum	--	--	4	--	21 *	--	--	--	--	--	--
Stellaria graminea	--	--	2	--	21 *	--	--	2	--	--	--
Colchicum autumnale	--	--	12	6	32 *	1	--	--	--	3	2
Primula vulgaris	--	--	--	--	14 *	--	--	--	--	--	--
Tragopogon pratensis agg.	11	13	4	17	54 *	8	5	11	4	22	5
Aquilegia vulgaris	--	--	4	6	21 *	--	--	--	--	--	--
Cirsium pannonicum	--	--	8	--	39 *	4	--	--	4	22	17
Rhinanthus minor	8	--	14	6	32 *	--	--	4	--	3	--
Festuca rubra agg.	15	7	33	39	57 *	7	15	7	4	3	--
Carex panicea	--	--	2	--	14 *	--	--	--	--	--	--
Hypochoeris maculata	--	--	2	--	25 *	--	--	2	--	9	7
Listera ovata	--	--	8	6	21 *	--	--	--	--	--	--
Potentilla erecta	8	--	16	6	29 *	1	--	--	--	--	--
Plantago lanceolata	61	40	39	67	86 *	15	5	35	4	53	2
Arrhenatherum elatius	18	33	49	28	86 *	48	45	13	8	34	50
Potentilla collina agg.	--	--	--	--	11 *	--	--	--	--	--	--
Prunella vulgaris	26	10	16	33	46 *	3	5	2	--	3	2
Holcus lanatus	7	--	8	6	21 *	1	--	--	--	--	--
Alchemilla glaucescens	--	--	2	--	11 *	--	--	--	--	--	--
Ranunculus auricomus agg.	--	--	2	--	11 *	--	--	--	--	--	--
Carum carvi	--	--	4	11	18 *	--	--	--	--	--	--
Lathyrus latifolius	--	--	--	--	21 *	3	--	--	--	9	12
Arabis hirsuta agg.	--	3	8	6	29 *	3	--	9	--	16	2
Trifolium medium	10	13	31	6	39 *	8	15	--	4	6	2
Carpinus betulus	8	--	14	6	25 *	8	--	--	--	--	2
Orchis morio	--	--	--	--	7 *	--	--	--	--	--	--
Hypochoeris radicata	--	--	--	--	7 *	--	--	--	--	--	--
Dactylorhiza sambucina	--	--	--	--	7 *	--	--	--	--	--	--
Lychnis flos-cuculi	--	--	--	--	7 *	--	--	--	--	--	--
Prunella laciniata	--	--	10	6	21 *	--	--	2	--	9	2
Phyteuma spicatum	2	--	2	--	11 *	1	--	--	--	--	--
Allium scorodoprasum	--	--	2	6	14 *	6	--	--	--	--	--
Crepis praemorsa	--	--	--	--	11 *	--	--	--	8	--	--
Myosotis arvensis	--	3	4	6	14 *	--	5	--	--	--	--
Briza media	75	73	65	78	86 *	10	20	35	44	62	38
Avenochloa pubescens	11	--	16	--	32 *	10	5	4	4	12	31
Non-valid group 2											
Coronilla varia	18	3	45	33	29	63 *	20	30	12	56	29

Origanum vulgare	5	7	24	--	7	27 *	--	--	4	9	10
Non-valid group 3											
Galium verum agg.	43	10	57	83	54	49	100 *	63	24	56	50
Cirsium eriophorum	--	--	--	--	--	3	15 *	2	--	--	2
Poa pratensis agg.	44	37	65	33	46	59	80 *	35	12	31	45
Non-valid group 4											
Centaurea paniculata agg.	3	--	2	--	--	3	--	33 *	4	6	--
Astragalus onobrychis	--	--	--	--	--	--	--	30 *	4	16	10
Eryngium campestre	2	--	2	11	--	20	10	59 *	40	31	21
Nonea pulla	--	--	--	--	--	1	--	15 *	--	--	2
Salvia nutans	--	--	--	--	--	--	--	9 *	--	--	--
Artemisia campestris	--	--	--	--	--	--	--	11 *	--	--	2
Festuca valesiaca	--	--	4	--	--	4	5	24 *	--	16	5
Campanula sibirica	--	--	--	--	--	1	--	17 *	4	9	2
Allium flavum	--	--	--	--	--	--	--	7 *	--	--	--
Silene otites	--	--	--	--	--	--	--	9 *	--	--	2
Stipa capillata	--	--	--	--	--	1	5	15 *	8	--	5
Euphorbia seguieriana	--	--	--	--	--	1	--	7 *	--	--	--
Peucedanum oreoselinum	--	--	4	--	--	1	--	11 *	4	--	--
Veronica spicata agg.	--	--	8	--	4	--	--	22 *	4	19	10
Seseli pallasii	--	--	--	--	--	--	--	7 *	--	--	2
E. Open grasslands on calcareous bedrock mostly from Bohemia											
Thymus praecox	13	--	--	11	--	4	--	13	68 **	6	--
Linum tenuifolium	--	--	--	--	--	--	--	13	32 *	19	2
Biscutella laevigata	--	--	--	--	--	--	--	--	8 *	--	--
Bromus pannonicus	--	--	--	--	--	--	--	--	8 *	--	--
Coronilla vaginalis	--	--	--	--	--	--	--	--	8 *	--	--
Jurinea mollis	--	--	--	--	--	--	--	--	8 *	--	--
Globularia punctata	--	--	2	--	--	1	--	2	16 *	6	2
Helianthemum canum	--	--	--	--	--	1	--	2	12 *	3	--
Euphorbia cyparissias	54	40	61	11	25	70	55	65	84 *	62	19
Non-valid group 5											
Chamaecytisus ratisbonensis	--	--	--	--	--	1	--	9	4	59 **	10
Aster amellus	--	3	--	--	--	10	--	--	12	66 **	19
Polygala major	--	--	8	--	7	1	--	4	8	47 *	12
Scabiosa ochroleuca	3	7	14	17	4	28	--	46	48	84 *	19
Stachys recta	7	--	2	--	--	20	--	20	4	47 *	29
Seseli libanotis	--	--	--	--	--	4	--	2	--	19 *	--
Viola rupestris	2	--	2	--	--	--	--	4	4	22 *	--

Pulsatilla grandis	--	--	--	--	--	4	--	9	4	28 *	12
Buphthalmum salicifolium	--	--	--	--	7	4	--	--	--	19 *	--
Prunella grandiflora	16	3	8	6	--	7	5	4	20	41 *	10
Hypericum elegans	--	--	--	--	--	--	--	--	--	9 *	--
Salvia pratensis	15	13	20	39	75	56	40	48	60	94 *	67
Orchis militaris	2	--	2	--	--	--	--	--	--	12 *	--
Thymus pannonicus	--	--	2	--	--	3	5	20	--	25 *	5
Anthericum ramosum	2	3	2	--	7	13	--	17	20	38 *	31
Onobrychis viciifolia agg.	13	3	8	--	14	10	--	17	24	41 *	21
Orobanche gracilis	--	--	--	--	--	--	--	--	--	6 *	--
Thymus glabrescens	--	--	4	--	--	6	--	15	--	22 *	14
Peucedanum cervaria	5	--	6	--	4	7	5	7	16	28 *	24
Euphorbia virgata	--	--	--	6	7	1	--	9	--	19 *	12
F. *Brachypodium* grasslands of the inner Carpathian Basin											
Euphorbia pannonica	--	--	--	--	--	1	--	2	8	--	62 **
Avenochloa adsurgens	--	--	--	--	--	--	--	2	--	--	38 **
Chamaecytisus austriacus	--	--	--	--	--	--	--	7	--	9	45 **
Agropyron intermedium	--	--	--	--	--	3	15	11	4	12	55 **
Tanacetum corymbosum agg.	--	--	14	--	4	10	5	9	4	25	62 *
Linum flavum	--	--	--	--	--	--	--	--	--	6	26 *
Thalictrum minus	--	--	--	--	--	4	--	7	--	9	33 *
Hieracium umbellatum	--	--	2	--	--	3	--	--	--	9	29 *
Galium glaucum	--	--	--	--	--	7	5	13	4	6	38 *
Peucedanum alsaticum	--	--	--	--	--	3	--	4	--	16	31 *
Lathyrus pannonicus	--	--	--	--	--	--	--	--	--	--	14 *
Inula hirta	--	3	2	--	--	6	5	2	4	6	29 *
Campanula bononiensis	--	--	--	--	--	--	5	--	--	--	14 *
Thesium arvense	--	--	--	--	--	--	--	4	--	--	12 *
Trifolium alpestre	--	--	18	--	4	4	5	9	8	19	33 *
Phleum phleoides	7	--	4	--	4	10	--	26	--	28	36 *
Veronica austriaca	--	--	--	--	--	--	--	2	4	9	17 *
Medicago prostrata	--	--	--	--	--	--	--	--	--	--	7 *
Adonis vernalis	2	--	2	--	--	4	10	15	8	3	26 *
Aster linosyris	--	--	--	--	--	1	--	11	16	22	26 *
Verbascum lychnitis	--	--	--	--	--	4	--	4	--	--	12 *
Pulmonaria mollis	--	--	2	--	4	--	--	--	--	3	12 *
Prunus fruticosa	--	--	--	--	--	1	--	--	--	--	7 *
Serratula radiata	--	--	--	--	--	--	--	--	--	--	5 *
Myosotis ramosissima	--	--	--	--	--	--	--	--	--	--	5 *

Torilis arvensis	--	--	--	--	--	--	--	--	--	--	5 *
Species diagnostic for more than one cluster											
Potentilla neumanniana	64 *	60 *	14	--	--	7	5	4	8	--	--
Scabiosa columbaria	61 *	60 *	8	22	--	--	5	2	4	--	--
Festuca ovina	62 *	77 **	16	6	--	6	15	--	--	--	--
Carex flacca	69 *	53 *	24	44	14	10	--	--	20	22	--
Sanguisorba minor	98 *	83	57	22	50	55	30	33	92 *	56	7
Thymus pulegioides	64 *	70 *	47	11	43	10	15	4	4	16	--
Leontodon hispidus	72 *	43	61	39	86 *	8	5	2	20	47	26
Carex caryophyllea	46 *	20	20	--	46 *	4	5	15	--	38	7
Lotus corniculatus agg.	79	90 *	63	17	93 *	37	15	35	64	66	12
Veronica chamaedrys agg.	7	--	47 *	6	75 **	17	--	4	--	3	7
Agrostis tenuis	11	--	43 *	17	50 *	4	25	11	12	--	--
Ranunculus acris	--	--	8	28 *	32 *	1	--	--	--	--	--
Taraxacum officinale agg.	25	3	24	39 *	54 *	8	--	4	--	3	5
Campanula glomerata	8	--	4	--	57 *	4	5	2	8	56 *	40
Filipendula vulgaris	3	--	16	6	75 *	17	55	37	16	19	74 *
Dactylis glomerata	34	23	37	50	96 *	35	80 *	24	16	66	67
Betonica officinalis	--	--	24	--	36 *	4	5	2	--	3	38 *
Carlina acaulis	16	10	45	--	50 *	15	5	7	12	66 *	2
Koeleria macrantha	3	--	6	--	--	7	10	59 *	16	53 *	19
Carex humilis	--	--	2	--	4	8	10	63 *	68 *	38	21
Potentilla arenaria	3	3	2	--	4	3	5	46 *	24	38 *	--
Astragalus austriacus	--	--	--	--	--	--	--	20 *	16 *	6	--
Bothriochloa ischaemum	--	--	--	--	--	3	--	20 *	--	25 *	--
Seseli hippomarathrum	--	--	--	--	--	3	5	22 *	20 *	9	--
Dianthus carthusianorum agg.	2	--	14	--	36	18	10	43 *	4	44 *	19
Asperula cynanchica	3	3	16	6	7	20	5	30	72 *	78 *	26
Bupleurum falcatum	10	10	14	--	--	35	10	20	64 *	72 *	10
Scabiosa canescens	--	--	--	--	--	3	15	17	28 *	31 *	2
Thesium linophyllon	--	--	4	6	7	7	--	15	8	56 *	36 *
Centaurea scabiosa agg.	39	27	29	17	29	45	10	43	52	97 *	74 *
Festuca rupicola	7	7	49	22	57	68	35	80	40	100 *	88 *
Dorycnium pentaphyllum agg.	--	--	12	--	4	7	--	30	16	47 *	36 *
Carex michelii	--	--	2	--	4	6	--	--	4	34 *	43 *
Seseli annuum	2	--	--	--	--	3	--	20	4	34 *	40 *
Inula ensifolia	--	--	2	--	--	1	--	7	12	28 *	26 *

Cirsium acaule	74 *	77 *	29	22	--	8	35	17	60 *	--	--
Bromus erectus	20	83 *	20	94 *	89 *	37	15	54	44	56	24
Ranunculus polyanthemos agg.	2	3	16	17	50 *	8	--	9	8	44 *	43 *
Teucrium chamaedrys	2	3	22	--	7	28	15	43	56 *	56 *	62 *
Other species with frequency > 20%											
Brachypodium pinnatum	97	70	94	56	46	83	100	70	88	100	98
Medicago falcata	15	--	33	6	39	35	50	50	36	56	52
Polygala comosa	39	37	27	17	39	6	--	4	8	--	5
Helianthemum nummularium agg.	30	--	29	--	46	25	5	20	28	34	12
Ononis spinosa	38	10	37	33	21	4	--	22	44	38	5
Agrimonia eupatoria	39	37	57	28	21	38	45	13	16	12	40
Salvia verticillata	3	--	29	6	25	18	--	9	12	19	5
Galium mollugo agg.	34	43	41	28	39	35	10	2	--	--	5
Centaurea jacea	44	17	43	33	39	23	35	15	56	28	24
Viola hirta	43	67	49	28	68	34	15	17	24	47	29
Hieracium bauhinii	3	--	18	--	25	3	--	9	16	12	5
Fragaria vesca	10	20	24	--	14	6	5	2	4	--	--
Daucus carota	34	30	39	28	32	7	10	9	--	25	--
Pimpinella saxifraga agg.	67	47	73	56	82	54	35	48	60	75	43
Knautia arvensis agg.	59	20	57	11	50	55	15	24	36	66	45
Campanula rapunculoides	11	7	16	6	21	8	5	--	12	3	2
Inula salicina	2	--	4	17	18	6	--	4	20	6	7
Hypericum perforatum	39	53	49	22	32	35	30	26	12	50	2
Picris hieracioides agg.	13	--	12	28	--	8	--	2	12	19	5
Achillea millefolium agg.	51	23	90	61	93	77	45	65	48	72	60
Carlina vulgaris agg.	56	57	24	22	4	10	15	13	44	56	14
Plantago media agg.	69	30	67	56	71	41	5	54	52	75	45
Fragaria viridis	23	17	39	6	32	56	45	43	8	56	33
Carex tomentosa	2	--	22	6	18	4	--	2	12	6	2
Potentilla heptaphylla agg.	8	3	33	28	29	25	5	9	32	28	5
Senecio jacobaea	13	20	18	11	7	6	--	11	4	9	--

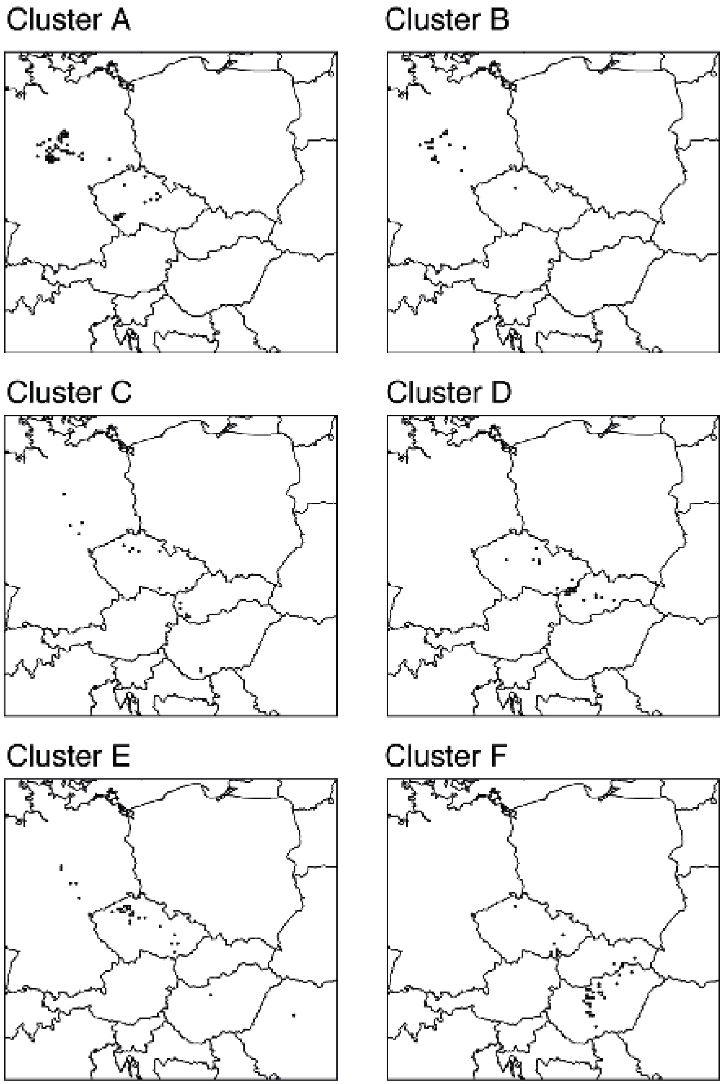


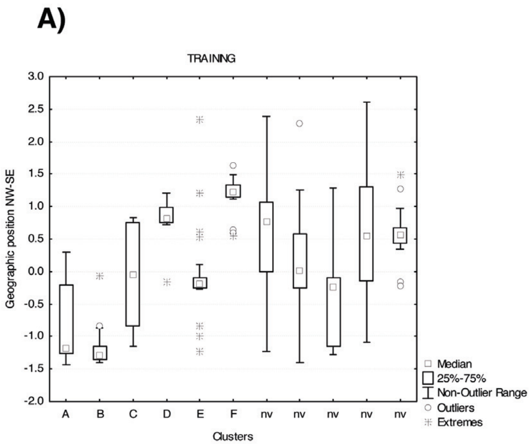
Fig. 8. Distribution maps of relevés of validated clusters A-F, based on the pooled data from the TRAINING and TEST data sets.

they contain 60-80 species per 16-25 m^2, thus belonging to the most species-rich grasslands of temperate Europe (Klimeš 1997). They occur on gentle slopes with deep soils over calcareous flysch sandstones and claystones. Outcrops of water-holding claystones may cause local waterlogging, but in dry periods of the year these places dry out, which supports species adapted to intermittently wet soils, such as *Betonica officinalis* and *Filipendula vulgaris*. The topsoil is usually slightly decalcified but a higher pH is maintained below (Tlusták 1975). The origin of these grasslands is secondary: they originated after the clearing of *Fagus*, *Carpinus* and *Quercus* forests. They largely correspond to *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939, and partly also to other species-rich grasslands which are transitional between the class *Festuco-Brometea* and the mesic meadows of the alliance *Arrhenatherion*.

Cluster E: These are open grasslands of steep slopes on calcareous bedrocks, occurring mostly in continental areas in Bohemia, but also in Moravia and Germany (Fig. 7.). Isolated sites are found in Hungary and Romania. The climate is subcontinental, with rather low annual precipitation and hot summers (Table 6.). The stands are dominated by *Brachypodium* or *Bromus*, although in some sites, narrow-leaved caespitose graminoids such as *Carex humilis* and *Festuca rupicola* can also be prominent. In the driest areas, they are usually found on north-facing slopes or footslopes, often in contact with narrow-leaved *Stipa-Festuca* dry grasslands. In areas with higher precipitation, they occupy the driest south-facing slopes. These grasslands are mostly secondary, developed as a replacement vegetation for oak, hornbeam or beech forests, but in some places they may be natural grasslands preserved for millennia on steep south-facing slopes, especially on slopes affected by solifluction and landslides (Studnička 1980). This vegetation corresponds to the *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933, but in different countries, these grasslands were traditionally assigned to different, locally described associations, e.g. in Germany to the *Adonido-Brachypodietum* (Libbert 1933) Krausch 1961, *Scorzonero hispanicae-Brachypodietum* Gauckler 1957 or *Festuco rupicolae-Brachypodietum* Mahn 1965, and in Slovakia to the *Salvio verticillatae-Brachypodietum* Ružičková 1986.

Cluster F: These are closed, dense and species-rich *Brachypodium* grasslands from the Pannonian region (Fig. 7., Fig. 8.). They are most common in the loess area of Mezőföld in central Hungary and in northern Hungary, southern Slovakia and southern Moravia. The climate is continental: the mean annual and July temperature and the January-July temperature difference is the highest of all clusters, while precipitation is low (Table 6.). They are typical of calcareous soils, developed mainly on deeper loess or other Quaternary and

Tertiary sediments. These grasslands are very rich in species, have a relatively high proportion of forest-steppe, forest-fringe and dry oak forest species (Fekete et al. 1998), and are usually dominated by *Brachypodium pinnatum*. They have a well-developed vertical structure and contain many broad-leaved herbs and tall forbs (Varga et al. 2000). The present stands are partly considered to be of primary origin, predominantly on extremely steep slopes, but mostly they are regarded as the extended and stabilized clearings of former foreststeppe forests (Borhidi 2003, Varga et al. 2000). This type corresponds to the *Polygalo majoris-Brachypodietum pinnati* Wagner 1941 or *Verbasco austriaci-Inuletum ensifoliae* Tlusták 1975. For these grasslands in Hungary Horváth (2002, 2009) recently proposed a new association, *Euphorbio pannonicae-Brachypodietum pinnati*. Formerly these stands were not named syntaxonomically or were erroneusly interpreted as *Salvio nemorosae-Festucetum rupicolae* Zólyomi ex Soó 1964 mainly in dicussions or in theses.



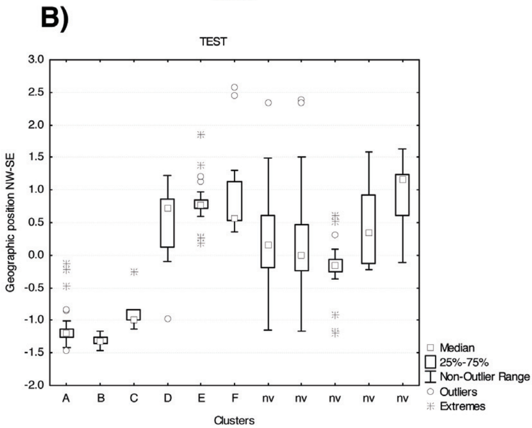


Figure 9. Geographic distribution along the NW-SE gradient of the clusters of the partitions of (**A**) TRAINING and **(B)** TEST data sets at the level of 11 clusters. Lower position on vertical axis represents a more NW distribution, higher position a more SE distribution. Letters A-F label corresponding valid clusters in TRAINING and TEST data sets; nv indicates non-valid clusters.

III. 2. Variation in species composition of Hungarian semi-dry grasslands

III.2.1. Patterns in the species composition of Hungarian semi-dry grasslands

The optimal number of clusters appeared at the level of 10 clusters where 7 clusters were found to be valid. The structure of the TRAINING and TEST dendrograms differed considerably. In our opinion it reflects that the compositional differences among the clusters are not sharp at least on higher levels, and even the species lists of relevés from the same site can be highly variable. This partly explains the difficulties of the classification of Hungarian semi-dry grasslands.

