



Comparative study on grasslands dominated by *Festuca vaginata* and *F. pseudovaginata* in the Carpathian Basin

Unterschiede zwischen *Festuca vaginata*- und *F. pseudovaginata*-Sandtrockenrasen im ungarischen Karpatenbecken

Gábor Szabó^{1,2,*}, Zita Zimmermann^{1,2}, Andrea Catorci³, Péter Csontos⁴, Barnabás Wichmann¹, Szilárd Szentes¹, Attila Barczy⁵ & Károly Penksza¹

¹Szent István University, Institute of Environment and Landscape Management, Department of Botany, 2100 Gödöllő, Páter K. u. 1, Hungary;

²Institute of Ecology and Botany, MTA Centre for Ecological Research, 2163 Vácraátót, Alkotmány u. 2–4, Hungary;

³School of Bioscience and Veterinary Medicine, University of Camerino, 62032 Camerino (MC), Via Pontoni 5, Italy;

⁴Institute for Soil Science and Agricultural Chemistry, Centre for Agricultural Research, Hungarian Academy of Sciences, 1022 Budapest, Hermann O. u. 10, Hungary;

⁵Szent István University, Institute of Environment and Landscape Management, Department of Nature Conservation and Landscape Ecology, 2100 Gödöllő, Páter K. u. 1, Hungary

*Corresponding author, e-mail: kabazit@gmail.com

Abstract

The aim of our study was to reveal the differences in the species composition and soil properties of open sandy grasslands dominated by different *Festuca* species, *Festuca vaginata* and *F. pseudovaginata*. Due to the arid conditions, sandy grasslands are generally covered by xerothermic vegetation in which *F. vaginata* is a typical dominant species. *Festuca pseudovaginata*, a species newly described by the authors, can also gain dominance in sandy grasslands. However, species composition and soil properties of grasslands dominated by this recently discovered species are still undiscovered. Based on previous coenological studies, we hypothesised that the grasslands characterised by the endemic *F. vaginata* are more species-rich than those with *F. pseudovaginata*.

Coenological sampling was carried out in May 2009 at two study sites using the Braun-Blanquet method in quadrats of 2 m × 2 m. Five relevés were sampled in stands dominated by *F. vaginata* and *F. pseudovaginata* respectively at two study sites in Central Hungary, resulting in a total of twenty relevés. Analyses were based on the cover scores of vascular plant species and cryptogam crust and values of seven soil properties (pH [KCl], pH [H₂O], humus, total N, Ca, P₂O₅ and K₂O) measured in the 0–15 and 15–30 cm soil layers. Soil properties of the grasslands dominated by *F. pseudovaginata* and *F. vaginata* (dependent variables) were compared by linear mixed models, where ‘grassland type’ was the fixed factor and ‘site nested in grassland type’ was considered as random factor. Data were analysed by cluster analysis, fusion algorithm was a combinatorial method (minimising increase of variance), and the correlation was used as comparative function. We compared the cover of subordinate species by Mann-Whitney U test.

We found that *F. pseudovaginata* and *F. vaginata* samples were well separated, and grasslands dominated by *F. pseudovaginata* had nearly two times more species than those dominated by *F. vaginata*. Based on the cluster analyses using plant cover and upper 0–15 cm soil layer data, *F. pseudovaginata*

and *F. vaginata* groups could be well separated. Linear mixed models revealed that *F. vaginata* grasslands were typical on soils with higher pH, nitrogen, phosphorous and potassium contents compared to *F. pseudovaginata* grasslands, which indicates a tight connection between the properties of the upper soil layer and the vegetation in sandy grasslands.

Keywords: coenosystematical elements, open sandy grasslands, Pannonian Biogeographical Region, sandy soil, species composition, soil properties

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Grasslands are important habitats for biodiversity conservation (TÄLLE et al. 2016, VALKÓ et al. 2016a), which is well reflected by the nature conservation priorities in the European Union (ZLINSZKY et al. 2015). Pannonic sand steppes are habitats protected by the Natura 2000 Habitats Directive. This habitat type occurs only in the Pannonian Biogeographical Region in an extent of 48.000 ha (HARASZTHY 2014). Pannonic sand steppes harbour several rare and protected plant species such as *Alkanna tinctoria*, *Corispermum* spp., *Dianthus serotinus* and *Helichrysum arenarium*. Due to the conservation importance of sandy grasslands it is crucial to get more information about their coenological and taxonomical characteristics.

Sandy soils are generally nutrient-poor, and their characteristic natural vegetation type is open sandy grasslands in the semi-arid areas (MOLNÁR 2003). On the sandy areas of the Danube-Tisza Interfluve, environmental conditions allow *Festuca vaginata* to become a dominant species. According to recent works describing the vegetation of Hungary (ŠMARDA et al. 2007, BORHIDI et al. 2012), there is vicariance among *Festuca* species typical of the *Festucetum vaginatae* (Rapaics ex Soó 1929 em Borhidi 1996) association (hereafter *F. vaginata* grassland). A high number of geographically separated taxa have similar functions in the sandy communities. One of them, *Festuca pseudovaginata*, has recently been described as a new taxon (PENKSZA 2003). The most important morphological distinguishing features of the two *Festuca* taxa are the following: the basal leaves of *F. vaginata* are hairless and glaucous. The sclerenchyma ring is thick, and it is uniform in the side of the mesophyll. The inflorescence is (4–)5–7 cm in length. There is no awn on the lemma. The chromosome number is $2n = 28$ (PENKSZA 2003). *Festuca pseudovaginata* has light green basal leaves, which are hairless and not glaucous. The sclerenchyma ring is extraordinarily thick, and it is not uniform in the side of the mesophyll. The inflorescence is 5–8.5 cm in length. The lower glume is 2.9–3.2 mm, the upper glume 3.9–4.1 mm long. The awn on the lemma is 1.2–1.8 mm long. The chromosome number is $2n = 14$ (PENKSZA 2003). There is only little information about the ecology of *F. pseudovaginata* (but see PENKSZA 2013). An important phenological characteristic of the species is that its flowering starts 2–3 weeks earlier than that of *F. vaginata*. Typical habitats of *F. pseudovaginata* are disturbed areas (BAJOR et al. 2016).

Ecological research of sandy areas of the Pannonian Biogeographical Region has a solid background (SZUIKÓNÉ LACZA & KOVÁTS 1993, BIRÓ et al. 2008, ERDŐS et al. 2015, TÖLGYESI et al. 2015). However, former studies on the natural vegetation in the region paid only little attention to disturbed areas, which are the most typical habitat of *F. pseudovaginata* (KÁRPÁTI & KÁRPÁTI 1954). In *F. vaginata* grasslands, soil moisture content was proven to be the most important limiting environmental factor; results of KOVÁCS-LÁNG & SZABÓ (1971) suggest that the water permeability of the light sandy soils is very high, the water

holding capacity is about 3–5% and the surface soil layers dry out very fast. During the summer drought period, the maximum soil moisture content is generally below 2% v/v in 20 cm depth (KOVÁCS-LÁNG & SZABÓ 1971, FEKETE et al. 1976).

Phytomass production of *F. vaginata* grasslands has two maximums during the year, one in late spring and the other one in autumn (KOVÁCS-LÁNG & SZABÓ 1971, NOSEK 1986), following the temporal distribution of yearly precipitation. Production maximum in autumn is higher than in late spring. An important characteristic of the association is that the majority of the roots can be found in the upper 20 cm layer, where soil moisture content is the lowest and the soil is exposed to the fastest drying (FEKETE et al. 1976). *Festuca vaginata* grasslands – mainly because of their low production – are usually utilised as sheep pasture (PENKSZA et al. 2009). Due to the low fertility of sandy soils, open sandy areas are less affected by intensive agricultural activities. However, sandy grasslands have been influenced by several human activities such as overgrazing, mining and military usage (KELEMEN et al. 2016). Due to these disturbances, new open, recently disturbed surfaces with new vegetation types have frequently been formed (BARTHA et al. 2008). The above-mentioned human impacts resulted in the appearance of new vegetation types in areas with a long history of human disturbance and regeneration processes. Grasslands dominated by the recently discovered *F. pseudovaginata* are typical in these disturbed sandy areas (PENKSZA 2003).

In former studies the two *Festuca* taxa were not distinguished (they were both recorded as *F. vaginata*); therefore, their ecological characteristics and the differences in species composition of their stands are still unknown. Our aim was to reveal the differences in species composition and soil conditions of grasslands dominated by *F. vaginata* and *F. pseudovaginata*. The aim of our study was to answer the following questions: (1) Do the species pools of *F. pseudovaginata* dominated grasslands differ from those dominated by *F. vaginata*? (2) Are there differences in the soil properties of the two grassland types?