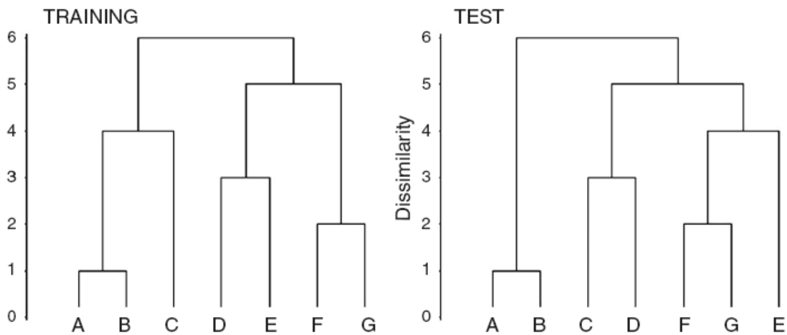


Figure 10. Topology of dendrograms based on the TRAINING and TEST data sets. Only valid clusters are shown.

Nevertheless, the topologies of the two dendrograms (Fig. 10.) have common features. Clusters A and B, which represent *Brachypodium pinnatum* or *Bromus erectus* dominated, species-rich meadow steppes on deep loess from central Hungary, are the closest to each other in both of the dendrograms, and they are the furthest from the cluster group E, F and G, which comprises stands from the cooler and more humid regions or the hilly parts of the county. The positions of clusters C and D are variable, indicating the transitional character of these relevés. Both of these clusters comprise stands from a single small area (C: meadow

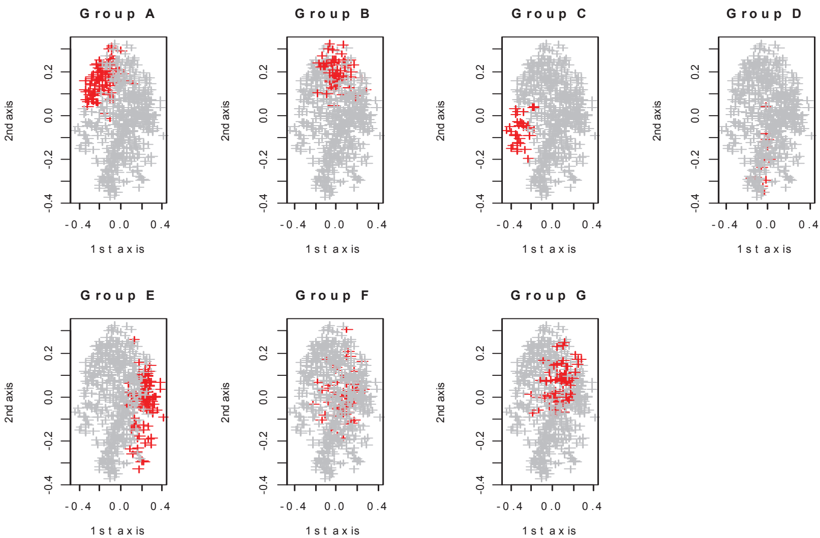


Figure 11. Spatial position of the valid clusters A-G along the first two axes in the PcoA plot. Presence-absence data with Sørrensen dissimilarity were used.

steppes near to the town Érd, D: semi-dry grasslands with montane character from the Bükk Mts). The structure of the dendrograms profoundly reflects the geographical differentiation of the clusters (Fig. 12.).

In order to visualise the spatial relations of clusters, we plotted the diagrams of the PCoA analysis run prior to the clustering process (Fig. 11). The positions of the valid clusters in the ordination space support the findings based on the dendrogram structure. Clusters A and B are positioned in the upper left-hand side part of the ordination space, while Clusters E, F and G are positioned in the middle and lower right hand side. Cluster C is positioned in the middle and lower left had side, while cluster D is in the middle bottom.

III.2.2. Description of the clusters

Cluster A: Most relevés of this cluster are from the Mezőföld region (loess plateau roughly in the middle of the country, western side of the Danube), others are from the eastern foothills of the Gerecse Mts. and some are from the upland along the Hernád River. These grasslands are typically found in loess valleys on steep, mostly north-facing slopes, and are dominated by *Brachypodium pinnatum*. The most important diagnostic species (*Euphorbia glareosa*, *Thalictrum minus* and *Viola ambigua*) are characteristic of parts of the Alföld with loess substrate and the foothills of the Magyar Középhegység. High constancies of *Euphorbia glareosa, Festuca valesiaca* agg., *Brachypodium pinnatum*, *Filipendula vulgaris*, *Salvia pratensis*, *Thalictrum minus*, *Galium glaucum* and *Carex michelii* define the cluster clearly.
Cluster B: Most of the relevés originate from the Mezőföld region and from the Gödöllői-dombság, along with some from the foothills of Gerecse and Pilis Mts. The species composition is highly similar to Cluster A and many diagnostic species are shared, which is reflected in both of the dendrograms and the ordination plot as well. The relevés are typically dominated by *Brachypodium pinnatum,* but occasionally by *Bromus erectus* and *Festuca valesiaca* agg. Faithful species of the cluster (*Campanula rotundifolia*, *Galium verum*, *Seseli annuum*) reflect a more open structure of the grassland in comparison to Cluster A, which might be caused by differences between the former and recent land use, since we know from field experience that some relevés were burnt regularly or slightly grazed by sheep.
Cluster C: These relevés are restricted to a very small area in the north-eastern part of the Mezőföld region, close to the town Érd. It is a relatively uniform cluster with a small number of relevés, the separation of which is most probably due to the presence of a few rare species (*Cotoneaster matrensis*, *Echinops spaerocephalon*) which are concentrated in this area (or

overrepresented in the relevés) and the higher frequencies of some shrub species (*Cornus sanguinea, Rhamnus catharticus, Rubus canescens*). The diagnostic species are to some extent shared with Clusters A and B and the geographical ranges of the three clusters are similar too, what is reflected well by the TRAINING dendrogram and the ordination plot. There are some species (*Aster amellus*, *Cirsium pannonicum*, *Linum flavum*, *Origanum vulgare*, *Peucedanum cervaria*) reaching higher constancies only in Clusters C and D, which explains the structure of the TEST dendrogram and also supported by the ordination plot.

Cluster D: These relevés are from the most hilly part of Hungary, from the higher elevations of the Bükk Mts. Their separation is clearly explained by the presence of montane elements (*Primula elatior, Dracocephalum ruyschiana, Carlina acaulis*, *Libanotis pyrenaica*), markedly showing montane influences. The relevés are from a well-defined smaller area, which is reflected in the considerable uniformity of species composition. These are very species-rich stands where the typical elements of semi-dry grasslands (*Asperula cynanchica*, *Geranium sanguineum*, *Cirsium pannonicum*, *Centaurea scabiosa* agg., *Filipendula vulgaris*, *Pulsatilla grandis*, *Dianthus pontederae*) reach medium or higher constancies. Presence of mesophilous species explains similarities with the Clusters E, F, and G in the TRAINING dendrogram. Shared higher constancies of *Aster amellus*, *Cirsium pannonicum*, *Linum flavum*, *Origanum vulgare* and *Peucedanum cervaria* explain the similarities to Cluster C in the TEST dendrogram.

Cluster E: Nearly all of the relevés are from the Dunántúli-középhegység and Dunántúli-dombság, and are dominated by *Bromus erectus* s.l. The relevés consist of common species of *Festuco-Brometea* (*Teucrium chamaedrys, Thymus odoratissimus, Galium verum, Salvia pratensis*). Species of higher and medium constancies indicate dry, shallow soils, while mesophilous species are also present. Some of the species reflect drier, locally open surface (*Acinos arvensis, Sanguisorba minor, Medicago minima, Trinia glauca, Bothriochloa ischaemum, Sedum sexangulare*). Most of the stands are located within the closer or broader surroundings of the Bakony Mts. on dolomite bedrock. The formerly widespread and rather intensive sheep grazing combined with the shallow rocky soils resulted in a simple structure and lack of broad-leaved forbs at these sites. The other stands in south-western part of the Dunántúli-dombság are from highly eroded, nutrient-poor loess soils, mostly abandoned vineyards and arable fields. It is interesting that the two different land use histories – overgrazing and development on the places of not long ago abandoned arable fields – can lead to highly similar species composition. The ordination plot shows considerable overlaps with Clusters F and G which is reflected by the classification results. Occurrence of some species of calcium-poor soils (*Luzula campestris*, *Anthoxanthum odoratum*) explains the similarity to Cluster F. The geographical distribution is rather similar to that of Cluster G, which is reflected by shared constant species.

Cluster F: The relevés of this cluster are mainly from the Északi-Középhegység (Fig. 1), and some are from the edges of the Mezőföld region and Gödöllői-dombság. The cluster is characterised by the presence and dominance of *Danthonia alpina*, although the species is present in half of the relevés only. Diagnostic and constant species (*Luzula campestris*, *Lychnis viscaria*, *Viola canina*, *Veronica officinalis*) reflect mesic soils poor in calcium. Species with high constancies (*Filipendula vulgaris*, *Trifolium montanum*, *T. alpestre*, *Salvia pratensis*) are character species of calcareous semi-dry grasslands (Soó 1964-80).

Cluster G: Most of the relevés of this cluster are from the hilly parts of Dunántúl (outside the Mezőföld plateau) located in the cooler and moister parts of the country. In these landscapes, semi-dry grasslands are located close to mesophilous forests and meadows, what is reflected in their species composition. Diagnostic species and species of medium constancies of Cluster G are mesophilous species (*Poa pratensis*, *Arrhenatherum elatius*, *Briza media*), or disturbance-tolerant species sensu Borhidi 1995 (*Galium mollugo*, *G. verum*, *Agrimonia eupatoria*, *Carlina biebersteini*, *Ononis spinosa*). From field experience, we know that most of the relevés of this cluster are of two typical types of origin: (1) young stands developing rapidly following recent abandonment of a former arable land or a vineyard, or (2) meadows that dried out due to canalisation. The lack of specialist dry- and semi-dry grassland species and the presence of meadow species give this cluster a transient character towards wet meadows (*Arrhenatheretalia*), and explain the similarity with cluster F in this analysis. Shared constant species explain the similarity with cluster E. The lack of specialist species in this cluster in indicated also by the scattered distribution of the relevés of this cluster in the ordination space.

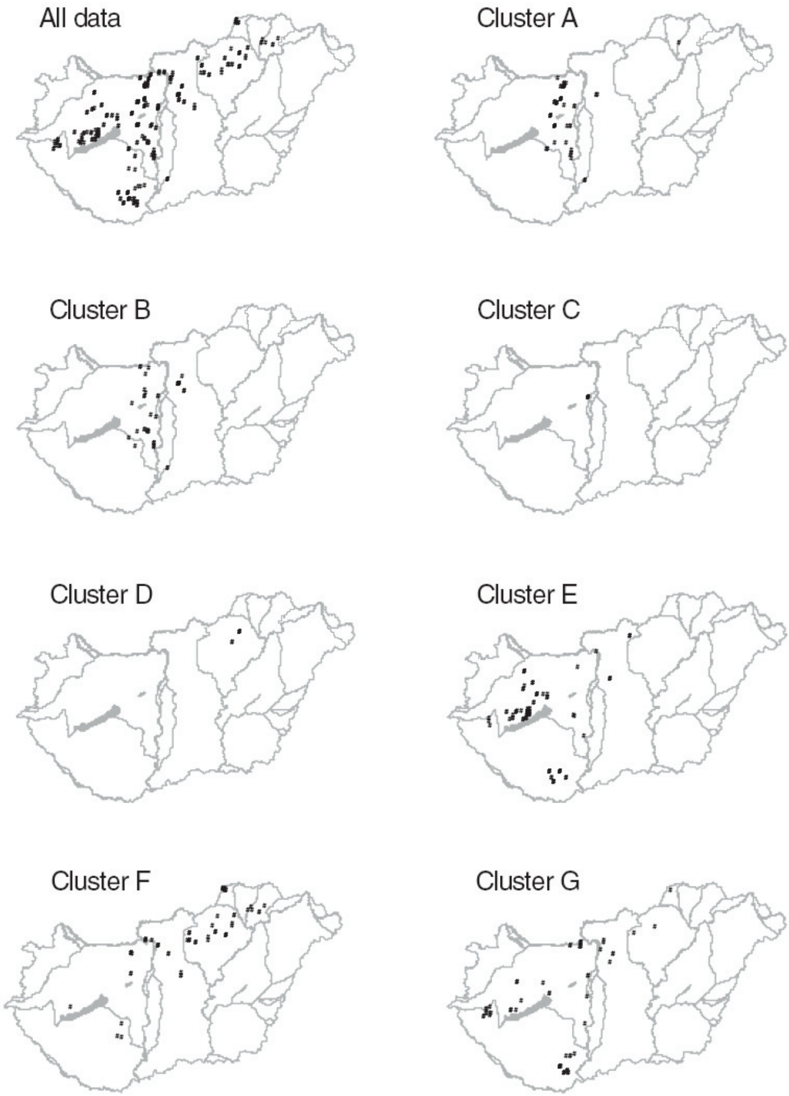


Figure 12. Distribution maps of all relevés included in the data set and relevés of validated clusters A-G, based on the pooled data from the TRAINING and TEST data set.

Table 7. Synoptic table of the 7 valid clusters of the joined TRAINING and TEST data set with percentage frequency (constancy) of species. Within blocks of diagnostic species, species are ranked by decreasing fidelity, measured by the phi coefficient for relevé groups of equalized size (*: $\Phi > 0.3$; **: $\Phi > 0.5$). Species with non-significant occurrence concentration in the given cluster were not included in the groups of diagnostic species, even if they had $\Phi > 0.3$ (Fisher's exact test, $P < 0.01$). The grass species used for the relevé selection are in bold. Other species with percentage > 20% are listed in alphabetical order, except the grass species used as selection criteria.

Group No.	**A**	**B**	**C**	**D**	**E**	**F**	**G**
No. of relevés	98	59	32	15	96	68	69
A. Core type of *Euphorbio pannonicae-Brachypodietum*							
Thalictrum minus	54 **	31	6	33	5	7	4
Viola ambigua	35 **	19	16	-	-	-	1
Thesium ramosum	21 *	8	-	-	-	9	-
Peucedanum arenarium	8 *	-	-	-	-	-	-
Elymus hispidus	58 *	46	44	-	6	28	7
Centaurea jacea sl.	40 *	15	-	-	23	25	33
B. *Bromus erectus* sub-type of *Euphorbio pannonicae-Brachypodietum*							
Campanula rotundifolia	16	44 **	-	-	-	7	1
Seseli annuum	52	69 **	6	-	19	43	19
Galium verum	39	88 *	-	47	66	69	61
Dactylis glomerata	59	76 *	38	-	46	22	59
Camelina microcarpa	-	7 *	-	-	-	-	-
C. Local type of *Euphorbio pannonicae-Brachypodietum* close to the town Érd							
Orobanche sp.	1	-	69 **	-	3	-	3
Chamaecytisus ratisbonensis	-	2	50 **	-	1	-	-
Stipa pulcherrima	7	3	47 **	-	1	7	-
Origanum vulgare	5	-	84 **	33	7	6	12
Hieracium umbellatum	33	7	72 **	-	3	10	19
Serratula tinctoria	17	-	59 **	7	-	9	4
Calamagrostis epigeios	2	7	56 **	-	7	19	23
Campanula glomerata	56	29	100 **	13	6	16	6
Serratula radiata	9	2	28 **	-	-	-	-
Scabiosa ochroleuca	7	12	78 **	33	16	22	13
Coeloglossum viride	-	-	12 **	-	-	-	-
Linum flavum	27	8	66 **	27	1	4	4
Colutea arborescens	-	-	16 **	-	-	-	4
Cornus sanguinea	2	2	28 **	-	1	3	10
Echinops sphaerocephalus	-	-	12 **	-	-	-	1

Rubus canescens	2	2	16 **	-	-	-	3
Rhamnus cathartica	8	-	28 **	-	2	1	4
Dorycnium germanicum	39	7	94 **	-	19	19	20
Aster amellus	26	2	81 **	33	1	3	4
Bupleurum falcatum	2	-	62 **	-	5	-	1
Inula ensifolia	31	3	97 **	53	7	10	14
Lembotropis nigricans	5	2	59 **	7	3	4	6
Peucedanum alsaticum	28	15	53 **	-	1	3	22
Scorzonera hispanica	1	-	69 **	-	1	3	4
Prunus cerasus	-	-	12 **	-	-	1	1
Linum tenuifolium	-	-	41 *	-	20	3	4
Thesium linophyllon	13	5	94 *	53	27	35	14
Viburnum lantana	1	-	22 *	-	1	1	4
Clematis vitalba	-	-	22 *	-	4	-	10
Campanula persicifolia	10	8	31 *	-	3	6	1
Prunus dulcis	-	-	9 *	-	-	-	1
Ulmus minor	3	2	12 *	-	-	1	3
Cotoneaster matrensis	-	-	6 *	-	-	-	-
Poa pratensis agg.	60	42	75 *	-	31	28	55
Buglossoides purpureo-coerulea	-	-	6 *	-	-	-	1
Koeleria cristata agg.	14	15	47 *	-	39	37	19
Prunus fruticosa	3	-	31 *	-	-	4	-
Peucedanum cervaria	23	7	94 *	40	9	32	13
Onobrychis arenaria	13	10	47 *	-	6	9	4
Inula hirta	46	7	53 *	-	1	21	1
D. *Polygalo majoris-Brachypodietum* grasslands of the Bükk Mountains							
Libanotis pyrenaica	-	-	-	80 **	1	-	-
Senecio erucifolius	-	-	-	33 **	-	-	-
Achillea setacea	3	3	-	40 **	-	-	-
Centaurea micranthos	3	-	3	47 **	9	-	12
Melampyrum arvense	1	-	-	53 **	2	3	3
Primula elatior	-	-	-	20 **	-	-	-
Ranunculus auricomus	-	-	-	33 **	-	-	-
Hieracium echioides	-	-	-	20 **	-	-	-
Thlaspi perfoliatum	2	2	-	27 **	4	3	-
Dracocephalum ruyschiana	-	-	-	13 **	-	-	-
Carex tomentosa	5	3	-	47 **	1	16	12
Iris sibirica	-	-	-	13 **	-	-	-
Verbascum chaixii sl.	1	2	-	20 **	-	1	1
Dorycnium herbaceum	-	2	-	53 **	10	28	22

Carlina acaulis	-	-	-	20 **	-	4	1
Asperula cynanchica	15	44	19	100 **	34	50	16
Cruciata glabra	-	-	-	33 **	-	1	-
Fragaria vesca	-	-	-	47 **	9	-	1
Viola hirta	8	17	-	67 *	7	47	22
Euphorbia polychroma	-	-	-	27 *	-	7	3
Potentilla argentea agg.	-	-	-	13 *	2	4	-
Geranium rotundifolium	-	-	-	7 *	-	-	-
Lathyrus pratensis	-	-	-	13 *	1	3	4
Symphytum tuberosum sl.	-	-	-	13 *	-	-	3
Hieracium pilosella agg.	-	3	-	27 *	25	6	1
Cirsium pannonicum	-	-	16	67 *	1	6	-
Geranium sanguineum	3	2	-	60 *	8	26	6
E. *Sanguisorbo minoris-Brometum erecti* grasslands of the Dunántúli-Középhegység							
Thymus odoratissimus	18	22	3	7	71 **	22	3
Acinos arvensis	-	-	-	-	20 **	3	1
Daucus carota	5	-	3	-	17 *	3	7
Onobrychis viciifolia	-	-	-	-	6 *	-	-
Plantago lanceolata	3	5	-	-	21 *	10	4
Sanguisorba minor	7	-	41	33	67 *	18	12
Sedum sexangulare	-	-	-	-	9 *	1	-
Vicia angustifolia	3	2	-	-	16 *	4	9
Trinia glauca	-	-	-	-	9 *	-	-
Achillea collina	6	25	-	-	57 *	50	30
***Bromus erectus* sl.**	8	32	3	-	71 *	13	16
Ranunculus sardous	-	-	-	-	5 *	-	-
F. *Trifolio medii-Brachypodium pinnatum* grasslands of the Északi-Középhegység							
Luzula campestris agg.	-	8	-	-	6	28 **	-
Danthonia alpina	-	-	-	-	2	44 **	-
Trifolium medium	-	3	-	-	2	19 *	1
Trifolium alpestre	29	8	9	7	7	60 *	6
Eryngium campestre	26	32	19	13	45	63 *	22
Cerastium brachypetalum	5	2	-	-	4	16 *	-
Seseli varium	6	-	9	-	1	19 *	1
Viola canina	-	-	-	-	-	10 *	3
Lychnis viscaria	-	-	-	-	-	7 *	1
Veronica officinalis	-	-	-	-	-	6 *	-
Trifolium ochroleucum	-	-	-	-	-	6 *	-
Verbascum phoeniceum	7	2	-	-	4	21 *	7
Anthoxanthum odoratum	-	2	-	-	7	18 *	3

Medicago x *varia*	-	-	-	-	-	4 *	-
Allium vineale	-	-	-	-	-	4 *	-
Trifolium montanum	33	31	-	40	24	65 *	10
G. Sites under succession and transitions to meadows							
Helleborus odorus	-	-	-	-	2	-	10 *
Galium mollugo	1	3	22	-	15	3	30 *
Knautia drymeia	-	-	-	-	-	-	6 *
Holcus lanatus	-	-	-	-	-	-	6 *
Scirpoides holoschoenus	-	-	-	-	-	-	4 *
Campanula trachelium	-	-	-	-	-	-	4 *
Species diagnostic for more than one cluster							
Bromus inermis	26 *	7	38 **	-	2	9	4
Euphorbia glareosa	95 **	80 **	91 **	-	8	15	7
Chamaecytisus austriacus	47 *	46 *	50 *	-	15	10	25
Galium glaucum	68 *	20	69 *	20	6	12	7
Filipendula vulgaris	93 *	92 *	75	47	19	84	33
Other species with frequency > 20%							
Brachypodium pinnatum	99	90	100	100	32	69	99
Avenula adsurgens	38	29	25	-	7	47	10
Avenula pubescens	34	12	9	-	6	10	12
Achillea pannonica	33	32	28	-	6	26	17
Adonis vernalis	42	25	31	27	8	19	28
Agrimonia eupatoria	24	47	34	7	47	38	42
Allium senescens ssp. *montanum*	-	-	-	27	2	-	-
Anthericum ramosum	19	19	66	7	3	21	4
Anthyllis vulneraria agg.	-	2	-	7	33	3	6
Arrhenatherum elatius	11	15	28	7	23	44	43
Aster linosyris	32	3	28	13	4	29	4
Briza media	30	22	3	-	30	38	41
Carex humilis	26	41	19	-	15	10	4
Carex michelii	56	27	22	20	7	25	7
Carlina biebersteini	6	3	34	27	17	15	26
Centaurea scabiosa agg.	73	63	91	80	33	35	52
Clinopodium vulgare	2	2	19	-	5	9	26
Crataegus monogyna	34	51	34	-	34	43	20
Dianthus pontederae	7	8	9	67	41	40	14
Dictamnus albus	3	8	28	-	-	4	1
Euphorbia cyparissias	12	24	-	33	52	43	26
Festuca valesiaca agg. (incl. *Festuca rupicola*)	96	95	100	100	86	96	58

Fragaria viridis	22	42	19	13	34	59	22
Genista tinctoria	27	8	-	-	-	35	3
Helianthemum nummularium sl.	3	25	-	7	21	16	9
Hypericum perforatum	2	12	6	20	32	29	6
Hypochaeris maculata	4	2	47	7	7	10	9
Knautia arvensis	59	46	-	7	34	40	35
Lotus corniculatus	16	17	6	7	46	37	23
Medicago falcata	54	61	3	-	48	34	22
Ononis spinosa	11	15	-	-	10	12	22
Phleum phleoides	24	37	16	33	12	21	-
Pimpinella saxifraga agg.	54	59	-	33	41	41	16
Plantago media	34	29	50	13	50	63	26
Polygala major	-	-	19	20	-	10	4
Potentilla arenaria	-	-	3	-	28	3	-
Prunella grandiflora	11	-	-	27	-	10	-
Prunus spinosa	10	12	3	-	11	28	13
Pseudolysimachion spicatum	7	17	-	-	7	29	3
Pulmonaria mollis	-	3	-	-	1	21	6
Pulsatilla grandis	2	-	6	47	-	13	-
Ranunculus acris	-	-	-	27	1	-	6
Ranunculus polyanthemos	46	47	22	-	10	24	23
Rosa canina agg.	7	3	25	7	11	13	7
Rumex acetosa	2	20	-	7	-	13	6
Salvia pratensis	64	49	62	13	58	56	48
Securigera varia	31	29	16	7	46	29	35
Silene vulgaris	12	25	22	7	14	4	12
Stachys officinalis	46	19	25	47	1	44	23
Stachys recta	41	12	9	27	11	18	10
Tanacetum corymbosum	48	7	62	20	1	28	3
Teucrium chamaedrys	62	73	19	53	71	59	42
Thymus pannonicus	3	15	19	-	-	37	-
Veronica austriaca	15	15	6	33	3	26	4

III. 3. Analysis of the factors affecting the naturalness based quality of semi-dry grasslands in Hungary at landscape level

Our results, in general, show that the naturalness of the semi-dry grasslands depends on both intra-patch (threats and landscape ecological attributes, like isolation or pattern) and matrix attributes [surrounding habitats and overall area of (semi-)natural vegetation in the cell] (Table 8.). Presence of other grassland types similar in ecological demands to the model habitat positively affects the naturalness of that type, while invasive alien species and diffuse pattern have negative effects. The higher proportions of (semi-)natural habitats in the cell, as well as the number of habitat types in the cell, have positive effects.