2. Materials and methods

The studied dry sandy grasslands are located in the Pannonian Biogeographical Region in Central Hungary. Sampling was performed at two sites: Tatárszentgyörgy and Imrehegy (Fig. 1). At the northern site (Tatárszentgyörgy), the mean temperature in the coldest month (January) is 3 °C, in the warmest month (July) 20.5 °C; the mean annual temperature is 9.5 °C. At the southern site (Imrehegy), the mean temperature in the coldest month (January) is 1.5 °C, it is 21.5 °C in the warmest month (July), and the mean annual temperature is 10.5 °C. Mean annual precipitation at the northern site is 550–600 mm, and it is 500–550 mm at the southern site (PÉCZELY 2006). Due to the low precipitation and poor water-holding capacity of the soil, both sites are characterised by an extremely dry and warm microclimate (PÉCZELY 2006).

The Tatárszentgyörgy site is characterised by sand hills, with mosaics of several subassociations of *Festuca vaginata* grasslands (BORHIDI et al. 2012): a pioneer subassociation with *F. vaginata* (*Festucetosum vaginatae* or *typicum*), an open *Fumana* subassociation (*Fumanetosum*), a *Stipa* subassociation on the hilltops (*Stipetosum*), a *Holoschoenus* subassociation at the feet of the hills (*Holoschoenetosum*) and a *Salix rosmarinifolia*-subassociation in the depressions between the hills (*Salicetosum rosmarinifoliae*). *Juniperus communis* forms *Junipero-Populetum albae* (Zólyomi ex. Soó 1950) patches with *Populus alba* and *P. nigra*. The study site was a military area churned up by tanks and characterised by anthropogenic holes and pits. When the vegetation recovered, the disturbed patches were mainly colonised by *F. pseudovaginata*. Besides the military usage, the area is grazed by sheep from April to September with 0.5–1 livestock units/ha (KISS et al. 2011). The other site, Imrehegy, is an open area with sandy hills. Vegetation types are similar to Tatárszentgyörgy (*Festucetosum vaginatae*,

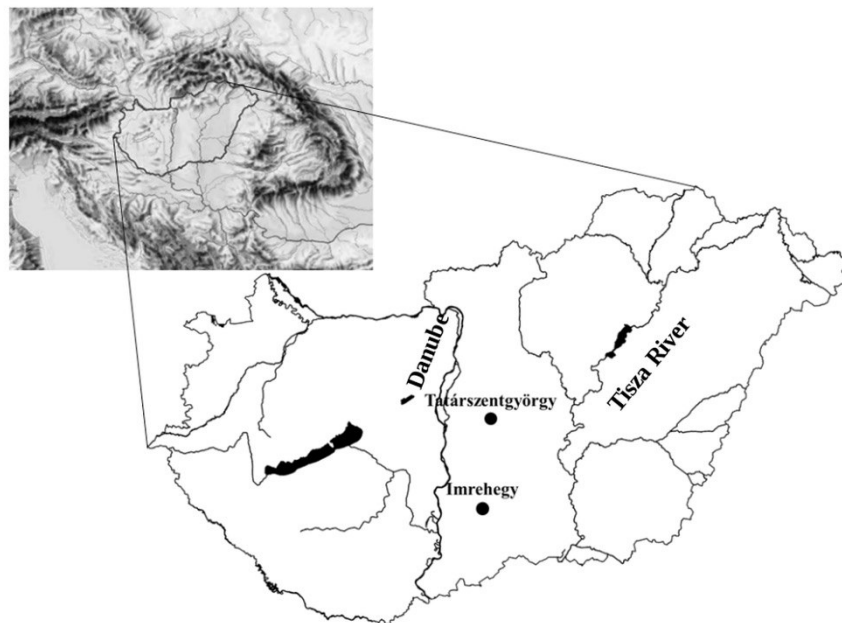


Fig. 1. Locations of the study sites (Tatárszentgyörgy and Imrehegy) in Central Hungary, in the Danube-Tisza Interfluve.

Abb. 1. Lage der Untersuchungsgebiete (Tatárszentgyörgy und Imrehegy) im Stromland zwischen Donau und Theiß in Zentral-Ungarn.

Fumanetosum, *Stipetosum*, *Holoschoenetosum* and *Salicetosum rosmarinifoliae*). The area has been continuously grazed by sheep for 30 years, with grazing pressure and pattern similar to Tatárszentgyörgy.