Table 8. Results of the individual generalised linear models. In the first column the name of the variable is given. The second column shows whether the variable is considered intra-patch or matrix. ANOVA p value shows the probability of a Type I. error. Direction signifies whether the variable has a negative or a positive effect on naturalness. Nagelkerke's R^2 indicates the importance of the effect of the variable (percentage variance explained by the factor). The higher the R^2, the larger the effect is. In the case of nominal variables, the results of the post-hoc tests are shown with uppercase letters after the names of the levels.

name of the factor	**matrix or intra-patch**	**ANOVA p value**	**direction**	**Nagelkerke R^2**
1. number of habitat types in the cell	m	3.50E-08	positive	3.73%
2. presence of closed thermophilous oak woodlands (L1)	m	5.31E-07	positive	3.09%
3. threat "presence of invasive alien species in the habitat type"	ip	1.37E-05	negative	2.33%
4. overall cover of (semi-)natural habitat types in the cell	m	2.75E-05	positive	2.17%
5. presence of calcareous open rock grasslands (G2)	m	5.33E-05	positive	2.02%
6. presence of slope steppes (H3a)	m	5.54E-04	positive	1.48%
7. pattern	ip	3.10E-03		1.43%
7.a three or more patches[a]			neutral	
7.b one or two patches[a]			neutral	
7.c diffuse[b]			negative	

III. 4. Factors explaining species richness, diversity and other compositional and structural characteristics of semi-dry grasslands in Hungary at stand level

III.4.1. Correlations between dependent variables

Most of the dependent variables are correlated with one another (Table 9., Fig.13.). This corresponds well with our expectations. The correlation analysis revealed two groups of variables which behave similarly. Within the groups the variables are correlated with each other positively, while among the groups the correlation is negative.

The first group is composed of the variables ‘species number’, ‘Shannon diversity’, ‘evenness’ and the ‘number of valuable species’ which are positively correlated to one another. The first three positive correlation is not surprising, however, the species number and the evenness could be independent theoretically. Nevertheless, the positive correlation of the number of valuable species to the other variables is interesting. It indicates that the most species rich stands host the highest number of valuable species.

The second group is formed by the variables ‘cover of valuable species’, ‘cover of *Brachypodium pinnatum*’ and ’cover of graminoids’, which are correlated positively to one another and mainly negatively to the first group. Positive correlation of ‘cover of *Brachypodium pinnatum*’ and ’cover of graminoids’ is well understood, however, association of the ’cover of valuable species’ to these to and negative correlation of it to the first group is interesting again. The reason for this is most probably that among the group of valuable species there are ones which sometimes reach high cover especially in more mesic stands where *Brachypodium pinnatum* highly dominates (e.g. *Geranium sanguineum*, *Trifolium alpestre*). Also, if one or some of these species reach higher cover together with *Brachypodium*, the number of species and species richness remains consequently lower due to spatial constraints coming from the fixed area of the plot.

Besides the two groups we found negative correlation between the variables ’cover of *Brachypodium pinnatum*’ and ’cover of *Bromus erectus*’. The negative correlation could indicate interspecific competition between these two grass species. However, according to our field experience this is not the most probable case. Difference in ecological demands and in site history is a more probable explanantion. During our field survey, we hardly ever found sites where both of the grasses were present with higher cover. This somewhat contradicts to the findings of Virágh and her colleagues in a study of semi-dry grassland patches in the Gödöllői-dombság (Virágh & Bartha 2003). In our opinion, the reason for this is that the site conditions and probably site history in their study area are quite unique in comparison to other Hungarian semi-dry grassland sites. This idea is supported by the floristic analysis of semi-dry grasslands as well, where we found that relevés from the Gödöllői-dombság form a separate cluster among Hungarian semi-dry grasslands (Illyés et al. 2009).

Interestingly enough we found that variable ’cover of *Helitotrichon praeusta*’ is positively associated with the number of valuable species. The significant correlation was unexpected, nevertheless suspected. During sampling we had the feeling that sites with high cover of *Helitotrichon praeusta* are „good” sites, but not necesserily because of their high species richness. However, it remained a feeling till this analysis. We hypothetise that *Helitotrichon praeusta* indicates somehow that the grassland patch is an ’ancient’ one. It usually occurs with higher cover in places which were grasslands for a very long time. Further study of the sites dominated by *Helitotrichon praeusta* seems to be an important task with conservation relevance, especially because the genus *Helitotrichon* poses taxonomical problems and very little is known of the ecology of this genus in Hungary. The reason why the special role was not detected by the synatonomical analysis is the fact that the number of sites where *Helitotrichon praeusta* reaches high cover was rather low in comparison to the number of relevés used for the analysis and thus they did not form a separate cluster.

We found no correlation with variables ‘cover of shrubs’ and ‘cover of trees’. We have two possible explanations for this. First, it is possible that the cover of trees and shrubs truly have no connections with the other studied variables in Hungarian grasslands. Second, sampling was carried out in such a way that shrubs and trees are underrepresented in the samples, and thus their effect is lessened. During sampling we focused on the documentation of semi-dry grasslands and we have to admit that very often we choose sample plots free from trees and shrubs even in places where trees and shrubs were widespread.

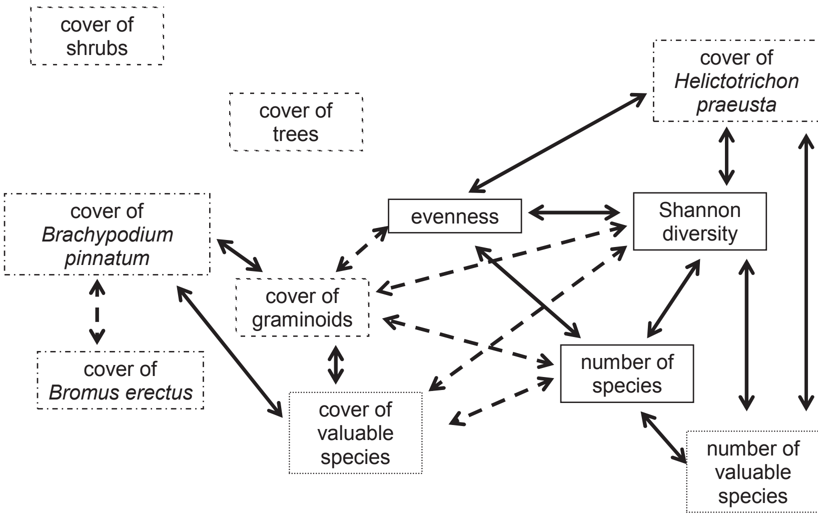


Figure 13. Correlations among the response variables. Arrows mean significant effects. Solid lines indicate positive, dashed lines indicate negative correlations. Contour line of the text boxes refer to the variable groups: ——— Species richness and diversity, ········ valuable species, -·-·-·-·- dominant grasses, - - - - - - - - - structural species group

Table 9. Correlations among the dependent variables. Only those correlations are shown which were found valid (p<0.05), i.e. they were significant both in the TRAINING and TEST datasets and the direction of the effect was also the same. The actual values present the results of the TEST database.

		number of species	Shannon diversity	evenness	cover of *Brachypodium pinnatum*	cover of *Bromus erectus*	cover of *Helitrotrichon paeusta*	number of valuable species	cover of valuable species	cover of trees	cover of graminoids
number of species	p	-	-	-	-	-	-	-	-	-	-
	rho	-	-	-	-	-	-	-	-	-	-
Shannon diversity	p	3.45E-06	-	-	-	-	-	-	-	-	-
	rho	5.85E-01	-	-	-	-	-	-	-	-	-
evenness	p	3.76E-02	2.20E-16	-	-	-	-	-	-	-	-
	rho	2.84E-01	9.27E-01	-	-	-	-	-	-	-	-
cover of Brachypodium pinnatum	p	ns	ns	ns	-	-	-	-	-	-	-
	rho	ns	ns	ns	-	-	-	-	-	-	-
cover of Bromus erectus	p	ns	ns	ns	2.95E-05	-	-	-	-	-	-
	rho	ns	ns	ns	-5.36E-01	-	-	-	-	-	-
cover of Helitrotrichon paeusta	p	ns	1.44E-02	2.67E-02	ns	ns	-	-	-	-	-
	rho	ns	3.31E-01	3.02E-01	ns	ns	-	-	-	-	-
number of valuable species	p	1.49E-03	5.60E-03	2.35E-02	ns	ns	2.07E-06	-	-	-	-
	rho	4.22E-01	3.72E-01	3.08E-01	ns	ns	5.95E-01	-	-	-	-
cover of valuable species	p	4.67E-02	5.65E-06	1.31E-06	5.74E-03	ns	ns	ns	-	-	-
	rho	-2.72E-01	-5.83E-01	-6.16E-01	3.71E-01	ns	ns	ns	-	-	-
cover of trees	p	ns	ns	ns	ns	ns	ns	ns	ns	-	-
	rho	ns	ns	ns	ns	ns	ns	ns	ns	-	-
cover of graminoids	p	2.20E-02	9.46E-08	2.78E-08	1.21E-02	ns	ns	ns	5.34E-05	ns	-
	rho	-3.11E-01	-6.69E-01	-6.91E-01	3.39E-01	ns	ns	ns	5.28E-01	ns	-
cover of shrubs	p	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	rho	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

III.4.2. Regression models

We built more than 700 models with the TRAINING dataset at the hypothesis generating phase. We gain 123 hypothesis to be validated ($p < 0.05$) on the TEST database, out of which 40 were proven to be significant. The rapid decrease in the number of significant effects warns us that even in large data sets the results depend highly on the input data thus validation of the results seems to be inevitable. In some cases we found the variable significant in both datasets, however, the direction of the effect was opposite in the TEST and TRAINING datasets. These cases are interpreted as non-valid. We do not interpret an effect either if the R^2 for the single model of the predictor (explanatory) variable was less than 0.01 (i.e. 1%).

III.4.2.1. Predictor variables without significant effects

Some tested potential predictor variables did not have significant effects on any of the response variables. In the following we list these variables starting from the 'patch variables' and we give a possible explanation for the lack of effect.

Many of the 'patch attributes' did not have effect on the response variables. From the soil parameters some particle size classes, mainly the ones from the middle size classes did not have significant effect on any of the response variables. Most probably these particle size classes are the most frequent and thus most plants are adapted to them. However, the smallest and the largest particle size classes did have significant effects which are described below.

According to our analysis, actual species richness, diversity and composition of semi-dry grasslands are not determined by local geographical attributes such as 'size of the grassland patch', 'exposition' and 'slope angle' either. These unexpected results suggest that the effects of wider landscape, the former and resent land use are more important factors in the determination of species richness and diversity of Hungarian semi-dry grasslands.

Potential dispersal attributes also did not have significant effects. These attributes – variables 'potential dispersal of the grassland species' and 'potential dispersal of the grassland patch' were documented since we think that these kinds of attributes are important and must have effects on actual species richness, however, in the present survey both of them were documented based on expert judgement and without sound knowledge on the real dispersal abilities of species per se and due to the configuration of the landscape.

Recent land use did not have significant effect on any of the response variables. This contradicts to the findings of some authors (Hurst & John 1999, Mitchley & Xofis 2005, Klimek et al. 2007). The reason for this can be twofold: in Hungary in our days only very few semi-dry grasslands are managed at all, which means that the database contained too few data on management which could result in non-significance. Another reason could be that the documentation of management of semi-dry grasslands meets many difficulties in this sampling design which is based on a single visit of a grassland patch. In many cases it is difficult to notice the traces of management, especially if it does not occur in each year. Most probably this was the reason why we could not detect significant effect of the threatening factor 'too low intensity of land use' and 'presence of any preserving factors'.

Usually a few variables had significant effect from the variable groups of the 'landscape attributes'. Some climatic variables, though, did not have effect on any of the response variables either (BIO1 = Annual Mean Temperature, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO13 = Precipitation of Wettest Month, BIO16 = Precipitation of Wettest Quarter, BIO18 = Precipitation of Warmest Quarter).

Former landcover types of the maps of the Military Surveys did not affect any predictor variables. The reason for this is can be manifold, possible explanations are the too coarse spatial and thematic resolution of the original mapping (Biró 2006) and the inadequate localisation of sampling sites on the old maps due to difficulties in the transformation of differing coordinate systems. Another reason can be the fact that since the last survey already 100-120 years passed, during which many changes happened in the landscape structure which could wipe out the effects of the former land cover types.

From the attributes used to describe the wider landscape context the variables 'area of fallow lands', 'area covered by invasive species' and 'total area of semi-natural habitat types' did not have significant effects on any of the response variables. This contradicts to the findings reported in the literature (Dauber et al. 2003) and even with our own results of the analysis of naturalness of semi-dry grasslands at landscape scale (Illyés et al. 2008). The reason for this can be a much coarser resolution of the data of the MÉTA database used for this analysis. However, it contradicts to the fact that other landscape attributes had significant effects. Another reason can be that the data derived from the MÉTA database belong to a 35 ha hexagon. The joining of the coordinates of the sampling sites and the hexagon could result in such a situation where a particular sampling site is located on a very edge of the hexagon and thus data from the adjoining hexagon would be more adequate for it, nevertheless this explanation is relevant to the other wider landscape attributes as well.

III.4.2.2. Response variables without predictors

Some of the response variables were not determined significantly by any predictor variables involved in the analysis. Response variables 'evenness', 'cover of *Brachypodium pinnatum*', 'cover of *Helictotrichon praeusta*', 'cover of shrubs' and 'cover of trees' were not affected by any predictors. However, it only means that the particular predictor variables chosen for the analysis did not explain the variation of these response variables.

In the case of the 'cover of *Brachypodium pinnatum*' this result is unexpected. According to our field experience and the literature (Bobbink & Willems 1987, Hurst & John 1999), we expected that extremely high cover of this dominant grass species is explained by climatic attributes and attributes which describe the former and recent land use. The independence of the cover of *Brachypodium* in the studied semi-dry grasslands, however, seems to indicate that the dominance of this grass species is not determined by a single factor but most probably by a combination of many effects the importance of which is different from site to site and therefore is provable by the used model building and testing procedure.

In the dataset there were only a few samples of semi-dry grasslands with the dominance of *Helictotrichon praeusta*, which can be the reason for the lack of significant relationships. However, the correlation analysis revealed that to stands rich in *Helictotrichon praeusta* valuable species are positively associated. This suggests that stands dominated by *Helictotrichon praeusta* are very important from conservation point of view, however the background reasons and mechanisms are hidden. Further study of this kind of stands is needed in the future in order to gain better understanding on the preference of valuable species.

The cover of trees and shrubs was not affected by any predictor variables involved in our analysis. A possible reason for this can be the sampling bias already mentioned above, namely that plots were placed in a way that shrub and tree individuals were underrepresented. Another explanation is that there are many different factors which affect the cover of trees and shrubs and the importance of them change site to site and thus every situation is a unique one impossible to generalise. Lack of significant relationship, however, is a bit disappointing since shrub encroachment is the most striking threatening factor of Hungarian semi-dry grasslands (Illyés & Bölöni 2007, Seregélyes et al. 2008). We hoped to find factors affecting the cover of shrubs since the identification of some single factors would help the task of conservation practice considerably. However, what is even more disappointing is that at this point we have no suggestion where to continue with the identification of factors affecting the cover of shrubs.

III.4.2.3. Number of species in the plots

According to our analysis, species number of semi-dry grasslands in Hungary is affected by many different kinds of factors (Table 10). Both ‘patch attributes’ and ‘landscape attributes’ affected species richness.

Variance in number of species is in the first place explained by geographical location, which explained 35% of variance. Other factors which explain relatively high amount, around 10% of variation are ‘patch parameters’ among which there are soil parameters (carbonate content, pH, humus content), local neighbourhood, disturbance by animals and elevation. Soil parameters are reported to have high impact on both species richness and species composition of grasslands (Sebastiá 2004, Löbel et al. 2006, Klimek et al. 2007). In our analysis humus and carbonate content positively affected species number, while pH had negative effect. We found these predictor variables to be relatively important, explaining more than 10% of the variation in species richness. Particle size distribution of the soil also influenced species number. Coarse particle class (0.25-0.05 mm particles) which corresponds to the sand fraction affected species number negatively, while smooth particle sizes corresponding to clay (0.01-0.005) and loam (0.005-0.002 mm particles) positively. However, the importance of these factors was lower. Elevation also had positive effect on species number and explained 11% of variance of species richness. Local neighbourhood affected species richness significantly, number of neighbours had positive effect with 11% importance. Landscape neighbourhood was also found to affect species number which is in agreement with the literature (Devictor & Jiguet 2007, Löbel et al. 2006). Number of habitat types, which can be understood as a kind of landscape heterogeneity and summed area of dry forests and every kind of forests and shrublands affected species number positively, while the total area of wet grasslands and marshes had negative effects. This corresponds well with our previous findings based on the analysis of the MÉTA database (Illyés et al. 2008), namely that the number and cover of semi-natural habitat types as well as the presence of dry oak forests affect naturalness positively. However, by the analysis of the MÉTA database the negative effect of marshes and wet grasslands was not detected (Illyés et al. 2008). The importance of the single variables describing landscape neighbourhood in the present analysis ranged between 3.4-11%, which corresponds to the variation explained by patch parameters.

Disturbance by animals affected species number positively and the importance of this factor was the highest among the significant ones (13.7%) as well. According to our results, besides geographical position species number of semi-dry grasslands is best predicted by animal disturbance at least on the scale of few square meters.

Climatic variables referring to precipitation positively affected species number, however, their importance was low, 1-3%. Temperature seasonality had negative effect and explained 4.8% of variance in species number.

The overlap between the geographical position and the other factors ranged between 0.3 and 10 % which is considered to be moderate. Unexplained variation remained around 60% for most of the model which is usual in these kind of studies (Dauber et al. 2003, Barbaro et al. 2007, Klimek et al. 2007). It is interesting that the model containing disturbance by animals explained the most of the variation, 48% and the overlap between the geographical location and disturbance by animals is the lowest (0.01%).

III.4.2.4. Shannon diversity

Interestingly enough, Shannon diversity was not affected by geographical location of the sample nor by most of the factors which affected the species number of the plot. Our analysis showed that Shannon diversity of Hungarian semi-dry grasslands is only affected by disturbance by animals (Table 11). It had positive effect with an importance of 10%. Again, we have to note that diversity is scale-dependent, and our results are relevant only to the scale of few square meters. Interestingly, this result is independent from the location of the sample.

III.4.2.5. Cover of *Bromus erectus*

The cover of *Bromus erectus* was significantly affected by geographical position (Table 12). Location of the sample explained 29% of the variation which is rather high. Among soil variables only the carbonate content affected the cover of *Bromus erectus*, it had positive effect and explained 9% of the variation. Structural parameter “denseness” affected the cover of *Bromus erectus* negatively but it explained only 4%. Among the attributes describing landscape neighbourhood only the area of semi-dry grasslands in the landscape had significant effect, it was positive, however, and the importance of this factor was only 3%. The overlap between the geographical position and the landscape attributes is the highest, 8%, which is considered to be low. The unexplained variation ranged between 63,5-67%.

III.4.2.6. Number of valuable species

The geographical position of the sample site affected the number of valuable species in the plot significantly, it explained 34% of variation which is high (Table 13). Structural attributes of the stand highly affected the number of valuable species. Both minimum and maximum height of the stand affected the number of valuable species positively (most probably different species were confined to low- and to high-growing stands), however, minimum height explained only 2% while maximum height explained 12%. Depth of the litter layer also had positive effects, which contradicts somewhat with the findings reported in the literature (Löbel et al. 2006), nevertheless, it explained less than 2%. Denseness affected the number of valuable species positively with importance of 25% which is high. Disturbance by animals also had positive effect, albeit with low importance of 4%. Besides the patch attributes, only climatic variables affected the number of valuable species. Temperature seasonality and mean temperature of the wettest quarter had negative effects while precipitation seasonality had positive effect. The importance of the climatic factors ranged from 3 to 8%, which is low. Unexplained variation ranged between 49-65%.

III.4.2.7. Cover of valuable species

Geographical location was found to affect cover of valuable species significantly and it explained 29% of variation (Table 14). The only variable which was found to have significant effect besides geographical location was conductivity of the soil which had negative effect with 10% importance. The unexplained variation for the model with this factor was 65, 9%.

III.4.2.8. Cover of graminoids

Geographical location had significant effects on the cover of graminoids as well, the importance of this factor was 41% (Table 15). Besides geographical location, only disturbance by animals was found to have significant effects. The effect was negative, however, explained only 1% of variance. Unexplained variation for this model remained 59%.

Table 10. Significant relationships for the response variable 'number of species in the plot'. Results of the GL models built for one explanatory variable. Geographical position (geo) itself had significant effect as well and thus it was incorporated in all of the models as a covariable. Variance partitioning of the effect of geo and the other factor was performed as well.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	un-explained
	Geographical location		0.0000	-	-	0.36	-	-	-	-
Patch attributes	Soil parameters	weight of stone pieces (m/m %)	0.0238	pos	0.36	0.05	0.31	0.00	0.04	0.64
		carbonate content (%)	0.0242	pos	0.36	0.12	0.24	0.00	0.12	0.64
		humus content (%)	0.0149	pos	0.38	0.13	0.25	0.02	0.11	0.62
		pH	0.0229	neg	0.36	0.10	0.25	0.00	0.10	0.64
		0.25-0.05 mm granules (m/m%)	0.0118	neg	0.39	0.03	0.35	0.03	0.00	0.62
		0.005-0.002 mm granules (m/m%)	0.0110	pos	0.39	0.09	0.29	0.03	0.06	0.61
		<0.002 mm granules (m/m%)	0.0235	pos	0.36	0.03	0.33	0.00	0.03	0.64
	Local geographical attributes	elevation	0.0135	pos	0.38	0.11	0.27	0.02	0.09	0.62
	Local neighbourhood	number of neighbouring habitat types with positive effects	0.0197	pos	0.36	0.11	0.25	0.01	0.11	0.64
	Treathening factors	disturbance by animals	0.0007	pos	0.48	0.14	0.34	0.12	0.01	0.52
Landscape attributes	Climatic data	temperature seasonality (standard deviation *100)	0.0235	neg	0.36	0.05	0.31	0.00	0.05	0.64
		annual precipitation	0.0079	pos	0.40	0.01	0.39	0.04	-0.03	0.60
		precipitation of driest month	0.0027	pos	0.44	0.02	0.42	0.08	-0.06	0.56
		precipitation of coldest quarter	0.0013	pos	0.46	0.03	0.43	0.11	-0.07	0.54
	Landscape neighbourhood	number of habitat types	0.0194	pos	0.37	0.03	0.33	0.01	0.03	0.63
		summed area of dry forests	0.0226	pos	0.36	0.07	0.28	0.00	0.07	0.64
		summed area of wet grasslands and marshes	0.0218	neg	0.36	0.04	0.32	0.00	0.03	0.64
		summed area of forests and shrublands	0.0238	pos	0.36	0.09	0.27	0.00	0.09	0.64

Table 11. Significant relationships for the response variable 'Shannon diversity'. Results of the GL models built for one explanatory variable.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	unexplained
geographical location			ns	ns	-	-	-	-	-	-
Patch attributes	treathening factors	disturbance by animals	0.0157	pos	-	0.11	-	-	-	-

Table 12. Significant relationships for the response variable 'cover of *Bromus erectus*'. Results of the GL models built for one explanatory variable. Geographical position (geo) itself had significant effect as well and thus it was incorporated in all of the models as a covariable. Variance partitioning of the effect of geo and the other factor was performed as well.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	unexplained
geographical location			0.0000	-	-	0.29	-	-	-	-
Patch attributes	Soil parameters	carbonate content (%)	0.0195	pos	0.37	0.10	0.27	0.08	0.02	0.64
	Structural attributes	denseness	0.0367	neg	0.34	0.05	0.28	0.05	0.01	0.66
Landscape attributes	Landscape neighbourhood	area of the semi-dry grasslands (H4)	0.0446	pos	0.33	0.12	0.21	0.04	0.08	0.67

Table 13. Significant relationships for the response variable ‘number of valuable species’. Results of the GL models built for one explanatory variable. Geographical position (geo) itself had significant effect as well and thus it was incorporated in all of the models as a covariable. Variance partitioning of the effect of geo and the other factor was performed as well.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	unexplained
geographical location			0.0013	-	-	0.35	-	-	-	-
Patch attributes	Structural attributes	minimum height of the stand (cm)	0.0285	pos	0.35	0.02	0.33	0.00	0.02	0.65
		maximum height of the stand (cm)	0.0018	pos	0.45	0.12	0.33	0.10	0.02	0.55
		deepness of the litter layer (cm)	0.0186	pos	0.37	0.019	0.35	0.02	0.00	0.63
		Denseness	0.0003	pos	0.50	0.26	0.24	0.15	0.10	0.50
	Treathening factors	disturbance by animals	0.0204	pos	0.36	0.04	0.32	0.016	0.03	0.64
Landscape attributes	Climatic data	temperature seasonality (standard deviation *100)	0.0184	neg	0.37	0.08	0.29	0.02	0.06	0.63
		mean temperature of wettest quarter	0.0216	neg	0.36	0.06	0.30	0.01	0.05	0.64
		precipitation seasonality (coefficient of variation)	0.0270	pos	0.35	0.03	0.31	0.00	0.03	0.65

Table 14. Significant relationships for the response variable 'cover of valuable species'. Results of the GL models built for one explanatory variable. Geographical position (geo) itself had significant effect as well was and thus it was incorporated in all of the models as a covariable. Variance partitioning of the effect of geo and the other factor was performed as well.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	unexplained
geographical location			0.0051	-	-	0.29	-	-	-	-
Patch attributes	Soil paramaters	conductivity	0.0341	neg	0.34	0.10	0.24	0.05	0.05	0.66

Table 15. Significant relationships for the response variable 'cover of graminoids'. Results of the GL models built for one explanatory variable. Geographical position (geo) itself had significant effect as well was and thus it was incorporated in all of the models as a covariable. Variance partitioning of the effect of geo and the other factor was performed as well.

			p value	direction	R^2 geo + factor	R^2 factor	pure effect of geo	pure effect of factor	overlap	unexplained
geographical location			0.0496	-	-	0.41	-	-	-	-
Patch attributes	Land use and threathening factors	disturbance by animals	0.0055	neg	0.41	0.01	0.40	0.00	0.01	0.59

Table 16. Summary of significant relationships found for the response variables with GL models. Significant effect of the geographical location is indicated by asterics. The directions of the effects are given.

			number of species in the plot	**Shannon diversity**	**cover of *Bromus erectus***	**number of valuable species**	**cover of valuable species**	**cover of graminoids**
Geographical location			**	ns	**	**	**	**
			direction of the effect					
Patch attributes	Soil parameters	weight of stone pieces (m/m %)	pos	-	-	-	-	-
		carbonate content (%)	pos	-	pos	-	-	-
		humus content (%)	pos	-	-	-	-	-
		conductivity	-	-	-	-	neg	-
		pH	neg	-	-	-	-	-
		0.25-0.05 mm granules (m/m%)	neg	-	-	-	-	-
		0.005-0.002 mm granules (m/m%)	pos	-	-	-	-	-
		<0.002 mm granules (m/m%)	pos	-	-	-	-	-
	Structural attributes	denseness	-	-	neg	pos	-	-
		minimum height of the stand (cm)	-	-	-	pos	-	-
		maximum height of the stand (cm)	-	-	-	pos	-	-
		deepness of the litter layer (cm)	-	-	-	pos	-	-
	Local geographical attributes	elevation	pos	-	-	-	-	-
	Local neighbourhood	number of neighbouring habitat types with positive effects	pos	-	-	-	-	-

	Treathening factors	disturbance by animals	pos	pos	-	pos	-	neg
Landscape attributes	Climatic data	temperature seasonality (standard deviation *100)	neg	-	-	neg	-	-
		mean temperature of wettest quarter	-	-	-	neg	-	-
		precipitation seasonality (coefficient of variation)	-	-	-	pos	-	-
		annual precipitation	pos	-	-	-	-	-
		precipitation of driest month	pos	-	-	-	-	-
		precipitation of coldest quarter	pos	-	-	-	-	-
	Landscape neighbourhood	area of semi-dry grasslands	-	-	pos	-	-	-
		number of habitat types	pos	-	-	-	-	-
		summed area of dry forests	pos	-	-	-	-	-
		summed area of wet grasslands and marshes	neg	-	-	-	-	-
		summed area of forests and shrublands	pos	-	-	-	-	-

IV. Discussion

IV. 1. Variation in species composition of Central European Brachypodium pinnatum and Bromus erectus dominated semi-dry grasslands

The training-and-test validation method used in the present study is one possibility for the critical interpretation of clusters resulting from numerical classification. The fact that about half of the relevés of both the TRAINING an TEST data sets belonged to clusters which were not identified by the same analysis of a very similar data set clearly demonstrates that results from the numerical analyses, even those based on large data sets, should be interpreted with caution. Classifications optained by numerical procedures may contain both robust clusters, which will be frequently recovered by other analyses in other data sets, and weak clusters, which are specific to the given classification of the given data set. Training-and-test validation seems to be a promising approach to discriminate between robust clusters, i.e. good candidates for obtaining the status of a formal syntaxon and being included in syntaxonomic overviews, and weak clusters with limited validity. Most of the valid clusters in our analysis had smaller geographic ranges and more diagnostic species than the non-valid clusters (Table 1.). This suggests that Central European semi-dry grasslands consist of a few geographically restricted types with ecologically specialized species, and other types, which mainly contain generalist species and have rather uniform species composition across large areas. Syntaxa are usually defined so as to include vegetation stands rich in specialized species, while the stands composed mainly of generalist species are often not considered in syntaxonomical systems, even if they cover large areas (Kopecký & Hejný 1978). Some attempts were made to include vegetation types without specialist species into the syntaxonomical systems by giving them a separate status of basal or derivative communities (Kopecký & Hejný 1978) or central syntaxa (Dierschke 1981). Our trial with the training-and-test validation of numerical classification suggests that such vegetation types are hardly robust due to the absence of specialist species, i.e. due to the lack of discrimination criteria against other vegetation types. If such vegetation types are included in syntaxonomic systems, they should preferably be broadly delimited, while locally restricted syntaxa that lack specialist species should better be avoided.

IV. 2. Variation in species composition of Hungarian semi-dry grasslands

Sound interpretation of clusters in syntaxonomical terms is difficult, due to the selection criteria (at least 10% cover of particular species) used. (However, we preferred to use consistent and repeatable selection techniques.) Moreover, the fact that we only analyzed the semi-dry grasslands and not all vegetation types of Hungary causes that the species which show fidelity to the clusters in our analysis are not character species in the classical syntaxonomical sense; rather they are differential species (Botta-Dukát & Borhidi 1999), which delimit the particular cluster from the others of the current dataset. Some of these species are even not typical species of semi-dry grasslands but are characteristic of special site conditions (e.g. *Sedum sexangulare* indicates stoniness in Cluster E) or to a geographical locality (e.g. *Primula elatior* is a very rare species and one of its localities was represented by some relevés of Cluster D).

Nevertheless, in order to make our results comparable to the former classifications of semi-dry grasslands in Hungary and to the recently revised systems of grassland vegetation in the surrounding countries, we review the literature regarding each cluster and besides the description for all clusters. We shall give syntaxonomical interpretation, wherever it is possible, and assign our clusters to described associations or proposed new associations when it is necessary (Illyés et al. 2009).

IV.2.1. Syntaxonomical interpretation of the clusters

The results of our clustering revealed a distinct semi-dry grassland type with central-Pannonian range (clusters A, B and C), characterised by many Pontic-Pannonian species like *Euphorbia glareosa*, *Chamaecytisus austriacus*, *Viola ambigua* and dominated mostly by *Brachypodium pinnatum* and sometimes by *Bromus erectus*. Based on the relevés sampled in a loess valley of the Mezőföld region, Bauer et al. (2001) note that those stands are not identical to any *Brachypodium pinnatum* association described from Hungary, thus the stands seem to represent a new association. Independently from this work, Horváth (2000, 2002, 2009) described a new type of *Brachypodium pinnatum* grassland from the central part of Mezőföld, which is extremely rich in Pontic-Pannonian species, and proposed the name *Euphorbio pannonicae-Brachypodietum*. However, in the previous papers of Horváth (2000, 2002) there was no valid description of the new association, since there was no table of relevés nor a holotype selected (see Weber et al. 2000). Recently Horváth (2009) compiled a new paper with the description and validation of the *Euphorbio pannonicae-Brachypodietum* association. Nevertheless, prior to these two publications, the way these kinds of grasslands were referred to was arbitrary. They were often mentioned as loess steppes or meadow steppes in oral communication among Hungarian botanists, sometimes even incorrectly specified as *Salvio-Festucetum rupicolae* Zólyomi ex Soó 1964, which is in fact a species-rich loess steppe dominated by narrow-leaved grasses (mainly *Festuca rupicola*, *F. valesiaca* and *Stipa capillata*). We consider clusters A and B equivalent to the *Euphorbio pannonicae-Brachypodietum* Horváth 2009 (*Euphorbia pannonica* = *E. glareosa*). According to Horváth (2002, 2009) this association is characterised by a dense, multi-layered structure, consists of broad-leaved graminoids and forbs and it is dominated by *Brachypodium pinnatum*. *Festuca rupicola*, *Salvia pratensis* and *Euphorbia glareosa* also reach high cover in the stands. Species shared with open oak woodlands (e.g. *Tanacetum corymbosum*, *Anthericum ramosum*, *Anemone sylvestris*, *Peucedanum cervaria*, *Campanula bononiensis*, *Ranunculus polyanthemos*, *Trifolium alpestre*) occur frequently in the stands. Although Clusters A, B and C show many similarities with *Polygalo majoris-Brachypodietum* (especially Cluster C) as well, based on the presence of many Pontic-Pannonian species, and the lack or low frequency of the characteristic species of *Polygalo majoris-Brachypodietum* (*Scorzonera hispanica*, *Onobrychis arenaria*, *Cirsium pannonicum* according to Wagner 1941), we agree with Horváth (2002, 2009) and recommend to distinguish this cluster as a separate association. We present 10 sample relevés of *Euphorbio pannonicae-Brachypodietum* in the file 'sample_releves.xls' on the CD attached to the thesis in order to give an impression for the readers on this association.

Cluster C shows transitional character towards *Polygalo majoris-Brachypodietum* Wagner 1941. The assignment of these relevés to any association, however, is questionable since all relevés are from the same locality and made by the same author.

Semi-dry grasslands of the Bükk Mountains are represented by cluster D in our analysis. These grasslands were intensively studied (Schmotzer & Vojtkó 1996, 1997, Vojtkó 1998) due to their high species richness and unique floristic composition. They were described as *Polygalo majoris-Brachypodietum* (Schmotzer & Vojtkó 1996, 1997, Vojtkó 1998). Their sites are considered secondary and the differences in the species composition among the stands are thought to be the consequence of the originally differing species composition of the distinct oak forest patches they were derived from. We are not totally convinced that the stands of Cluster D belong to the *Polygalo majoris-Brachypodietum* since the species composition of the relevés in this cluster differ considerably from the original description by Wagner (1941), and several characteristic species are missing (*Scorzonera hispanica*, *Seseli annuum*, *Onobrychis arenaria*, *Galium glaucum*) or are present only with low frequency (e.g. *Hypochaeris maculata*). Nevertheless, we should not conceal that all of the relevés from the Bükk Mountains in the dataset and from this cluster were made by the same authors (A. Schmotzer & A. Vojtkó), and subjective preference of valuable species at sampling sites is shown by the extremely high frequency of them (*Asperula cynanchica*, *Cirsium pannonicum*, *Dianthus pontederae*, *Geranium sanguineum*, *Polygala major*). Nevertheless, we have to admit as well that the Bükk Mountains are very rich in semi-dry grasslands and from the higher altitudes we have only a few relevés, which do not represent the area well. On the other hand, species composition of the stands shows considerable similarities to *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 (Chytrý et al. 2007, Janišová et al. 2007). This association is described from the White Carpathians, a mountain range at the border of the Czech and Slovak Republic, but the ecological conditions in the Bükk Mountains could be very similar. Taking all these facts into consideration, we suggest a consensus solution that the relevés of Cluster D represent the *Polygalo majoris-Brachypodietum* Wagner 1941. Further studies of the semi-dry grasslands of the higher altitudes of the Bükk Mountains may support this idea. Sample relevés of this association are presented in the file 'sample_releves.xls' on the CD attached to the thesis.

In spite of the fact that the *Bromus erectus* dominated Cluster E shows some similarities to the *Bromion erecti* alliance, especially if one reads the description of the latter in Borhidi (2003) and not in other sources (e.g. Mucina & Kolbek 1993), Cluster E lacks the typical meadow and atlantic species of the alliance. In our opinion, Cluster E cannot be identified as a member of the tall mown meadows of *Onobrychido viciaefoliae-Brometum erecti* or as *Carlino acaulis-*

Brometum because of the lack of mesophilous species and the presence of drought-adapted species (*Acinos arvenis, Sanguisorba minor*, *Teucrium chamaedrys, Thymus odoratissimus*). Moreover, the soils of these stands are not deep but shallow and rocky. Semi-dry grasslands of the Dunántúli-középhegység have been hardly studied so far (or at least the results have not been published yet). Isépy (1998) suggested – based on his own relevés and on the work of Debreczy (1966) – that the "*Xerobrometum*-like" *Bromus erectus* dominated grasslands of this part of the country developed in place of former *Quercus pubescens*-*Q*. *cerris* forests, and therefore they should be dealt together. He also proposed the name *"Lathyro pannonici-Brometum erecti"* based on a synthetic table of 10 relevés (Isépy 1998); however, this is not a valid publication, since it does not contain original relevés. Moreover, the study of Isépy (1998) covers a small area of the Dunántúli-középhegység. Nevertheless, we agree to separate these grasslands as a distinct association. However, connections to and distinctions from *Festucion valesiacae* and *Bromo pannonici-Festucion pallentis* need to be revealed in the future. This cluster shows considerable similarities to the description of *Onobrychido viciifoliae-Brometum erecti* T. Müller 1966 in Janišová et al. (2007). However, it differs considerably from the description of the same association in the Hungarian syntaxonomical textbooks (Borhidi & Sánta 1999, Borhidi 2003). We proposed a new association with the name *Sanguisorbo minoris-Brometum* Illyés, Bauer et Botta-Dukát 2009 (Illyés et al. 2009), since the name proposed by Isépy (1998) is less adequate due to the absence of *Lathyrus pannonicus* from most of the sampled grassland sites (Weber et al. 2000). Sample relevés of this new association are presented in the file 'sample_releves.xls'on the CD attached to the thesis.

Cluster F is characterised by the presence and dominance of *Danthonia alpina*. In the syntaxonomical literature regarding the territory of Hungary, there are only a few references to this species, while no relevés or association names have been published for stands dominated or co-dominated by this species. *Danthonia alpina* is known to occur frequently and even to dominate in places (Varga & Varga-Sipos 1999, p. 52) in semi-dry grasslands of Hungary, which is not the case in other countries (Chytrý 2007, Janišová et al. 2007). A recent study of *Danthonia alpina* grasslands in the Carpathian Basin and its surroundings (Kovács 2008) revealed that *Danthonia alpina* dominated stands belong to several alliances and associations, namely to the *Cirsio pannonici-Brachypodion pinnati*, *Danthonio-Brachypodion* Boşcaiu 1972, *Danthonio-Brachypodietum pinnati* Soó (1946) 1947, *Danthonio alpinae-Stipetosum stenophyllae* Ghisa 1941 and *Danthonio-Chrysopogonetum grylli* Boşcaiu (1970) 1972. Sanda (2002) gives constant species and localities of these associations in Romania. The geographical ranges of these alliances include Hungary, parts of Romanian Transylvania, and the Balkan Peninsula. A comprehensive international study of the *Danthonia alpina* grasslands is needed in the future with special focus on the Balkan and East-Carpathian areas. Nevertheless, finally we proposed a new association for the relevés of Cluster F with the name *Trifolio medii-Brachypodietum pinnati* Illyés, Bauer et Botta-Dukát 2009 (Illyés et al. 2009). Sample relevés of this new association are presented in the file 'sample_releves.xls'on the CD attached to the thesis.

Stands of transitional character between alliances or stands which are undergoing succession always make the interpretation of classification results loose and subjective. In our case, the relevés of Cluster G are considered to be transitions to mesophilous meadows according both to their species pool and site conditions. We know from field experience that many relevés of Cluster G represent relatively young stands or recently abandoned ones. We think that at present it is not feasible to name this cluster as an association especially without an extended analysis considering *Molinio-Arrhenatheretea*.

IV.2.2. A proposed new syntaxonomic system for Hungarian semi-dry grasslands

Since there was no detailed analysis of the Hungarian semi-dry grassland vegetation prior to our work, the recently published synopsis of Hungarian plant associations (Borhidi 2003) was still based on small-scale or local studies in case of semi-dry grasslands. The results of the numerical analysis with large amount of data enabled us to propose a new system for semi-dry grasslands (Illyés et al. 2009), which brings considerable, yet expected changes. We propose the following system for the Hungarian semi-dry grasslands (originally published in Illyés et al. 2009):

Order: *Brometalia erecti* Br.-Bl. 1936
  Alliance: *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951
   Association:
    (1a) *Polygalo majoris-Brachypodietum* Wagner 1941

(1b) *Euphorbio pannonicae-Brachypodietum* Horváth 2009

(1c) *Sanguisorbo minoris-Brometum erecti* Illyés, Bauer et Botta-Dukát 2009

(1d) *Trifolio medii-Brachypodietum pinnati* Illyés, Bauer et Botta-Dukát 2009

As it was revealed by the previous analysis at a larger scale (Illyés et al. 2007a) and earlier recognized by Soó (1973), most probably, there are no stands of *Bromion erecti* in Hungary. Our analysis of the current extended dataset supports this finding. Therefore, we agree with Varga (1997) that all of the semi-dry grasslands of Hungary belong to the *Cirsio-Brachypodion* alliance and thus none of the relevés in this analysis belongs to the associations *Onobrychido viciifoliae-Brometum erecti* T. Müller 1966 or *Carlino acaulis-Brometum* Oberdorfer 1957.

The concept of associations *Lino tenuifolio-Brachypodietum pinnati* (Dostál 1933) Soó 1971, *Hypochoerido-Brachypodietum pinnati* Less 1991 and *Poo badensis-Caricetum montanae* V. Sipos & Varga 1996 listed in Borhidi (2003) could not be supported by this analysis. Here we have to add that we met difficulties in documentation of these associations even during sampling, although localities given in the literature (Less 1991, Varga-Sipos & Varga 1998) were re-visited and sampled. In the case of *Hypochoerido-Brachypodietum pinnati* Less 1991 we were unable to find any grassland in the area mentioned in the original publication. In our opinion, the description of these stands as separate associations should be rejected, since there are no published tables which would serve as a sound basis for comparison and the repeatability of their species composition is rather questionable since none of them could be convincingly documented.

IV.2.3. Non-valid clusters

There were 140 relevés (24.2%) which could not have been assigned to any of the valid clusters. This ratio is not high compared to the previous analysis at a larger scale where it was around 50% (Illyés et al. 2007a). The non-valid clusters comprise relevés from rather small, isolated areas, the species composition of which is very unique. These stands seem to have developed under unique site conditions (mesoclimate, soil properties, and surrounding vegetation types) with special management history, so there is only a little chance that a similar species composition occurs in any other place which is a requirement for validity in this sense. We recommend interpreting these relevés on the level of alliance *Cirsio-Brachypodion pinnati* (compare with the deductive approach of Kopecký & Hejný 1974), together with stands under successional processes represented in our analysis by cluster G.

IV.3. Analysis of the factors affecting the naturalness based quality of semi-dry grasslands in Hungary at landscape level

IV.3.1. General conclusions

Our results are in correspondence with the literature, namely that the naturalness of the model habitat – as a qualitative measure of the habitat – depends upon intra-habitat attributes (size, land use type) and both structural and compositional matrix variables (Barbaro et al. 2007), i.e. the landscape surrounding the habitat (other habitat types in the vicinity, connectedness, overall area of the (semi-)natural habitats in the sampling unit), as it has been stated by many authors (Duelli 1997, Wagner et al. 2000, Söderström et al. 2001, Campagne et al. 2006, Devictor & Jiguet 2007, Raatikainen et al. 2007).

Factors reflecting management (and threats) were found to have significant effects on naturalness (see Campagne et al. 2007, Klimek et al. 2007), as well as factors reflecting landscape structure (see Barbaro et al. 2007). Intra-patch factors – i.e. factors that characterise the habitat patch itself – seem to have smaller effects in the case of highly fragmented semi-dry grasslands according to our analysis based on the MÉTA database. This indicates the increased impact of the surrounding landscape on fragmented grassland patches. In the case of fragmented grasslands in particular, the habitat quality can be even more affected by the landscape context than the patch itself. Consequently, for effective conservation of Hungarian semi-dry grasslands it is not enough to focus on the grassland patch, but the effects of the surrounding landscape should be considered as well, and potential negative factors need to be identified and managed to be able to conserve the quality of the habitat patch.

Nevertheless, it has to be mentioned that our analysis is restricted to only one scale, namely the 35 ha hexagons of the MÉTA project. The results are only valid at this scale, because it is generally accepted that ecological processes act on different levels and factors determining habitat quality are expected to differ with spatial scales (Raatikainen et al. 2007, Barbaro et al. 2007).

IV.3.2. Conclusions concerning the Hungarian semi-dry grasslands

Most of the factors determining the naturalness of Hungarian semi-dry grasslands according to our analysis based on the MÉTA-database are matrix variables and not the attributes of the specific habitat type, which is reflected in their proportions and their overall effects as well. One of the main determining factors of a high naturalness value was a form of landscape diversity – the number of habitat types within the cell. This corresponds well with the findings that landscape diversity enhances biodiversity (Wagner et al. 2000, Honnay et al. 2003, Celesti-Grapow et al. 2006, but see Dauber et al. 2003, Moreno-Rueda & Pizarro 2007), and that the habitat composition of the surrounding matrix may influence patch habitat quality (Barbaro et al. 2007). The fact that the presence of termophilous oak woodlands indicates higher naturalness reflects that forest steppe meadows originally occurred in forest-steppe-like foothill landscapes (current lack of forests is due to human impact in most cases) (Fekete et al. 1998), and often form mosaic patterns with open oak forests and other dry grassland types (H3a, G2), often on rocky soils. On the forest fringes these habitats had a better chance to survive. The overall cover of (semi-)natural vegetation in the cell reflects a better landscape health status (Bertollo 2001), which corresponds well with the literature related to species richness (Dumotier et al. 2002, Paltto et al. 2006). The effect of invasive alien species is negative, which is quite well documented in the literature (Cronk & Fuller 2001, Botta-Dukát 2008b). Diffuse spatial pattern in the cell (for explanation see Molnár et al. 2007) indicates that the habitat type was maintained in small and rather isolated strips, which are most probably embedded in an agricultural landscape and are not wide or long enough to buffer the infiltration of chemicals. Fragmentation of the habitat is also reflected by the fact that matrix factors affect the naturalness twice as much as intra-patch attributes, possibly meaning that the patches are not large enough by themselves to hamper the landscape effects.

All of the significant variables together explained only 10.05 percent of the naturalness of the forest steppe meadows for two reasons. First, the habitat ‘forest steppe meadows’ comprises vegetation patches with different origin and former land use. Half of the stands are secondary and relatively young (10-80 years old), developed in abandoned fields, vineyards or after the canalisation of meadows (Mojzes 2003). Second, the diverse and high-quality stands of forest steppe meadows might not be determined by the factors surveyed in the MÉTA project, but rather by other environmental and historical factors like climate and land use history (Fekete et al. 1998, Mojzes 2003, Barbaro et al. *2007*).

IV. 4. Factors explaining the species richness, the diversity and other compositional and structural characteristics of semi-dry grasslands in Hungary at stand level

IV.4.1. Correlations between the dependent variables

IV.4.1.1. Species richness, diversity and valuable species

The fact that the variable 'number of valuable species' was positively correlated to the variables 'number of species ', 'Shannon diversity' and 'evenness' indicates that the list of the valuable species compiled by us does have significant conservation relevance. Further analysis and editing the list of valuable species are needed in the future to gain a more complete list of indicator species of Hungarian semi-dry grasslands. Using a list of indicator species for determining the conservation value of a stand is highly advised in conservation practice (Margules and Pressey 2000) since it is relatively quick and much less labour-intensive than relevé sampling. The monitoring of Natura2000 sites is planned to be based partly on the monitoring of indicator species. Prior to our analysis, indicator species of Hungarian semi-dry grasslands were identified purely by field experience and expert judgement. Our new analysis has an advantage of having statistical background.

At the same time, the result that variable 'cover of valuable species' was associated negatively to species richness and diversity and positively to the cover of graminoids warns us not to pay high attention to the cover of possible indicator species. To document the presence of a species is much easier and raises less methodological questions than the documentation of its cover. According to our results, for monitoring purposes and for inventories for conservation practice the documentation of presence/absence of the indicator species is recommended instead of relevé making.

IV.4.1.2. Cover of graminoids

Interestingly enough, we did not find negative correlation between the cover of *Brachypodium pinnatum* and species number, diversity and evenness, although, it is widely reported in the literature (Bobbink & Willems 1987, Hurst & John 1999, Willems 2001). In western Europe the cover of *Brachypodium pinnatum* is increasing due to the abandonment of traditional management and possibly due to nitrogen deposition from the air. This aggressively spreading species causes severe threat to species richness and diversity of calcareous grasslands (Bobbink & Willems 1987, Hurst & John 1999, Klimek et al. 2007). This effect of *Brachypodium pinnatum* could not be proven for Hungarian semi-dry grasslands by our analysis. Macroclimatic differences might be in the background of this, i.e. in the Pannonian region where Hungary lies the climate is more continental and the Sub-Mediterranean climatic effects are important in several parts of the country as well. This means that the yearly precipitation is much lower while the mean annual temperature is higher and especially the summers are much drier than in western Europe which might hinder the overdominance of *Brachypodium pinnatum*. Another reason could be that semi-dry grasslands in Hungary have been hardly ever fertilised which results in much lower fertility compared to western European sites. *Brachypodium pinnatum* otherwise is considered to be a character species of forest steppe vegetation complex the presence of which in a site is usually thought to indicate historical forest cover at the area of the site (Fekete et al. 1998, Fekete et al. 2000).

The cover of graminoids negatively affected species number and Shannon diversity as well, and it was positively correlated to the cover of *Brachypodium pinnatum*. This indicates that there is some competition between grasses and forbs, which is a general rule for grassland communities.

IV.4.2. Regression models

IV.4.2.1. Species richness (species number, diversity and evenness)

Species richness and diversity of semi-dry grasslands is reported in the literature to be affected by several factors. Patch attributes like habitat quality, soil characteristics, slope, angle and elevation are shown to have significant effects on species richness (Bennie et al. 2006, Löbel et al. 2006, Klimek et al. 2007). In some studies soil fertility and pH were found to be the most important determinants of species richness (Sebastiá 2004, Löbel et al. 2006¸ Raatikainen et al. 2007). Our results confirm the importance of soil characteristics in Hungarian semi-dry grasslands, however, there are considerable differences in comparison to the literature.

Other publications emphasise the role of the landscape characteristics surrounding the grassland patch, especially the proportion of grasslands and (semi-)natural habitat types or that of urban elements (Söderström et al. 2001, Mitchley and Xofis 2005, Wellstein et al. 2007). We found positive relationships between species richness and number of semi-natural habitat types and the area of forest and shrubland habitats. However, we could not detect the negative effect of the dominance of agricultural or urban elements in the landscape (Bobbink & Willems 1987, Dumortier et al. 2002, Mitchley and Xofis 2005, Devictor & Jiguet 2007).

Sometimes historical landscape configuration is even more important factor determining the species richness of a particular grassland patch than recent landscape configuration (Eriksson et al. 2002, Cousins 2006, Helm et al. 2006, Cousins et al. 2007). However, we could not prove any effect of historical landscape on the species richness of Hungarian semi-dry grasslands.

The effect of management is emphasised by many studies, sometimes even reported as the key factor determining species richness (Hurst & John 1999, Willems 2001, Klimek et al. 2007), nevertheless, others do not find management significant (Löbel et al. 2006). We could not find any connection with management in case of species richness either.

Raatikainen et al. (2007) investigated the effects of climatic variables on community composition and they found that temperature had significant effect while the effect of precipitation was non-significant. On the contrary, we found variables describing precipitation to have positive effects on species richness, while temperature seasonality had negative effects. Positive effect of precipitation is most probably explained by the fact that most of the characteristic species of semi-dry grasslands survive under dry conditions but rather favour moderately mesic situations.

Disturbance by animals was found to be one of the most important factors affecting positively the species richness in our analysis. Although, the high importance of small-scale disturbance in Hungarian semi-dry grasslands is surprising, the positive effect was not unexpected, since small-scale disturbance is known to be favourable for local species richness also from basic ecology and from field studies (Lavorel et al. 1994, 1998, Willems 2001, Wellstein et al. 2007). Since most of the Hungarian semi-dry grasslands have not been managed recently, the small-scale disturbance which is needed for the regeneration and turnover of short-lived and small-sized plants might only be provided by the activity of animals. Disturbance by small animals seems to be a key factor for Hungarian semi-dry grasslands though, since this was the only factor proven to have significant and positive effect on Shannon-diversity in our study.

Interestingly enough, despite the fact that shrub encroachment and the cessation of use are widely reported as main threats to semi-dry grasslands all over Europe as well as in Hungary (Willems 2001, Mitchley & Xofis 2005, Raatikainen et al. 2007, Illyés et al. 2007b, Seregélyes et al. 2008), recent studies do not take into account the possible effect of them (an experimental study is presented in Willems 2001). We included several threats to our analysis, on two spatial scales, at the scale of the vegetation samples and at landscape scale, however, we found no connection between species richness and threatening factors. One possible explanation of this can be the delayed response of grassland species to threats, thus the effect of the currently documented threat might be detectable only after a longer period of time.

To sum it up, determining the factors affecting species richness is an important task both from scientific and from conservation point of view, however, it seems that there are no general rules. Different factors were proven to be significant for different grassland types in different studies, and most probably this reflects the true situation. Our analysis revealed that the species richness of semi-dry grassland patches in Hungary are most probably determined by both patch and landscape attributes. These findings in general correspond with our previous results on the naturalness of Hungarian semi-dry grasslands (Illyés et al. 2008). Nevertheless, the potential predicting factors involved in the two analyses differed (e.g. we did not use climatic and soil data during the MÉTA survey), which hinders the direct comparison of the results. After all, it is worth to be noted that both of our studies are relevant to a particular spatial scale and since species richness is scale-dependent, the results only can be generalized with caution.

IV.4.2.2. The cover of dominant grasses and graminoids

The cover of *Brachypodium pinnatum* was not affected by any of the factors involved in our analysis, which was a rather unexpected result. For western-European calcareous grasslands, lack of management was found to be a highly important factor explaining the increased cover of *Brachypodium pinnatum* (Bobbink & Willems 1987, Hurst & John 1999, Mitchley & Xofis 2005). This is in accordance with our previous expectations based on the experience gained during the field survey. The reason for the lack of connections might be explained by the fact that stands of highly different dynamical state and of environmental condition were involved in our analysis. The samples included relatively young stands developed secondarily in abandoned ploughlands or vineyards and orchards as well as ancient grassland patches. The species richness of these sites differed significantly from one another, however, in many cases it was unaffected by the cover of *Brachypodium pinnatum* but by other effects, most probably by the age of the grassland patch and dispersal possibilites of grassland species.

However, the increase in cover of *Brachypodium pinnatum* is possible after abandonment in Hungarian semi-dry grasslands as well, we saw newly spreading policormons of *Brachypodium* pinnatum in many places, nevertheless, we do not have data at hand unfortunately on the speed and mode of spreading of *Brachypodium pinnatum*. The study of the spread of this species would need sophisticated reconstruction studies of former land use. Most of the ancient semi-dry grasslands were used as pastures for centuries in Hungary mainly till the 1960-ies when collectivisation occurred (Illyés & Bölöni. 2007). In that time, most of the grasslands were abandoned while other ones became to get overused since the kolhoz system favoured one big pasture for one big flock or herd close to the sted instead of small pastures for many small herds and flocks. At the same time, many small orchard and vineyard plots became abandoned since local people had to join the kolhoz and no time and energy remained to cultivate the traditional small-plot orchards and vineyards. In these places, secondary semi-dry grasslands started to develop and till now valuable species rich grassland patches have evolved. In most territories the pastures became totally abandoned around 1990 when due to the change in the political system most kolhozes collapsed. In the last ten years pasturing is re-introduced in more and more places as a revived form of rural land use, nevertheless, size of flock or herd may vary considerably year to year as well as the area grazed. Most of these changes in the land use system are not documented, aerial photos are only sporadically available and mostly from the further past only with bigger time lags (10-20 years). Consequently, it is very hard if not impossible to gather reliable data on recent and former land use and on the intensity of management. However, the questions whether *Brachypodium pinnatum* is spreading and whether it has any effect on species richness and diversity of Hungarian semi-dry grasslands are important and relevant for both from pure scientific viewpoint and for conservation managament. Further studies of this topic even with the establishment of management experiments are required.

According to field experience, it seems that the ecological tolerance of *Bromus erectus* is narrower than that of *Brachypodium pinnatum*, since it was found in much fewer localities and tended to occur with high cover on shallow, rocky soils. (Nevertheless, there is most probably a competition between these two grasses, since the results of the correlation analysis revealed significant negative relationships.) Cover of *Bromus erectus* was positively affected by carbonate content of the soil. Soil characteristics were reported to have significant effects both on species richness and composition of the community (Sebastiá 2004). *Bromus erectus* is though to be a grassland species, it is considered to be a relatively disturbance tolerant and some cases are hypothetised to be sown for the agricultural impovement of the grassland (Poschlod & Wallis De Vries 2002, Baumann 2006). We found that the total area of semi-dry grasslands in the landscape positively affected the cover of *Bromus erectus* which contradicts the assumption that it is a disturbance tolerant species.

Cover of graminoids in general was negatively affected by disturbance of animals. From the gaps and small open surfaces created by this activity, graminoids are rooted out in most cases, thus the negative relation is well understood. We could not prove the positive correlation of the amount of litter and the cover of graminiods or to dominant grasses, however, it is documented in the literature (Hurts & John 1999). Moreover, litter removal is suggested as a high priority conservation management for stands dominated by *Brachypodium pinnatum* (Hurts & John 1999) in order to facilitate the establishment and performance of valuable species supressed by the high amount of litter. Recently Ildikó Judit Türke started similar experiments in Hungarian semi-dry grasslands, however, the results are not published yet.

IV.4.2.3. Valuable species

The number of valuable species was mainly affected by structural attributes of the stand. Both the minimum and maximum height of the stand had positive effect, however, the importance of maximum height was much higher. The height of the stand is determined by environmental and management characteristics, more humid and shaded stands are usually higher as well as stands free from grazing and mowing. Depth of litter layer and denseness of the stand also positively affected the number of valuable plant species. Since all of these explanatory attributes are characteristic of unmanaged grasslands, the results indicate indirectly that the number of valuable species is higher in non-managed sites (we found no significant relationship with management attributes). These results are quite unexpected and are in contradiction with the findings published in the literature (Hurst & John 1999, Mitchley and Xofis 2005, Klimek et al. 2007), where the importance of slight management for the maintenance of species richness of calcareaous grasslands is emphasised. The clue for this contradiction might be that the explanatory variables in our analysis not only indicate lack of management but in case of Hungarian semi-dry grasslands they are somehow related to non-disturbed ancient grasslands. Another and possible solution can be that there is a time-lag in the response of valuable species to the abandonment of the management meaning that the height and dense structure documented by us now is a result of recent abandonment which affected the structure but did not have impact on species presence yet. Slow response of grassland species to the envionmental changes is widely documented in the literature (Helm et al. 2006, Cousins et al. 2007). Further studies are needed to find out the true explanation, since the above mentined two solutions indicate radically different suggestions for nature conservation practice.

The number of valuable species was found to be affected by climatic parameters as well. Temperature seasonality and mean temperature of the wettest quarter were found to have negative, while precipitation seasonality was found to have positive effect. We already mentioned that the only publication we found which tested the effect of climatic variables on community composition (Raatikainen et al. 2007), showed that temperature had significant effect while the effect of precipitation was non-significant.

Investigation of the occurence and density of valuable species showed that number and proportion of suitable habitats in the landscape had important positive effects, which is in good correlation with the findings of others (Mitchley and Xofis 2005, Paltto et al. 2006).

IV.4.2.4. Soil variables

The results of our analysis confirmed that the soil characteristics play important role in the composition of Hungarian semi-dry grasslands. However, our results are somewhat contradictory to what is published in the literature. Klimek et al. (2007) and Sebastiá (2004) report that the higher was the quality of the soil, the less species were found in the plots. On the contrary, we found positive relationship between the carbonate and humus content of the soil and species richness. The reason for this difference can be traced back to the differing land use practise in Hungary and in other parts of Europe, namely that in Hungary semi-dry grasslands are not fertilised at all and thus the soil is much less fertile, and most probably the most fertile soils are still considered to be rather poor from European context. According to our results, pH did not affect species richness of the grasslands, while the major importance of it was reported from alvar grasslands (Löbel et al. 2006). The reason for the difference might come from the fact that soils of Hungarian semi-dry grasslands are mostly calcareous (pH ranged between 5.6 and 8.2), while the soil pH of the alvar grasslands included acidic and calcareous sites as well (pH ranged between 3.5 to 8.1) (Löbel et al. 2006). Importance of pH was reported from Finnish boreal grasslands as well, however, soils were mostly acidic there too (Raatikainen et al. 2007).

Grain size classes were investigated by Raatikainen et al. (2007) but these did not have significant effect on the species composition of boreal grasslands, while we found relationships between the particle size distribution and species richness.

Soil parameters were proven by us to affect species richness, cover of *Bromus erectus* and cover of valuable species, however, Shannon-diversity, number of valuable species, cover of *Brachypodium pinnatum* and cover of graminoids remained independent. This again contradicts to the findings of others. Sebastiá (2004) reported the soil characteristics to have important effect on the composition of the community and on dominant grasses. In our analysis, conductivity was found to have negative effect on the cover of valuable species. Conductivity is correlated to the ion concentration of the soil, and since salt content is moderately tolerated by many grassland specialist, this can be a reason for this negative connection.

IV.4.2.5. Geographical position

Geographical position was found to be very important for all of the response variables which had significant relation except Shannon diversity. Geographical location alone explained around 30-40 % of the variation in the response variables, which is rather high. Similar figures are found by most authors taking into consideration the geographical location (Vandvik & Birks 2002, Barbaro et al. 2007, Paltto et al. 2006). However, in other studies the effect of location is not analysed at all (Wagner et al. 2000, Sebastiá 2004, Raatikainen et al. 2007) which in our opinion is a problem since it seems to be evident that geographical location is highly important.

It means that there is an inherent pattern of most of the attributes of Hungarian semi-dry grasslands, which in fact exists only because of the sites are located in different places. Therefore, the variance explained by geography and the other factors in question has to be separated by partitioning.

The location of the stand was the most important factor determining the species richness as well, meaning that there are areas in the country where semi-dry grasslands are rich in species and other areas where they are poor. This corresponds well with the distribution of the species of semi-dry grasslands which are concentrated to the Magyar Középhegység and its surroundings.

Local geographical attributes, like elevation, slope, angle and exposition were found to be important factors in determining composition and species richness of grasslands (Sebastiá 2004, Benie et al. 2006, Raatikainen et al. 2007). In our analysis, positive effect of elevation on species richness can be explained by the fact that at lower elevation nearly all of the potential semi-dry grassland habitats were or are ploughed, thus the present landscape either does not contain semi-dry grasslands or contains mostly secondary ones developed after the cessation of agricultural use. However, except species richness we did not find the local geographical attributes to be significant.

IV.4.2.6. Disturbance factors and threats

Small scale disturbance is inevitable to maintain stand-level species richness of grasslands. Species coexistence in highly species rich plant communities is ensured by small-scale heterogeneity, which is partly provided by the heterogeneity of environmental factors (soil depth, stoniness) but significant part of which is created by disturbance. Semi-dry grasslands originated and extended under special conditions after humans cleared the primeval forests over large areas several thousand years ago (Willems 2001). In western Europe, their maintenance completely depends on human impact, viz. grazing and mowing (Willems 2001). Especially grazing provides the kind of small-scale heterogeneity needed for long-term species coexistence. In case of lack of management, the species richness of semi-dry grasslands in western Europe decline rapidly, and thus moderate grazing is a widely used conservation measure for the maintenance of semi-dry grasslands (Willems 2001, Barbaro et al. 2004, Klimek et al. 2007). In most of the Hungarian semi-dry grasslands, recently there has been no management or any kind of land use, which might cause the decline of the species richness in the long run. However, it seems that activity of wild animals can substitute the lack of management at least locally and in the short run. Our analysis revealed the positive effects of animal disturbance on species richness, on Shannon-diversity and the number of valuable species. In most cases, we documented the activity of ants and small rodents, which affect only a few square decimeters in the grassland. The gaps and open surfaces created this way favour the establishment of small or short-living plants. Activity of small animals, however, affected the cover of graminoids negatively according to our results, which means again that disturbance favours forbs to grasses.

Shrub encroachment and too low intensity of management are reported as main threats to calcareous grasslands in western Europe (Hurst & John 1999, Klimek et al. 2007). However, we found no reference to the analysis of threatening factors to species richness or composition of grasslands. In our analysis we included several threats, at the scale of the vegetation samples and at landscape scale, however, we found no connection between any response variable and any threatening factor. One possible explanation of this can be the delayed response of grassland species and composition to threats, thus the effect of the currently documented threat is detectable only after a longer period of time.

IV.4.2.7. Climatic parameters

Although vegetation is known to be shaped by climatic effects significantly, we found only one publication where the effects of climatic variables on the composition of grasslands were investigated (Raatikainen et al. 2007). Temperature was found to have significant effect on the composition of boreal grasslands, while precipitation had no effect (Raatikainen et al. 2007). In our analysis we found climatic variables to affect the species richness and the number of valuable species of the plots, however, different climatic attributes were responsible for the significant effect. The data of the WORLDCLIM database are derived for a grid of 1 by 1 km, thus the resolution of them is much coarser than our sampling. Using of climatic data of finer resolution most probable would be more suitable for this analysis. Microclimatic parameters of different grassland types in the same locality has been shown to be different (Horváth 2002, Bauer & Kenyeres 2006), thus different microclimatic parameters most probably influence the floristic composition of grassland patches.

IV.4.2.8. Local and landscape neighbourhood

Landscape composition is reported to be a key factor for explaining species richness of a particular vegetation patch in the landscape (Wagner et al. 2000, Löbel et al. 2006, Paltto et al. 2006, Barbaro et al. 2007, Devictor & Jiguet 2007). In was shown by numerous studies that local and landscape factors together determine the species composition, species richness or diversity of a vegetation stand. Our results partly confirm these ideas for Hungarian semi-dry grasslands, however, only species richness and cover of *Bromus erectus* were found to be significantly affected by landscape attributes, and there was no such effect detectable in case of Shannon-diversity, valuable species and cover of graminoids.

Species richness was positively affected by both landscape heterogeneity (number of habitat types) and proportion of forests and shrublands while the proportion of wet grasslands and marshes had negative effect. This indicates that the overlap between the species pool of semi-dry grasslands and dry forest is higher than between semi-dry grasslands and wet grasslands, (at least in Hungary) and thus dry forests and shrublands act as sources of species richness for semi-dry grasslands. These results confirm the results of our previous analysis on the factors affecting naturalness of Hungarian semi-dry grasslands.

IV.4.2.9. Potential dispersal parameters

Our analysis did not prove that dispersal attributes have significant effects on any response variables. However, dispersal attributes are proven to play important role in the determination of species richness and diversity of grasslands (Poschlod et al. 1998), and thus they must have high relevance for conservation practice. Therefore, detailed studies of the actual dispersal abilities of semi-dry grassland species as well as landscapes rich in semi-dry grasslands are needed in the future. As far as we know there are no published studies in this topic from Hungary.

IV.4.2.10. Former land cover types, land use history and recent management

In spite of the fact that former land use and landscape configuration are to be important for species richness of grasslands (Eriksson et al. 2002, Cousins et al. 2007) and thought to be highly important in case of Hungarian grasslands as well, it seems that only by using the maps of the Military Surveys it is not possible to prove the effect of historical land use on Hungarian grasslands. There is no comprehensive map available for the whole country more recent than the 3rd Military Survey and maps for smaller areas rather hard to get access to. Analysis of the effects of former land use types and former landscape configuration is highly labour intensive though and most probably not possible to perform adequately for such a large dataset used in the present analysis.

In a future analysis for a filtered subset of the sampling sites the study of former land cover types and land use is adviseable, since the effects of former landscape are reported to be even more important for the current species richness and diversity of grassland patches than the actual landscape configuration (Eriksson et al. 2002, Helm et al. 2006, Cousins et al. 2007).

We could not find any effect of former or recent land use on the studied variables in Hungarian semi-dry grasslands in spite of the fact that Klimek et al. (2007) reported that management regime explained the highest amount of variation in species richness and several other papers (Mitchley & Xofis 2005, Raatikainen et al. 2007) also emphasise the importance of management on the prediction of high diversity. On the other hand, Löbel et al. (2006) did not find the effect of management significant on species richness. Thus, the effects of management seem to be indeterminate, most probably the results depend on many factors, for example, on sampling design and management intensity as well. Limited access to information on management and the non-systematic execution of the management activities result in other problems hard to handle in scientific analysis.

V. Conclusions from conservation point of view

The floristic composition of semi-dry grasslands of central Europe show gradual changes along a NW-SE gradient from S Germany to E Romania. Semi-dry grasslands of Hungary show similarities to the grasslands of the surrounding countries, however, grassland types characteristic only for the central part of the Pannonian Basin could be identified by the large-scale international analysis. The results of the large-scale analysis of the floristic patterns of central European semi-dry grasslands as well as the detailed study of the Hungarian ones support earlier findings on the uniqueness of Hungarian semi-dry grasslands and steppes (Zólyomi & Fekete 1994, Varga 1989, 1997, Horváth 2009). The sense of scientifically sound vegetation surveys and studies from the conservation point of view is exactly lies in the recognition of previously neglected vegetation types, since the main aim of conservation is to maintain the diversity of nature, in our case the diversity of semi-dry grasslands.

The conservation of semi-dry grasslands can only be effective if representatives of all types of semi-dry grasslands can be maintained in the long run. Therefore, the national and European level conservation policy should incorporate the results of recent vegetation studies. The periodic review of the Natura2000 network could provide an excellent occasion to exchange knowledge between vegetation scientists and conservationists. Semi-dry grasslands of central Europe are recognized by the European Communities as endangered habitat types, and "Sub-Pannonic steppic grasslands" (6240) as Natural Habitat Types of Community Interest according to Annex I of the Habitats Directive (92/43/EEC). Nevertheless, this habitat type has only unclear delimitation and was not supported by data at the European level (Demeter 2002). For effective inventory and monitoring of this habitat type detailed description and list of characteristic species would be needed at the European scale based on sound scientific data and then subtypes of regional importance should be identified based on the results of national vegetation surveys and analyses.

In this thesis the main types of Hungarian semi-dry grasslands were identified. In order to make them comparable to the literature and other vegetation studies, they were assigned into associations. The description of these associations could serve as a basis for the refinement of the definition and description of the “Sub-Pannonic steppic grasslands“ (6240) Natural Habitat Types of Community Interest according to Annex I of the Habitats Directive (92/43/EEC);and for the identification of Pannonian subtypes of these habitat types which is in my opinion inevitable for effective conservation practice.

Little has been known on what makes a grassland „good” from nature conservation point of view, what are the factors which predict and contribute to high species richness, presence of many protected species and so on. At the first glimpse these questions seem to be important only from pure scientific view, however, if we turn the question over in a way that ’what are the places or situations where it is possible to find a „good” grassland?’ it becomes a high priority issue for effective conservation planning. In my thesis I tried to answer the question ’what circumstances make a semi-dry grassland „good” from conservation point of view at two spatial scales, at landscape and on stand level’. At landscape level the richness of the surrounding landscape in natural habitat types had the largest positive effect. Presence of natural woodlands and grasslands also predicted good quality. This indicates that conservation efforts focusing on semi-dry grasslands are recommended to take place in areas with different grasslands and dry forest habitats present in the vicinity of the semi-dry grasslands embedded into a relatively diverse landscape, since there the conservation of grasslands is predicted to be effective in the long run. This approach needs the harmonisation of the conservation of different habitat types and rather recommends to conserve landscape units as a whole rather than single habitat patches.

At stand level, the results are quite similar. I did not address naturalness at the stand level, yet I used different quality attributes. The number of species per plot in Hungarian semi-dry grasslands was positively affected by landscape heterogeneity (number of habitat types in the surroundings) and the area covered by (semi-)natural habitats, especially forests (wetland and marshes had negative effect). However, the most important factor with positive effect was the disturbance by animals, which also affected positvely the diversity and the number of valuable species. I recorded small-scale disturbance, mostly as the effect of ants and small rodents. There were only a few sites which were grazed, so the effects of grazing could not be revealed, although in my opinion the effects of slight grazing are similar to the ones of animal disturbance. The high importance and positive effect of small-scale disturbance on species richness are not surprising, there are well-documented in vegetation ecology. Our results prove again the well-known fact that for the effective conservation of the diversity of semi-dry grasslands management actions must be taken. Without management, the quality of semi-dry grassland habitats decreases rapidly and there is no way to get the lost values back. Proper habitat management run exclusively for conservation purposes, however, is expensive and in many cases difficult to perform. Re-establishment of traditional forms of land-use instead would be a far more economical – and at the same time ecological – solution. The proper strategy would amalgamate rural developmental strategies, ecologically sustainable agriculture and nature conservation. For instance, by supporting eco-tourism or ecologically sustainable husbandry run by families of smaller communities, simultaneous use of semi-dry grasslands for economical and ecological purposes would be feasible. Nevertheless, to reach this goal, collaboration of higher political circles as well as local decision makers, farmers and people from nature conservation is needed.

VI. Summary

The focus of my thesis is the semi-dry grasslands of Hungary. These grasslands hold high aesthetic and conservational value and they used to play a key role in the traditional farming system. I address my work as a scientific contribution to the conservation of these habitat types. First I evaluate the internal floristic patterns on two spatial scales, in order to answer the questions 'What are these grassland?' and 'How do they look like'? Then I turn my focus to quality by asking the question 'What factors determine the naturalness, species richness and diversity of semi-dry grasslands?'.

The relationships of Hungarian semi-dry grasslands to the central European ones were not clear, therefore we performed a large-scale analysis of floristic patterns. We used vegetation data along a 1200 km long transect as a gradient of increasing continentality from central Germany to NW Romania. Species composition changed along the NW-SE gradient and valid clusters were geographically well-separated. From the six valid clusters two from Germany and the Czech Republic corresponded to the *Bromion erecti*; two clusters from the Czech Republic and Hungary to the *Cirsio-Brachypodion*, and two clusters were transitional between these two alliances.

In the next part of my thesis I present a cluster analysis of Hungarian semi-dry grasslands. 699 relevés were geographically selected by the 10%> cover of 6 dominant grass species. The number of valid clusters was the highest at the level of ten clusters, where seven clusters appeared to be valid, which were assigned to five associations, two of them were newly described; and a new system for the syntaxonomy of Hungarian semi-dry grasslands was proposed as well. I suggest the revealed types to serve as a basis for ecological stratification in conservation practice.

The following parts of the thesis analyses the factors affecting the quality of Hungarian semi-dry grasslands on two spatial scales. For the landscape scale analysis, I used data from the MÉTA database; while for the stand level analysis I used relevé data supplemented by additional data collected on the field and from other sources. In both analyses the diversity and proportion of semi-natural habitat types in the surrounding landscape had positive effects. While at the stand level small-scale disturbance of animals became the most important positive effect. I suggest the conservation of whole semi-natural landscape instead of single grassland patches and I recommend the re-establishment of traditional grazing.

VII. Összefoglalás

Dolgozatom a magyarországi félszáraz gyepekkel foglalkozik. A félszáraz gyepek esztétikai és természetvédelmi értéke igen nagy, a hagyományos gazdálkodásnak is fontos elemei voltak. Dolgozatommal ezeknek a gyepeknek a megőrzéséhez szeretnék tudományos igénnyel hozzájárulni. Az első részben bemutatom a gyepek belső kompozíciós mintázatát, két térléptékben. Az első kérdéseim: "Milyenek ezek a gyepek, hogy néznek ki?". Aztán a milyenség felől a minőség felé fordulok, a megválaszolandó kérdésem: "Milyen tényezők határozzák meg a félszáraz gyepek természetességét, az állományok fajszámát, diverzitását?."

A magyarországi félszáraz gyepek közép-európai kapcsolatai mindeddig feltáratlanok voltak. Ezért a kompoziós mintázat feltárására egy nagyléptékű elemzést végeztünk, Közép-Németországtól Romániáig tartó 1200 km-es transzekt mentén készült cönológiai felvételek alapján. A fajkészlet változott az ÉNY-DK irányú gradiens mentén, és a 6 valid csoport földrajzilag is elkülönült. A *Bromion erecti* rendbe tartozik egy német- és egy csehországi, egy *Cirsio-Brachypodion* rendbe egy cseh- és egy magyarországi csoport, és van két átmeneti csoport.

A dolgozat következő részében a magyarországi félszáraz gyepek osztályozását mutatom be. 699 felvételt választottunk ki 6 domináns fűfaj egyenként legalább 10%-os borítása alapján. A valid csoportok maximális száma 7 volt, melyet 10 csoportnál találtunk. Ezeket 5 társulásba soroltuk. 2 új társulást írtunk le, és javasoltunk egy új szüntaxonomiai rendszert a magyarországi félszáraz gyepekre. Felvetettem, hogy az 5 fő típust (asszociációt) a továbbiakban ökológiai alapú rétegzésre lehetne felhasználni a félszáraz gyepeket érintő természetvédelemi tervezésben.

Dolgozatom következő részében két elemzést mutatok be a magyarosrzági félszáraz gyepek minőségét meghatározó tényezőkről két térbeli léptékben. A táji léptékhez a MÉTA adatbázis adatait használtam fel, míg az állományszintű elemzésnél cönológiai felvételek adatait, kiegészítve más, a terepen gyűjtött adatokkal és egyéb források adataival (pl. történeti térképek). Mindkét elemzés eredménye azt mutatja, hogy a környező táj változatásságának és a természetközeli élőhelyek kiterjedésének kedvező hatása van a félszáraz gyepekre. Állomány léptékben a kisléptékű zavarás szerepe igen jelentős, pozitív hatása van a fajszámra és a diverzitásra is. Javasoltam egész tájrészletek védelmét egyes kis, önálló gyepfoltok helyett, valamint lehetőség szerint a hagyományos tájhasználati formák, a legeltetés visszaállítását.

VIII. Acknowledgement

First of all I would like to thank my supervisor, Sándor Bartha for guiding me through all the process that leads to a PhD. I appreciate greatly his critical approach and patience towards my headstrongness. The help of my colleague Botta-Dukát Zoltán, co-author in all of my papers was inestimable; he always had time and energy to help me to find the correct way in the labyrinth of data analysis and statistics. I am also thankful to Zsolt Molnár for helping me to become a vegetation scientist; he always encouraged me both mentally and scientifically, together with her wife, Mariann Biró. Ferenc Horváth also gave kind help of several kinds immediately, whenever I asked him. I am thankful to all of my colleagues for creating a fruitful and very inspiring atmosphere of a workplace which is typical to the Institute of Ecology and Botany of the HAS. I liked to work there very much, and I hope it will continue in the future.

I enjoyed the cooperation with Monika Janosová, Iveta Škodová, Wolfgang Willner, Ute Jandt, Ondřej Hajek, Csaba Molnár, Norbert Bauer, János Garadnai and Tibor Tóth, and in the field with György Szollát from which I have learned a lot. Special thanks are due to Milan Chytrý, who was not only my supervisor for a while and regular reviewer of my manuscripts, but became an ideal of mine as a scientist.

I am thankful for the many people who gave their unpublished relevés for builing up the releve database of Hungarian semi-dry grasslands: Kornél Baráth, Anikó Csecserics, János Csiky, Júlia Erős-Honti, András Horváth, Júlia Kállayné Szerényi, András Kun, Attila Lengyel, Attila Mesterházi, Csaba Molnár, Zsolt Molnár, Dragica Purger, Tamás Rédei, Eszter Ruprecht, Gábor Schmidt, Imelda Somodi, György Szollát, Ildikó Judit Türke and Klára Virágh. Mariann Mózes gave invaluable help during the analysis of the soil samples. Thanks are due to Imelda Somodi who corrected my English several times.

I would like to express my great thanks to my family. My husband, János Bölöni supported me in many various ways during the PhD process. My parents, Eszter Balog and Antal Illyés regularly took care of my little daughters to enable me to work on my thesis.

The studies were founded through the Czech-Hungarian academic exchange programme and the Jedlik Ányos Program of the Hungarian Government "Interaction of natural and man-made ecosystems: landscape ecological studies of biodiversity and ecosystem functions in the Great Hungarian Plain, 2005–2008" (NKFP 6–0013/2005).

IX. References

Archibald, O.W. (1995): Ecology of world vegetation. – Chapman & Hall, London.

Barbaro, L., Dutoit, Th., Anthelme, F. & Corcket, E. (2004): Respective influence of habitat conditions and management regimes on prealpine calcareous grasslands. – Journal of Environmental Management 72: 261-275.

Barbaro, L., Rossi, J.P., Vetillard, F., Nezan, J. & Jactel, H. (2007): The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. – Journal of Biogeography 34: 652-664.

Bartha, S. (2007): Kompozíció, differenciálódás és dinamika az erdőssztyep biom gyepjeiben [Composition, differentiation and dynamics of the grasslands in the forest steppe biome] – In: Illyés, E. & Bölöni, J. (eds.): Lejtősztyepek, löszgyepek és erdőssztyeprétek Magyarországon [Slope steppes, loess steppes and forest steppe meadows in Hungary]. – Budapest, pp. 72-103 and 194-210.

Bartha, S., Campatella, G., Canullo, R., Bódis, J. & Mucina, L. (2004): On the importance of fine-scale spatial complexity in vegetation restoration. – International Journal of Ecology and Environmental Sciences 30: 101-116.

Bastian, O. (1996): Biotope mapping and evaluation as a base of nature conservation and landscape planning. – Ekológia 15: 5-17.

Batáry, P., Báldi, A., Samu, F., Szűts, T. & Erdős, S. (2008): Are spiders reacting to local or landscape scale effectsin Hungarian pastures? – Biological Conservation 141: 2062-2070.

Bauer, N. Kenyeres, Z. & Mészáros, A. (2001): A berhidai Koldustelek löszvölgyének flórája és vegetációja (Veszprém megye) [Flora and vegetation of the loess-valley of Koldustelek at Berhida (Veszprém County, Hungary)]. – Folia Musei Historico-Naturalis Bakonyiensis 17: 65–86.

Bauer, N. & Kenyeres, Z. (2006): Data to the microclimate of some characteristic grassland associations of the Transdanubian mountains. – Acta Botanica Hungarica 48: 9-27

Baumann, A. (2006): On the vegetation history of calcareous grasslands in the Franconian Jura (Germany) since the Bronze Age. – Dissertaciones Botanicae 404., J. Cramer, Berlin, Stuttgart.

Bennie, J., Hill, M.O., Baxter, R. & Huntley, B. (2006): Influence of slope and aspect of on long-term vegetation change in British chalk grasslands. – Journal of Ecology 94: 355-368.

Bertollo, P. (2001): Assessing landscape health: A case study from Northeastern Italy. – Environmental Management 27**:** 349-365.

Biró, M. (2006): Történeti vegetációrekonstrukciók a térképek botanikai tartalmának foltonkénti gazdagításával [Reconstructions of historical vegetation by the method of 'teaching' maps]. – Tájökológiai Lapok 4: 357-384.

Bobbink, R. & Willems, J.H. (1987): Increasing dominance of *Brachypodium pinnatum* (L.) Beuv. in chalk grasslands: a theat to a species-rich ecosystem. – Biological Conservation 40: 301-314.

Borcard, D., Legendre, P. & Drapeau, P. (1992): Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.

Borhidi, A. (1961): Klimadiagramme und Klimazonale Karte Ungarns. – Acta. Univ. Sci. Budapestiensis de Rolando Eötvös, Sect. Biol. 4: 21-50.

Borhidi A. (1995): Social behaviour types, their naturalness and relative ecological indicator values of the higher plants of the Hungarian Flora. – Acta Botanica Hungarica 39: 97–182.

Borhidi, A. (1996): An annotated checklist of the Hungarian plant communities, I. The non-forest vegetation. – In: Borhidi, A. (ed.), Critical Revision of the Hungarian Plant Communities. Janus Pannonius Univ., Pécs, pp. 43-94.

Borhidi, A. (2003): Magyarország növénytársulásai [Plant communities of Hungary] – Akadémiai Kiadó, Budapest.

Borhidi, A. & Sánta, A. (1999): Vörös Könyv Magyarország növénytársulásairól [Red data book of Hungarian Plant communities]. – Természetbúvár Alapítvány Kiadó, Budapest.

Botta-Dukát, Z. (2008a): Validation of hierarchical classifications by splitting dataset. – Acta Botanica Hungarica 50(suppl.): 73–80.

Botta-Dukát Z. (2008b): Invasion of alien species to Hungarian (semi-) natural habitats. – Acta Botanica Hungarica 50(Suppl.): 219-227. Botta-Dukát, Z. & Borhidi, A. (1999): New objective method for calculating fidelity. Example: the Illyrian beechwoods. – Annali di Botanica 57: 73–90.

Botta-Dukát, Z., Chytrý, M., Hájková, P. & Havlová, M. (2005): Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. – Preslia 77: 89-111.

Bölöni, J., Molnár, Zs., Illyés, E. & Kun, A. (2007): A new habitat classification and manual for standardized habitat mapping. – Annali di Botanica 7: 105-126.

Bölöni, J., Molnár, Zs., Horváth, F. & Illyés, E. (2008): Naturalness based habitat quality of Hungarian (semi-)natural vegetation. – Acta Botanica Hungarica 50(Suppl.): 149-159.

Braun-Blanquet, J. (1936): Über die Trockenrasengesellschaften des *Festucion vallesiaceae* in den Ostalpen. – Berichte der Schweizerischen Botanischen Gesellschaft 46: 169–189.

Campagne, P., Roche, Ph. & Tatoni, T. (2006): Factors explaining shrub species distribution in hedgerows of a mountain landscape. – Agriculture, Ecosystems and Environment 116: 244-250.

Celesti-Grapow, L., Pyšek, P., Jarošik, V. & Blasi, C. (2006): Determinants of native and alien species richness in the urban flora of Rome. – Diversity and Distributions 12: 490-501.

Chambers, J.M. & Hastie, T.J. (eds.) (1992): Statistical Models in S. – Wadsworth & Brooks, Cole.

Chytrý, M. (ed.) (2007): Vegetace České republiky 1. Travinná a keříčková vegetace [Vegetation of the Czech Republic. 1. Grasslands and dry vegetation]. – Academia, Praha.

Chytrý, M., Kučera, T. & Kočí, M. (eds.) (2001): Katalog biotopů České republiky [Habitat catalogue of the Czech Republic]. – Agentura ochrany přírody a krajiny ČR, Praha.

Chytrý, M. & Rafajová, M. (2003): Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – Preslia 75: 1-15.

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, Z. (2002): Determination of diagnostic species with statistical fidelity measures. – Journal of Vegetation Science 13: 79-90.

Ciurchea, M. (1964): Aspecte de vegetație de pe Valea Boholțului (Raionul Făgărăs) [Apects of the vegetation of the Boholt valley, Fogaras county]. – Contribuții Botanice, Cluj Napoca, 4: 249-264.

Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006): Propagule pressure: a null model for biological invasions. – Biological Invasions 8:1023–1037.

Cousins, S.A.O. (2006): Plant species richness in midfield islets and road verges - the effect of landscape fragmentation. – Biological Conservation 127: 500-509.

Cousins, S.A.O., Ohlson, H. & Eriksson, O. (2007): Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. – Landscape Ecology 22: 723-730.

Cronk, Q.C.B. & Fuller, J.L. (2001): Plant Invaders. The Threat to Natural Ecosystems. – Earthscan Publication Ltd., London and Sterling.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A. & Wolters, V. (2003): Landscape structure as an indicator for biodiversity: matrix effects on species richness. – Agriculture, Ecosystems and Environment 98: 321-329.

Debreczy, Zs. (1966): Die xerothermen Rasen der Péter- und Tamás-Berge bei Balatonarács. – Ann. Hist.-Nat. Mus. Nat. Hung. 58: 223–241.

Demeter, A. (ed.) 2002: Natura2000 – Európai hálózat a természeti értékek megőrzésére [Natura2000 – European network for the conservation of natural values]. – Öko Rt, Budapest, pp. 66–86.

Denk, T. (2000): Flora und Vegetation der Trockenrasen des tertiaren Hügellandes nördlich von St. Pölten aus arealkundlicher sowie natursutzfachlicher sicht. – Stapfia 72: 1–209.

Devictor, V. & Jiguet, F. (2007): Community richness and stability in agricultural landscapes: The importance of surrounding habitats. – Agriculture, Ecosystems and Environment 120: 179-184.

Dierschke, H. (1981): Zur syntaxonomischen Bewertung schwach gekennzeichneter Pflanzengesellschaften. – In: Dierschke, H. (ed.): Syntaxonomie, J. Cramer, Vaduz, pp. 109-122.

Dierschke, H. (1984): Natürlichkeitsgrade von Pflanzengesellschaften unter besonderer Berücksichtigung der Vegetation Mitteleuropas. – Phytocoenologia 12: 173-184.

Dirzo, R. & Raven, P.H. (2003): Global state of biodiversity and loss. – Annual Review of Environmental Resources 28: 137-167.

Dobson, A.J. (1990): An Introduction to Generalized Linear Models. – Chapman and Hall, London.

Domin, K. (1928): The Plant-Associations of the Valley of Radotin. – Preslia 7: 3–67.

Dúbravková, D., Chytrý, M., Willner, W., Illyés, E., Janišová, M., Kállayné Szerényi, J. (2009): Dry grasslands in the Western Carpathians and the northern Pannonian Basin: a numerical classification – submitted to Preslia.

Duda, R.O., Hart, P.E. & Stork, D.G. (2001): Pattern classification. – 2nd ed., John Wiley & Sons, New York.

Duelli, P. (1997): Biodiversity evaluation in agricultural landscapes: An approach at two different scales. – Agriculture, Ecosystems and Environment 62: 81-91.

Dumortier, M., Butaye, J., Jacquemyn, H., Van Camp, N., Lust, N. & Hermy, M. (2002): Predicting vascular plant species richness of fragmented forests in agricultural landscapes in central Belgium. – Forest Ecology and Management 158: 85-102.

Dutoit, D. (1924): Les associations végétales des sous-alpes de Vevey (Suisse). – Thése Univ., Lausanne.

Dutoit, Th., Buisson, E., Roche, Ph., & Alard, D.(2003): Land use history and botanical changes in the calcareous hillsides of Upper-Normandy (north-western France): new implications for their conservation management. – Biological Conservation 115: 1-19.

Ehrendorfer, F. (ed.) (1973): Liste der Gefäßpflanzen Mitteleuropas. – 2nd ed., Gustav Fischer Verlag, Stuttgart.

Eijsink, J., Ellenbroek, G., Holzner, W. & Werger, M.J.A. (1978): Dry and semi-dry grasslands in the Weinviertel, Lower Austria. – Vegetatio 36: 129-148.

Eriksson O., Cousins, S.A.O. & Bruun, H.H. (2002): Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. – Journal of Vegetation Science 13: 743-748.

European Commission (1999): Agriculture, environment, rural development. Facts and Figures.

Fekete, G., Molnár, Zs. & Horváth, F. (eds.) (1997): A magyarországi élőhelyek leírása és határozókönyve. A Nemzeti Élőhely-osztályozási Rendszer [Guide and description of the Hungarian habitats. The National Habitat Classification System]. – Természettudományi Múzeum, Budapest.

Fekete, G., Virágh, K., Aszalós, R. & Orlóci, L. (1998): Landscape and coenological differentiation of *Brachypodium pinnatum* grasslands in Hungary. – Coenoses 13: 39-53.

Fekete, G., Virágh, K., Aszalós, R. & Précsényi, I. (2000): Static and dynamic approaches to landscape heterogeneity in the Hungarian forest-steppe zone. – Journal of Vegetation Science 11: 375-382.

Gauch, H.G., Jr. (1982a): Multivariate analysis in community ecology. – Cambridge University Press, Cambridge.

Gauch, H.G., Jr. (1982b): Noise reduction by eigenvector ordinations. – Ecology 63: 1643-1649.

Gauckler, K. (1938): Steppenheide und Steppenheidewald der Fränkischen Alb in pflanzensoziologischer, ökologischer und geographischer Betrachtung. – Berichte der Bayerischen Botanischen Gesellschaft 23: 5-134.

Grabherr, G., Koch, G., Kirchmeir, H. & Reiter, K. (1998): Hemerobie österreichischer Waldökosysteme. – Veröffentlichungen des Österreichischen MaB-Programms, Band 17. Universitätsverlag Wagner, Innsbruck.

Hallgren, E., Palmer, M.W. & Milberg, P. (1999): Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. – Journal of Ecology 87: 1037-1051.

Hastie, T. J. & Pregibon, D. (1992): Generalized linear models. – In: Chambers, J.M. & Hastie, T.J. (eds.), Statistical Models in S. –Wadsworth & Brooks, Cole.

Heikkinen, R., Louto, M., Virkkala, R. & Rainio, K. (2004): Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. – Journal of Applied Ecology 41: 824-835.

Helm, A., Hanski, I., & Pärtel, M. (2006): Slow response of plant species richness to habitat loss and fragmentation. – Ecology Letters 9: 72-77.

Hennekens, S.M. & Schaminée, J.H.J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. – Journal of Vegetation Science 12: 589-591.

Hill, M.O., Bunce, R.H.G. & Shaw, M.W. (1975): Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. – Journal of Ecology 63: 597-617.

Honnay, O., Piessens, K., Van Landuyt, W., Hermy, M. & Gulink, H. (2003): Satellite based land use and landscape complexity indices as predictors for plant species diversity. – Landscape and Urban Planning 63: 241-250.

Honti, J. (2004): A fajkészlet eloszlása egy több gyeptársulás alkotta tájmozaikban [Distribution of the species pool in a landscape mosaic consisted of different kinds of grasslands]. – MSc. Thesis, Eötvös Loránd University, Budapest.

Horváth, A. (1998): A mezőföldi fátlan löszvegetáció florisztikai és cönológiai jellemzése [Floristic and coenological description of the treeless loess vegetation of the Mezőföld]. – Kitaibelia 3: 91-94.

Horváth, A (2000): Horváth, A. (2002): A mezőföldi löszvegetáció términtázati szerveződése. [Spatial organisation of loess vegetation of the Mezőföld]. – PhD Thesis, University of Szeged, Szeged.

Horváth, A. (2002): A mezőföldi löszvegetáció términtázati szerveződése [Spatial organisation of loess vegetation of the Mezőföld]. – Scientia Kiadó, Budapest.

Horváth, A. (2009): Validation of description of the xeromesophilous loess grassland association, *Euphorbio pannonicae-Brachypodietum pinnati*. – Acta Botanica Hungarica 51 (3-4). Submitted.

Horváth, F., Dobolyi, K., Karas, L., Lőkös, L., Morschhauser, T. & Szerdahelyi, T. (1995): FLÓRA Adatbázis 1.2. Taxon-lista és attribútum-állomány [FLORA database 1.2. Taxon list and attributes]. – Institute of Ecology and Botany of the Hungarian Academy of Sciences, Vácrátót.

Horváth, F. & Polgár, L. (2008): MÉTA SQL expert interface and access service. – Acta Botanica Hungarica 50(Suppl.): 35-45.

Hothorn, T., Bretz, F. & Westfall, P. with contributions by Heiberger, R. M. (2007): multcomp: Simultaneous Inference for General Linear Hypotheses. – R package version 0.992-4.

Hurst, A. & John, E. (1999): The biotic and abiotic changes associated with *Brachypodium pinnatum* in chalk grassland in south-east England. – Biological Conservation 88: 75-84.

Illyés, E. & Bölöni, J. (eds.) (2007): Lejtősztyepek, löszgyepek és erdőssztyeprétek Magyarországon [Slope steppes, loess steppes and forest steppe meadows in Hungary]. – Budapest.

Illyés, E., Bauer, N. & Botta-Dukát, Z. (2009): Classification of semi-dry grassland vegetation of Hungary. – Preslia 81: 239–260.

Illyés, E., Botta-Dukát, Z. & Molnár, Zs. (2008): Patch and landscape factors affecting the naturalness-based quality of three model grassland habitats in Hungary. – Acta Botanica Hungarica 50 (Suppl.): 179-197.

Illyés, E.; Chytrý, M.; Botta-Dukát, Z.; Jandt, U.; Škodová, I., Janišová, M.; Willner, W. & Hájek, O. (2007a): Semi-dry grasslands along a climatic gradient across Central Europe: Vegetation classification with validation. – Journal of Vegetation Science 18: 835-846.

Illyés, E., Molnár, Cs., Garadnai, J. & Botta-Dukát, Z. (2007b): Északi-középhegységi erdőssztyeprétek természetvédelmi állapotának felmérése – esettanulmány [Survey and evaluation of the threats of forest steppe meadows in the North Hungarian Range – a case study]. – Természetvédelmi Közlemények 13: 163-172.

Ioan, G. (1970): Asociatii stepice montane din partea nordica a Munților Trăscălului [Steppic montane associations in the north part of Trascaluli Hills]. – Contribuții Botanice, Cluj Napoca, 10: 167-181.

Isépy I. (1998): Diverzitás-vizsgálatok hazai száraz és félszáraz gyepekben [Diversity studies in Hungarian dry and semi-dry grasslands]. – Kitaibelia 3: 75–80.

Jäger, C. & Mahn E.G. (2001): Die Halbtrockenrasen im Raum Questen berg (Südharz) in Beziechung zu ihrer Nutzungsgeschicte. – Hercynia 34: 213–235.

Jandt, U. (1999): Kalkmagerrasen am Südharzrand und im Kyffhäuser. Gliederung im überregionalen Kontext, Verbreitung, Standortsverhältnisse und Flora. – Diss. Bot. 322: 1-246.

Janišová, M. (ed.) (2007): Travinnobylinná vegetácia Slovenska – elektronický expertný systém na identifikáciú syntaxónov. [Grassland vegetation of Slovak Republic –

electronic expert sysetm for identification of syntaxa] – Botanický ústav SAV, Bratislava.

Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.B, Bekker, R.M., Fillat, F. & Oomes, M.J.M. (1998): Relationships between soil chemical factors and grassland diversity. – Plant Soil 202: 69-78.

Jeannaret, Ph., Schüpbach, B. & Luka, H. (2003): Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. – Agriculture, Ecosystems and Environment 98: 311-320.

Juhász-Nagy, P. (1976): Spatial dependence of plant populations. Part 1. Equivalence analysis (an outline for a new model). – Acta Bot. Acad. Sci. Hung. 22: 61-78.

Juhász-Nagy, P. (1993): Notes on compositional diversity. – Hydrobiol. 249: 173-182.

Juhász-Nagy, P. & Podani, J. (1983): Information theory methods for the study of spatial processes in succession. – Vegetatio 51: 129-140.

Klika, J. (1931): Studien über die xerotherme Vegetation Mitteleuropas I. Die Pollauer Berge im südlichen Mähren. – Beih. Bot. Centralbl. 47: 343–398.

Klika, J. (1933): Studien über die xerotherme Vegetation Mitteleuropas. II. Xerotherme Gesellschaften in Böhmen. – Beih. Bot. Centralbl., Abt. II, 50: 707-773.

Klika, J. (1936): Studien über die xerotherme Vegetation Mitteleuropas IV. – Beih. Bot. Centralbl. 54: 489–514.

Klika, J. (1939): Die Gesellschaften des *Festucion vallesiacae*-Verbandes in Mitteleuropa. – Stud. Bot. Čech. 2/3: 117-157.

Klimek, S., Kemmermann, R.G.A., Hofmann, M. & Isselstein, J. (2007): Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. – Biological Conservation 134: 559 – 570

Klimeš, L. (1997): Druhové bohatství luk v Bílých Karpatech [Species rich meadow in the White Carpathians]. – Sborn. Přír. Klubu Uh. Hradiště 2: 31-42.

Knapp, R. (1953): Wald und Steppe im östlichen Nieder-Österreich. – Biol. Zentralbl. 70: 85–91.

Knollová, I., Chytrý, M., Tichý, L. & Hájek, O. (2005): Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. – Journal of Vegetation Science 16: 479–486.

Kopecký, K. & Hejný, S. (1978): Die Anwendung einer 'deduktiven Methode syntaxonomischer Klassifikation' bei der Bearbeitung der strassenbegleitenden Pflanzengesellschaften Nordostböhmens. – Vegetatio 36: 43-51.

Kovács, J.A. (2008): A *Danthonia alpina* dominálta félszáraz gyepek cönológiai viszonyairól a Kárpát-medencében [About the coenological relations of *Danthonia alpina* dominated semi-dry grasslands in the Carpathian Basin]. – Proceedings of the conference Aktuális Flóra- és Vegetációkutatás a Kárpát-medencében VIII. – Kitaibelia 13: 171.

Krausch, H.D. (1961): Die kontinentalen Steppenrasen (*Festucetalia valesiacae*) in Brandenburg. – Feddes Repert. Beih. 139: 167-227.

Kun, A. (1996): A Gödöllői-dombvidék Tájvédelmi Körzet bővítésére tervezett területek botanikai állapotfelmérése. A Kratyinka, a Túzberek és az Erdey-dülő növényzete. [Botanical survey of the areas planned to be joined to the Natural Protected Area of Gödöllő Hills. Vegetation of the sites Kratyinka, Túzberek and Erdey-dülő]. – Manuscript, Vácrátót.

Kun, A., Ruprecht, E., Bartha, S., Szabó, A. & Virágh, K. (2007): Az Erdélyi Mezõség kincse: a gyepvegetáció egyedülálló gazdagsága. [Unique diversity of grassland in the Transylvanian Lowland]. – Kitaibelia 12: 88-96.

Lájer, K., Botta-Dukát, Z., Csiky, J., Horváth, F., Szmorad, F., Bagi, I., Dobolyi, K., Hahn, I., Kovács, J. A. & Rédei, T. (2008): Hungarian Phytosociological database (COENODATREF): sampling methodology, nomenclature and its actual stage. – Annali di Botanica nuova series 7: 197-201.

Lambert, J.M. & Williams, W.T (1966): Multivariate methods in plant ecology. VI. Comparison of association analysis and information analysis. – Journal of Ecology 54: 635-664.

Lavorel, S., Lepart, S., Debusche, M., Lebreton, J. D. & Beffy, J. L. (1994): Small scale disturbance and the maintenance of species diversity in Mediterranean old fields. – Oikos 70: 455– 473.

Lavorel S., Touzard B., Lebreton J.D. & Clement B. (1998): Identifying functional groups for response to disturbance in an abandoned pasture. – Acta Oecologica 19: 227–240.

Lavrenko, E.M. & Karamysheva, Z.V. (1993): Steppes of the former Soviet Union and Mongolia. – In: Coupland, R.T. (ed.): Ecosystems of the world. – Volume 8B, Elsevier, Amsterdam, pp: 3-59.

Legendre, P. & Legendre, L. (1998): Numerical ecology. – 2nd ed., Elsevier, Amsterdam.

Less N. (1991): A Délkeleti-Bükk vegetációja és xerotherm erdőtársulásainak fitocönológiája [Vegetation of the southeastern Bükk and phytosociology of xerotherm forest communities]. – Thesis, Debreceni Egyetem, Debrecen.

Louto, M., Rekolainen, S., Aakkula, J. & Pykälä, J. (2003): Loss of plant species richness and habitat connectivity in grassland s associated with agricultural change in Finland. – Ambio 32: 447-452.

Löbel, S. & Dengler, J. (2008): Dry grassland communities on southern Öland: phytosociology, ecology, and diversity. – Acta Phytogeogr. Suec. 88: 13-32.

Löbel, S., Dengler, J. & Hobohm C. (2006): Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. – Folia Geobotanica 41: 377-393.

Mahn, E.-G. (1965): Vegetationsaufbau und Standortsverhältnisse der kontinental beeinflußten Xerothermrasengesellschaften Mitteldeutschlands. – Abh. Sächs. Akad. Wiss., Math.-Naturw. Kl., 49: 1-138.

Margules, C.R. & Pressey, R.L. (2000): Systemetic conservation planning. – Nature 405: 243-253.

Mägi, M. & Lutsar, L. (2001): Inventory of seminatural grasslands in Estonia. - Report, Estonian Fund for Nature, Tallinn.

McCune, B. & Mefford, M.J. (1999): PC-ORD. Multivariate analysis of ecological data. Version 4. – MjM Software Design, Gleneden Beach, OR, US.

MEA (2005): Millennium Ecosystem Assessment, Ecosystems and Human Well-Being. Our human planet – Summary for Decision-Makers. Island Press, Washington D.C.

Meelis, P., Kalamees, R., Zobel, M. & Rosen, E. (1999): Alvar grasslands in Estonia: variation in species richness and community structure. – Journal of Vegetation Science 10: 561-568.

Meusel, H. (1939): Die Vegetationsverhältnisse der Gipsberge im Kyffhäuser und im südlichen Harzvorland. Ein Beitrag zur Steppenheidefrage. – Hercynia 2: 1–313.

Milchunas, D.G. & Laurenroth, W.K. (1993): Quantitative effects of grazing on vegetation and soils over a global range of environments. – Ecological Monographs 63: 327-366.

Mitchell, M.S., Rutzmoser, S.H., Wigley, T.B., Loehle, C., Gerwin, J.A., Keyser, P.D., Lancia, R.A., Perry, R.W., Reynolds, C.J., Thill, R.E., Weih, R., White, D. & Bohall Wood, P. (2006): Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. – Forest Ecology and Management 221: 155-169.

Mitchley, J. & Xofis, P. (2005): Landscape structure and management regime as indicators of calcareous grassland habitat condition and species diversity. – Journal of Nature Conservation 13:171-183.

Mojzes, A. (2003): A tollas szálkaperje (*Brachypodium pinnatum* L.) Beauv.) és az általa dominált félszáraz gyeptársulások jellemvonásai Nyugat-Európában és hazánkban [Characteristics of the perennial grass *Brachypodium pinnatum* (L.) Beauv. And its semiarid grassland communities in Western Europe and in Hungary]. – Természetvédelmi Közlemények 10: 51-72.

Molnár, Zs., Bartha, S., Seregélyes, T., Illyés, E., Botta-Dukát, Z., Tímár, G., Horváth, F., Révész, A., Kun, A., Bölöni, J,. Biró, M., Bodonczi, L., Deák, J.Á., Fogarasi, P., Horváth, A., Isépy, I.., Karas, L., Kecskés, F., Molnár, Cs., Ortmann-né Ajkai, A. & Rév, Sz. (2007): A grid-based, satellite-image supported, multi-attributed vegetation mapping method (MÉTA). – Folia Geobotanica 42: 225–247.

Molnár, Zs., Biró, M., Bölöni, J. & Horváth, F. (2008a): Distribution of the (semi-)natural habitats in Hungary I. Marshes and grasslands. – Acta Botanica Hungarica 50 (Suppl.): 59-106.

Molnár, Zs., Bölöni, J. & Horváth, F. (2008b): Threatening factors encountered: actual endangerment of the Hungarian (semi-)natural habitats. – Acta Botanica Hungarica 50 (Suppl.): 119-217.

Moreno-Rueda, G. & Pizarro, M. (2007): The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. – Acta Oecologica 32: 50-58.

Mucina, L. & Kolbek, J. (1993): Festuco-Brometea. – In: Mucina, L., Grabherr, G. & Ellmauer, T. (eds.), Die Pflanzengesellschaften Österreichs. Teil I., Anthropogene Vegetation, pp. 420-481. – Gustav Fischer Verlag, Jena.

Nagelkerke, R.J.D. (1991): A note on the general definition of the coefficient of variation. – Biometrika 78: 691–692.

Németh, F. & Seregélyes, T. (1989): Természetvédelmi információs rendszer: Adatlap kitöltési útmutató. [Information system of nature conservation: Guide for filling-in the data sheets]. – Manuscript, Környezetgazdálkodási Intézet (Institute of Environmental Management), Budapest.

Oberdorfer, E. (ed.) (1993): Süddeutsche Pflanzengesellschaften. Teil II: Sand- und Trockenrasen, Heide- und Borstgras-Gesellschaften, alpine Magerrasen, Saum-Gesellschaften, Schlag- und Hochstauden-Fluren. – 3rd ed., Gustav Fischer Verlag, Jena.

Oksanen, J., Kindt, R. & O'Hara, R.B. (2005): VEGAN: Community Ecology Package version 1.6-10. http://cc.oulu.fi/~jarioksa.

Otýpková, Z. & Chytrý, M. (2006): Effects of plot size on the ordination of vegetation samples. – Journal of Vegetation Science 17: 465–472.

Paltto, H., Nordén, B., Götmark, F. & Franc, N. (2006): At which spatial scales does landscape context affect local density of Red Data Book and Indicator species? – Biological Conservation 133: 442-454.

Parkes, D., Newell, G. & Cheal, D. (2003): Assessing the quality of native vegetation: The 'habitat hectares' approach. – Ecological Management and Restoration. 4: 29-38.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996): The species pool and its relation to species richness: evidence from Estonian plant communities. – Oikos 75: 111-117.

Peet, R. K., Glenn-Lewin D. C. & Walker-Wolf J.W. (1983): Prediction of man's impact on plant species diversity. – In: Holzner, W., Werger, M.J.A., Ikusima, I. (eds.), Man's impact on vegetation. – Junk Publishers, The Hague, pp. 41-54.

Pielou, E.C. (1977): Mathematical ecology. – John Wiley & Sons, New York.

Poschlod, P., Kiefer, S., Trankle, U., Fischer, S., & Bonn, S. (1998): Plant species richness in calcareous grasslands as affected by dispersability in space and time. – Applied Vegetation Science (1): 75-90.

Poschlod, P. & Wallis De Vries, M.F. (2002): The historical and -socio-economic perspective of calcareous grasslands –lessons from the distant and recent past. – Biol. Conserv. 104, p. 361–376.

Pott, R. (1995): The origin of grassland plant species and grassland communities in Central Europe. – Fitosociologia 29: 7-23.

Pykälä, J., Louto, M., Heikinnen, R. K. & Kontula, T. (2005): Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. – Basic and Applied Ecology. 6: 25-33.

R Development Core Team (2005): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raatikainen, M.K., Heikkinen, R.K. & Pykälä, J. (2007): Impacts of local and regional factors on vegetation of boreal semi-natural grasslands. – Plant Ecology 189: 155-173.

Ratiu, O., Kovacs, A. & Silaghi, Gh. (1969): Fitocenoze din împrejurimile Blajului [Plant association of the surroundings of the village Blaj]. – Contribuții Botanice, Cluj Napoca 9: 169-189.

Riecken, U., Ries, U. & Ssymank, A. (1994): Rote Liste der gefährdeten Biotoptypen der Bundesrepublik Deutschland. Schriftenr. – Kilda Verlag, Greven.

Rodwell, J.S. (ed.) (1992): British plant communities. (Vol. 3.). Grasslands and montane communities. – Cambridge University Press, Cambridge.

Rodwell, J.S., Schamineé, J.H.J., Mucina, L., Pignatti, S., Dring, J. & Moss, D. (2002): The Diversity of European Vegetation – An overview of phytosociological alliances and their relationships to EUNIS habitats. – Rapp. EC-LNV 2002/054: 168 S., National Reference Centre for Agriculture, Nature and Fisheries, Wageningen.

Royer, J.M. (1991): Synthèse eurosibérienne, phytosociologique et phytogéographique de la classe des *Festuco-Brometea*. – Diss. Bot. 178: 1-296.

Ruprecht, E., Kun, A. & Szabó, A. (2003): Száraz gyepek térbeli mintázatanak összehasonlitása az Erdelyi Mezőségben [Comparison of spatial patterns of dry grasslands in the Transylvanian Mezőség]. – Erdélyi Múzeum füzetek, Új sorozat 12: 92-113.

Ružičková, H., Halada, L., Jedlička, L. & Kalivodová, E. (1996): Biotopy Slovenska [Habitats of Slovakia]. - Ústav krajinnej ekológie, SAV.

Sanda, V. (2002): Vademecum ceno-structural privind covorul vegetal din România [Coeno-structural Vademecum regarding the vegetal layer in Romania]. – Vergiliu, Bucureşti.

Schmotzer, A. & Vojtkó, A. (1996): Investigation of *Brachypodium pinnatum*-dominated semi-dry grasslands in the Bükk Mountains (North-east Hungary). – Proceedings of Research, Conservation, Management Conference, Aggtelek, Hungary. pp. 385-391.

Schmotzer, A. & Vojtkó, A. (1997): Félszáraz gyepek bükki állományainak cönológiai összevetése az eredeti erdőtársulások aljnövényzetével [Syntaxonomical comparison of semi-dry grassland stands of the Bükk Mountains with the herb layer of original forest communities]. – Kitaibelia 2: 304.

Schneider-Binder, E. (1971): Pajiştile xeromezofile din depresiunea Sibiului şi colinele ei marginale [Xeromesophilous pastures in the Sibiu valley and the sorroundingd hills] – Stud. şi Comunic. Muz. Brukenthal, ser. Şt. Naturale 16: 135-172.

Sebastiá, M-T. (2004): Role of topography and soils in grassland structuring at the landscape and community scales. – Basic and Applied Ecology 5: 331-346.

Seregélyes, T., Molnár, Zs., Bartha, S. & Csomós, Á. (2008): Regeneration potential of the Hungarian (semi-) natural habitats. – Acta Botanica Hungarica 50(Suppl.): 229-248.

Simon, T. (2000): A magyarországi edényes flóra határozója. Harasztok – virágos növények . [Key of the Hungarian flora. Pteridophytes - Angiosperms]. – Nemzeti Tankönyvkiadó, Budapest.

Sokal, R.R. & Rohlf, F.J. (1995): Biometry. 3rd ed. – W.H. Freeman & Co., San Francisco.

Soó, R. (1933): Balatonvidék növényszövetkezeteinek szociológiai és ökológiai jellemzése [Sociological and ecological descriptions of the plant communites in the surroundings of lake Balaton]. – Math. Term. Tud. Ért. 51: 669–712.

Soó, R. (1949): Les associations végétales de la Moyenne-Transylvanie. – Alföldi Nyomda, Debrecen.

Soó, R. (1964-80): A magyar flóra és vegetáció rendszertani - növényföldrajzi kézikönyve. I-VI. [Synopsis systematico-geobotanica florae vegetationisque Hungariae I-VI.] – Akadémiai Kiadó, Budapest.

Söderström, B., Svenssen, B., Vessby, K. & Glimskär, A. (2001): Plants, insects and birds in semi-natural pastures in relation to local habitat and lanscape factors. – Diversity and Conservation 10: 1839-1863.

Stanová, V. & Valachovič, M. (eds.) (2002): Katalóg biotopov Slovenska [Habitat Catalogue of Slovakia]. – DAPHNE, Bratislava.

Studnička, M. (1980): Vegetace bílých strání Českého středohoří a dolního Pohoří [Vegetation of the meadows of Czech Medium mountains and the Pohor Hills]. – Preslia 52: 155–176.

Şuteu, Ş. (1979): Cercetări de vegetație pe Coasta Alunaşului (Tirimia - Jud. Mureş) [Vegetation investigations on the Alunaş Slope (Tirimia, District of Mureş)]. – Contribuții Botanice, Cluj Napoca, 19: 143-154.

Szabó, A. (2001): A Fertőmelléki-dombsor sziklagyepeinek vizsgálata [Studies of the rock grasslands of the Fertőmelléki-dombsor Hills] – Msc. Thesis, West Hungarian University, Faculty of Forestry, Sopron.

Szerényi, J. (1997): Az Alföld természetes növénytakarójának maradványfoltjai Érden és környékén [Remnants of the former natural vegetation of the Alföld near the town Érd]. – MSc Thesis, Eötvös Loránd University, Budapest

Szirmai, O. (2008): Botanikai és tájtörténeti vizsgálatok a Tardonai-dombság területén. [Botanical and landscape historical researches in the area of the Tardonai Hills]. – PhD Thesis, Szent István University, Gödöllő.

Täuber, F., Weber, P. (1976): Dealul cu bulbuci (Trollius europaeus L.) de lingă Mediaş [Trollius europeaus in the Mediaş meadow] – Ocrotinea Naturi si Mediului inconjurator 1: 23-34.

ter Braak, C.J.F. & Šmilauer, P. (2002): CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination Version 4.5. – Microcomputer Power, Ithaca.

Tichý, L. (2002): JUICE, software for vegetation classification. – Journal of Vegetation Science 13: 451-453.

Tichý, L. & Chytrý, M. (2006): Statistical determination of diagnostic species for site groups of unequal size. – Journal of Vegetation Science 17: 809-818.

Tlusták, V. (1975): Syntaxonomický přehled travinných společenstev Bílých Karpat [Syntaxonomical evaluation of the grassland communities of the White Carpathians]. – Preslia 47: 129-144.

Valachovič, M. (1999): Centrálna databáza fytocenológických zápisov (CDF) na Slovensku [Central database of phytosociological relevés of Slovakia]. – In: Zborník 7. zjazdu SBS, Hrabušice, Podlesok, pp. 218-220.

Vandvik, V. & Birks, H.J. (2002): Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: are the patterns determined by environment or by land-use? – Plant Ecology 162: 233-245.

Varga, Z. (1989): Die Waldsteppen des pannonischen Raumes aus biogeographisher Sicht. – Düsseldorfer Geobot. Kollq. 6: 35–50.

Varga, Z. (1997): Trockenrasen im pannonischen Raum: Zusammenhang der physiognomischen Struktur und der florischtischen Komposition mit den Insektenzönosen. – Phytocoenologia 27: 509–571.

Varga Z. (2000): Félszáraz és szekunder gyepek ökológiai és cönológiai viszonyai az Aggteleki-karszton [Ecological and coenological relations of semi-dry and secondary grasslands in the Aggtelek Karst]. – In: Borhidi A. & Botta-Dukát Z. (eds), Ökológia az ezredfordulón II. Esettanulmányok [Ecology on the millenium II. Case studies], p. 187–221, Magyar Tudományos Akadémia, Budapest.

Varga Z. & Varga-Sipos J. (1999): 18.3.4.1. Pacsirtafüves szálkaperjerét (*Polygalo majori-Brachypodietum pinnati* H. Wagner 1941) [*Polygalo majori-Brachypodietum pinnati* H. Wagner 1941 grasslands]. – In: Borhidi A. & Sánta A. (eds), Vörös könyv Magyarország növénytársulásairól [Red data book of Hungarian plant communities], p. 51–55, Természetbúvár Alapítvány Kiadó, Budapest.

Varga, Z., Varga-Sipos, J., Orci, M.K. & Rácz, I. (2000). Felszáraz gyepek az Aggteleki karszton [Semi-dry grasslands in the Aggtelek Karst]. – In: Virágh, K. & Kun, A. (eds.), Vegetáció és Dinamizmus [Vegetation and Dynamics], MTA ÖBKI, Vácrátót, pp. 195-238.

Varga-Sipos, J. & Varga, Z. (1998): Az Aggteleki-karszt félszáraz gyepeinek (*Cirsio pannonicae-Brachypodion pinnati*) fitocönológiai jellemzése [Phytosociological description of the semi-dry grasslands of the Aggtelek Karst]. – Kitaibelia 3: 347–348.

Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M. (2005): Implementing false discovery rate control: increasing your power. – Oikos 108:643-647.

Virágh, K. & Bartha, S. (1998): Interspecific associations in different successional stages of *Brachypodium pinnatum* grasslands after deforestation in Hungary. – Tiscia 31: 3-12.

Virágh, K. & Bartha, S. (2003): Species turnover as a function of vegetation pattern. – Tiscia 34: 47-56.

Virágh, K., Bartha, S. & Botta-Dukát, Z. (2000): Fine-scale coalition structure in Brachypodium grassland. – Proc. IAVS Symp., 2000. Opulus Press, Uppsala, p. 102.

Virágh, K., Horváth, A., Bartha, S. & Somodi, I. (2006): Kompozíciós diverzitás és términtázati rendezettség a szálkaperjés erdőssztyepprét természetközeli és zavart állományaiban [Compositional diversity and spatial pattern organisation in the natural and degraded stands of *Brachypodium pinnatum* dominated forest steppe meadows]. – In: Molnár E. (ed.), Kutatás, oktatás, értékteremtés [Research, education, accomplishing values]. MTA ÖBKI, Vácrátót, pp. 89-110.

Virágh, K., Horváth, A., Bartha, S. & Somodi, I. (2008): A multiscale methodological approach for monitoring the effectiveness of grassland management. – Community Ecology 9: 237-246.

Virágh, K., Kun, A., Aszalós, R. & Krasser, D. (2001): A Gödöllői-dombvidék Tájvédelmi Körzet és a bővítésre tervezett területei erdőssztyepp mozaikjainak botanikai és természetvédelmi felmérése és értékelése [Botanical and conservational survey and evaluation of the forest-steppe mosaic areas planned to suplement the Gödöllő Hills Protection Area]. – Manuscript, MTA ÖBKI, Vácrátót.

Vojtkó, A. (1998): A Bükk hegység sziklagyepjeinek és sztyeprétjeinek jellemzése [Description of rock and steppic grasslands of the Bükk Mts.]. – In: Csontos P. (ed.), Sziklagyepek szünbotanikai kutatása [Synbotanical resarch of rock grasslands], Scientia Kiadó, Budapest, pp. 133–155.

Wagner, H. (1941): Die Trockenrasengesellschaften am Alpenostrand. Eine Pflanzensoziologische Studie. – Denkschr. Akad. Wiss. Wien., Math.-Nat. Kl. 104: 1-81.

Wagner, H., Wildi, O. & Ewald, K. (2000): Additive partitioning of plant species diversity in an agricultural mosaic landscape. – Landscape Ecology 15: 219-227.

Weber H. E., Moravec J. & Theurillat J.-P. (2000): International Code of Phytosociological Nomenclature. 3rd edition. – Journal of Vegetation Science 11: 739–768.

Wallis De Vries, M.F., Poschlod, P. & Willems, J.H. (2002): Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. – Biological Conservation 104: 265-273.

Wellstein, C., Otte, A. & Waldhardt, R. (2007): Impact of site and management on the diversity of central European mesic grassland. – Agriculture, Ecosystems and Environment 122: 203-210.

Wendelberger, G. (1953): Die Trockenrasen im Naturschutzgebiet auf der Perchtolsdorfer Heide bei Wien. – Angewandte Pflanzensoziologie 9: 1–51.

Willems, J.H. (1982): Phytosociological and geographical survey of *Mesobromion* communities in Western Europe. – Vegetatio 48: 227-240.

Willems, J.H. (2001): Problems, approaches and results in restoration of Dutch calcareous grasslands during the last 30 years. – Restoration Ecology 9: 147-254.

Willner, W., Jakomini, C., Sauberer, N. & Zechmeister, N. (2004): Zur Kenntnis kleiner Trockenrasensinseln in Osten Österreichs. Tüxenia 24: 215-226

Zar, J.H. (1999): Biostatistical analysis. – 4th ed., Prentice & Hall, Upper Saddle River.

Zólyomi, B. (1958): Budapest és környékének természetes növénytakarója [Natural vegetation of Budapest and its surroundings]. – In: Pécsi M. (ed.), Budapest természeti képe [The landscape of Budapest]. Akadémiai Kiadó, Budapest, pp. 509-642.

Zólyomi, B. & Fekete, G. (1994): The Pannonian loess steppe: differentiation in space and time. – Abstracta Botanica 18: 29-41.

X. Appendix

X.1 Availability of the relevés used in the syntaxonomical analyses

A) Czech relevés

The Czech relevés used for the analysis of Central-European semi-dry grasslands were from the Czech national phytosociological database (Chytrý & Rafajová 2003). The relevés of this Turboveg database are available for scientific analysis upon request to the coordinator of the database. Each relevé in the database has an unique identification number. The following relevés were used in our analysis:

100020, 100021, 100041, 100042, 100043, 100044, 100155, 100156, 100157, 100161, 100162, 100163, 100164, 100165, 101013, 101014, 101015, 101016, 101017, 101018, 101020, 101038, 101039, 101040, 101041, 101042, 101043, 101044, 101045, 101046, 184001, 184047, 184049, 184054, 184079, 184080, 184081, 184083, 184084, 184088, 184091, 184095, 184101, 184103, 184105, 184119, 184122, 209503, 209510, 209513, 209518, 209519, 209520, 209524, 209540, 209563, 209564, 209566, 209568, 209576, 209577, 209581, 209587, 209589, 209591, 209593, 209594, 209596, 209598, 209599, 209610, 209613, 210030, 210270, 210351, 210548, 211133, 211212, 216089, 216095, 216102, 216381, 217001, 217008, 217009, 217010, 217011, 217012, 217018, 217025, 217033, 217034, 217041, 217047, 217052, 217053, 217058, 217059, 217062, 217066, 217072, 217073, 217079, 217080, 217081, 217082, 217083, 217088, 217090, 217091, 217096, 217097, 217100, 217111, 217112, 217116, 217117, 217118, 217120, 217122, 217123, 217125, 217126, 217130, 217131, 217134, 217135, 217136, 217137, 217138, 217142, 217147, 217149, 217151, 217152, 217153, 217154, 217158, 217168, 217173, 217184, 217186, 217188, 217189, 217190, 217193, 217195, 217196, 217198, 217202, 217206, 217208, 217209, 217212, 217213, 217214, 217218, 217221, 217222, 217224, 217225, 217226, 217229, 217233, 217236, 217237, 217238, 217240, 217244, 217246, 217252, 217253, 217255, 217256, 217257, 217261, 217263, 217268, 217269, 217276, 217620, 217645, 217647, 217651, 217656, 217666, 217671, 217697, 217707, 217709, 217722, 217727, 217735, 217744, 217749, 217750, 217751, 217752, 217753, 217763, 217782, 217793, 217794, 217795, 217804, 217805, 217836, 217852, 217871, 217873, 217874, 217875, 217891, 283027, 283196, 283222, 283225, 343640, 350002, 350003, 350004, 350009, 350010, 350014, 350017, 350020, 350025, 350028, 350029, 350030, 350040, 400179, 400185, 400190, 400191, 400194, 400395, 400754, 400763, 400765, 400786, 400787, 400794, 400795, 400834, 401307, 401744, 401745, 401748, 401749, 401750, 401751, 402023, 402038, 402044, 402049, 402050, 402051, 402052, 402059, 402120, 402180, 402188, 402214, 402215, 402217, 402221, 402269, 402272, 402296, 402309, 402329, 402330, 402332, 402337, 402338, 402339, 402340, 402342, 402424, 402458, 402992, 402993, 403020, 403021, 403032, 403067, 403102, 403115, 403118, 403135, 403175, 403188, 403193, 403204, 403208, 403209, 403217, 403218, 403226, 403227, 403231, 403238, 403240, 403242, 403247, 403249, 403250, 403253, 403254, 403256, 403257, 403258, 403259, 403260, 403261, 403262, 403266, 403268, 403270, 403271, 403272, 403276, 403278, 403279, 403280, 403282, 403283, 403284, 403285, 403338, 403339, 403340, 403342, 403343, 403345, 403347, 403349, 403350, 403352, 403353, 403354, 403355, 403356, 403358, 403359, 403360, 403361, 403362, 403363, 403364, 403365, 403366, 403367, 403373, 403374, 403375, 403376, 403377, 403378, 403381, 403382, 403383, 403384, 403385, 403387, 403388, 403389, 403390, 403391, 403392, 403393, 403394, 403395, 403396, 403397, 403398, 403399, 403400, 403401, 403402, 403404, 403405, 403406, 403475, 403505, 403533, 403534, 403535, 403536, 403538, 403541, 403542, 403544, 403545, 403546, 403547, 403552, 403553, 403554, 403555, 403558, 403559, 403560, 403561, 403562, 403563, 403564, 403565, 403568, 403569, 403575, 403578, 403579, 403580, 403581, 403582, 403586, 403588, 403589, 403590, 403591, 403592, 403593, 403594, 403596, 403597, 403598, 403599, 403600, 403601, 403602, 403604, 403605, 403608, 403609, 403611, 403613, 403614, 403620, 403622, 403623, 403625, 403629, 403636, 403637, 403638, 403653, 403654, 403655, 403658, 403666, 403667, 403670, 403672, 403673, 403675, 403676, 403677, 403678, 403679, 403681, 403682, 403683, 403684, 403686, 403687, 403688, 403689, 403690, 403691, 403692, 403693, 403695, 403697, 403699, 403700, 403701, 403702, 403703, 403704, 403710, 403712, 403713, 403714, 403715, 403717, 403719, 403720, 403721, 403722, 403723, 403724, 403725, 403726, 403728, 403729, 403730, 403731, 403732, 403736, 403857, 403977, 403997, 403998, 403999, 404006, 404013, 404213, 404215, 404988, 404989, 404994, 405421, 405465, 405584, 405587, 405595, 405624, 405626, 405628, 405635, 405642, 407546, 407547, 407624, 407627, 407628, 407629, 407630, 407631, 407632, 407638, 407639, 407640, 407641, 407642, 407643, 407644, 407645, 407646, 407648, 407649, 407650, 407653, 407654, 407657, 407658, 407660, 407661, 407662, 407663, 407664, 407665, 407667, 407668, 407670, 407671, 407672, 407673, 407674, 407675, 407676, 407679, 407684, 407686, 407687, 407690, 407691, 407692, 407693, 407694, 407696, 407697, 407698, 407700, 407701, 407702, 407704, 407705, 407706, 407707, 407708, 407709, 407710, 407711, 407713, 407716, 407723, 407724, 407725, 407726, 407728, 407729, 407730, 407732, 407733, 407734, 407735, 407738, 407744, 407745, 407749, 407755, 407756, 407757, 407758, 407759, 407760, 407761, 407762, 407763, 407764, 407765, 407766, 407767, 407768, 407769, 407770, 407771, 407772, 407773, 407790, 407793, 407795, 407798, 407799, 407801, 407802, 407803, 407804, 407805, 407806, 407807, 407808, 407809, 407820, 407823, 407844, 407850, 407853, 407883, 407903, 407919, 407921, 407934, 407937, 407938, 407942, 407958, 408067, 408068, 408069, 408076, 408077, 408088, 408089, 408090, 408091, 408093, 408098, 408102, 408105, 408159, 408162, 408521, 408522, 408524, 408525, 408539, 408541, 408805, 408993, 409003, 409004, 409006, 409007, 409011, 409013, 409242, 409246, 409248, 409259, 409260, 409261, 409262, 409263, 409264, 409265, 409266, 409267, 409268, 409269, 409270, 409271, 409272, 409273, 409274, 409275, 409276, 409277, 409278, 409284, 409285, 409286, 409288, 409289, 409291, 409292, 409293, 409295, 409296, 409297, 409298, 409303, 409304, 409305, 409307, 409322, 409324, 409325, 409327, 409328, 409330, 409331, 409333, 409334, 409335, 409336, 409337, 409345, 409348, 409349, 409353, 409356, 409357, 409358, 409359, 409360, 409362, 409363, 409364, 409366, 409367, 409368, 409369, 409371, 409374, 409375, 409377, 409384, 409388, 409389, 409390, 409391, 409392, 409393, 409395, 409397, 409452, 409453, 409454, 409455, 409593, 409598, 409852, 409947, 409948, 409950, 409951, 409963, 410130, 410132, 410133, 410135, 410139, 410149, 410186, 410247, 410322, 410324, 410338, 410765, 410766, 410817, 410863, 410985, 411343, 411363, 411365, 411366, 411367, 411368, 411369, 411370, 411371, 411372, 411374, 411375, 411376, 411377, 411379, 411380, 411381, 411382, 411390, 411391, 411392, 411864, 411983, 412130, 412489, 412508, 412509, 412510, 412567, 412568, 412583, 412587, 412763, 412789, 413422, 413446, 413448, 413449, 413450, 413451, 413452, 413453

B) Slovakian relevés

The Slovakian relevés used for the analysis of Central-European semi-dry grasslands were from the Slovak national phytosociological database (Valachovič 1999). The relevés of this Turboveg database are available for scientific analysis upon request to the coordinator of the database. Each relevé in the database has an unique identification number. The following relevés were used in our analysis:

1, 2, 3, 10, 13, 14, 16, 19, 32, 33, 34, 35, 37, 39, 68, 99, 100, 108, 120, 126, 130, 148, 151, 1103, 1105, 1109, 1200, 1216, 1219, 1222, 6001, 100014, 100015, 100017, 100018, 100019, 100020, 100022, 100028, 100030, 100034, 100036, 100037, 100040, 100041, 100044, 100074, 600003, 600005, 600012, 20056, 403097, 600113, 600114, 600115, 600116, 601940, 602163, 602167, 602168, 602169, 602170, 602171, 602226, 602227, 602231, 602233, 602235, 602238, 602239, 602240, 602241, 603319, 603350, 603351, 603355, 603444, 603445, 603446, 603497, 603498, 603499, 603500, 603501, 603502, 603503, 603504, 603505, 603506, 603507, 603508, 603509, 603510, 603511, 603512, 603513, 603514, 603515, 603516, 603522, 604304, 604305, 604307, 604411, 604413, 604416, 604422, 604423, 604424, 604425, 604429, 604432, 604433, 604436, 604437, 604439, 604440, 604441, 604443, 604444, 604445, 604446, 604447, 604450, 604451, 604452, 604455, 604456, 604457, 604459, 604461, 604463, 604466, 604467, 604472, 604474, 604477, 604752, 604753, 604754, 604755, 604756, 604757, 604758, 604759, 604760, 604761, 604907, 604908, 604909, 604910, 604912, 605482, 606231, 606493, 606494, 606496, 606497, 606498, 606499, 606714, 606769, 606770, 606802, 606824, 606826, 606827, 606828, 606829, 606830, 606831, 606832, 606833, 606834, 606835, 606875, 606876, 606877, 606878, 606879, 607034, 608923, 609476, 609478, 609880, 611262, 611684, 611685, 611686, 611852, 611853, 611939, 611940, 612669, 612700, 612702, 612703, 612705, 612706, 612708, 612712, 612713, 612714, 612715, 612716, 613058, 613061, 613062, 613063, 613111, 613112, 613113, 613114, 613539, 613541, 613575, 613588, 613837, 613912, 613990, 613995, 614704, 614705, 614879, 614884, 616591, 616592, 616593, 616594, 616595, 616600, 617339, 617612, 617636, 34, 736120, 736125, 736163, 74, 92, 7, 10, 13, 17, 19, 24, 25, 33, 34, 35, 39, 45, 46, 48, 49, 52, 55, 60, 64, 74, 79, 80, 81, 82, 85, 87, 88, 92, 93, 94, 96, 98, 102, 103, 107, 118, 120, 122, 125, 127, 139, 140, 149, 150, 156, 157, 159, 162, 164, 167, 169, 174, 177, 179, 180, 181, 182, 185, 186, 190, 205, 206, 213, 214, 217, 219, 220, 222, 223, 227, 232, 234, 236, 237, 238, 239, 240, 242, 243, 244, 245, 246, 247, 248, 250, 251, 253, 254, 255, 256, 257, 258, 262, 264, 269, 271, 275, 276, 278, 279, 283, 284, 285, 289, 290, 292, 293, 294, 295, 297, 298, 304

C) German relevés

The German relevés used for the analysis of Central-European semi-dry grasslands were from the database compiled by Ute Jandt (1999). The identification number and the biblioreference of these relevés are in the Excel file entitled ’Headers_of_German_rels.xls’ on the CD attached to the thesis. The relevés are available for futher analysis with the permission of Ute Jandt.

D) Austrian relevés

The Austrian relevés used for the analysis of Central-European semi-dry grasslands were digitalised from the published literature. The identification number and the biblioreference of these relevés are in the Excel file entitled ’Headers_of_Austrian_rels.xls’ on the CD attached to the thesis. The relevés are stored in a Turboveg database and are available for futher analysis from Eszter Illyés.

E) Romanian relevés

The Romanian relevés used for the analysis of Central-European semi-dry grasslands were mostly digitalised from the published literature. The identification number and the biblioreference of these relevés are in the Excel file entitled ’Headers_of_Romanian_rels.xls’ on the CD attached to the thesis. The relevés are stored in a Turboveg database and are available for futher analysis from Eszter Illyés.

E) Hungarian relevés

The Hungarian relevés used for the analyses of Central-European and Hungarian semi-dry grasslands were collected from various sources by Eszter Illyés. Most of the relevés are unpublished and were used with the permission of the author. Part of the relevés was digitalised from published relevé tables, and part of them was newly sampled by Eszter Illyés. The identification number, the authors and localities of these relevés are given in the Excel file ’Headers_of_Hung_rels.xls’ on the CD attached to the thesis. For the further analysis of the relevés the authors of them have to be contacted. The relevés newly sampled by Eszter Illyés are available on the CD attached to the thesis as a Turboveg backup file.

X.2 List of the documents on the CD attached to the thesis

- List_of_valuable_species.doc
- Headers_of_Austrian_rels.xls
- Headers_of_German_rels.xls
- Headers_of_Romanian_rels.xls
- Headers_of_Hung_rels.xls
- Sample_releves.xls
- TurbovegDbBackup_Releves_of_Eszter_Illyes.zip
- PhD_Diss_Illyes.doc
- PhD_Diss_Illyes.pdf
- Theses_of_PhD_Diss_Illyes.pdf
- Tézisek_Illyés.pdf