Environmental conditions of the studied areas also have a mosaic character (TÖLGYESI & KÖRMÖCZI 2012, TÖLGYESI et al. 2014, ERDŐS et al. 2015). According to TÖLGYESI (2016), patches of different vegetation types have developed along the environmental gradients in the sandy areas of the Danube-Tisza Interfluve. Physical parameters, e.g., soil moisture, soil texture, exposure or temperature, can change along these gradients (BARTHA et al. 2008, COURTWRIGHT & FINDLAY 2011, BÁTORI et al. 2014); however, biotical factors are also important. VADÁSZ et al. (2016) provide an example for this in their study on effects of different natural grazing and trampling intensities on the vegetation. According to TÖLGYESI (2016), ecotones that were formed in the contact zone of different vegetation types are important for the survival of species and ensure appropriate environmental conditions for them. In the Danube-Tisza Interfluve, the interaction of grasslands and forests lead to the development of forest edge ecotones (TÖLGYESI 2016, ALIGNIER & DECONCHAT 2011). In the last centuries, there were remarkable changes in the relationship of forests and grasslands, e.g., grasslands have taken the place of forests, meadows have disappeared (BIRÓ et al. 2008). In the transition zone of forests and grasslands and in the place of the former forests, open sandy surfaces have developed, which have been colonised by plants in a relatively short time (CSECSERITS & RÉDEI 2001, CSECSERITS et al. 2011, BARTHA et al. 2014). These patches remained for a long time after anthropogenic impact had ended (PÁNDI et al. 2014). In the place of the former forests, succession set in and resulted in the development of grasslands (PRACH et al. 1997, 2001, TÖRÖK et al. 2011).

Coenological sampling was carried out in May 2009, using the BRAUN-BLANQUET (1951) method in quadrats of 2 m × 2 m. Five relevés were recorded in the centre of patches dominated by *F. vaginata* and *F. pseudovaginata* at both study sites, resulting in a total of 20 relevés. In one relevé both species

occurred (*F. pseudovaginata* was dominant, and *F. vaginata* appeared with 1% cover). Species names follow the nomenclature of KIRÁLY (2009). Associations were named based on BORHIDI et al. (2012). Soil samples were also taken at the time of the botanical surveys from the depth of 0–15 and 15–30 cm from each quadrat. Soil analyses were carried out for the following parameters and with the following methods: pH (H₂O, KCl) (electrometry); CaCO₃ (Scheibler type calcimeter); ammonium lactate (AL) soluble P₂O₅; AL soluble K₂O, humus (Turin method). The total nitrogen content was measured in an accredited laboratory (Szent István University, Soil Chemistry Laboratory). The effects of ‘grassland type’ (*F. pseudovaginata* or *F. vaginata* dominated grasslands, fixed factor), and ‘site nested in grassland type’ (Tatárszentgyörgy and Imrehegy, random factor) on the studied soil properties were tested by linear mixed models (LMM, ZUUR et al. 2009). Soil properties that did not have normal distribution were log-transformed. For comparing the cover of the most abundant species (with cover more than 5%) in the different grassland types, Mann-Whitney U test was applied. Data were analysed using SPSS 20.0 software. Multivariate analyses of the relevés were based on the following data: (1) cover values of the vascular plant species and the cryptogam crust; (2) values of soil properties (pH [KCl], pH [H₂O], humus, total N, Ca, P₂O₅ and K₂O) measured in the 0–15 cm and 15–30 cm soil layers. We used an agglomerative cluster analysis technique (HMCL2, SYN-TAX program package): The fusion algorithm was a combinatorial method (minimising the increase of variance), and the correlation was used as comparative function (PODANI 1997). Calculations were made by the SYN-TAX software (PODANI 2001).

3. Results

3.1 Botanical results

Altogether 76 vascular plant species occurred in the relevés of the two study sites. Twenty-three species were found in both associations, four species appeared only in *Festuca vaginata* grasslands, while 49 species occurred only in *F. pseudovaginata* grasslands. We revealed a remarkable difference in the species number of the two grassland types. *F. pseudovaginata* grasslands had a higher mean species number: The average number of species per quadrat was 19.6 (SD = 1.1) in Tatárszentgyörgy and 25.2 (SD = 4.0) in Imrehegy, while in case of the *F. vaginata* type, this value was 10.0 (SD = 3.4) in Tatárszentgyörgy and 11.4 (SD = 1.3) in Imrehegy. Two moss species (*Polytrichum piliferum* and *Tortula ruralis*) and two lichen species (*Cladonia magyarica* and *C. rangiformis*) occurred in the *F. vaginata* grasslands, while in *F. pseudovaginata* grasslands, there were no cryptogam species. Supplement E1 shows the dominance-abundance data of the relevés. *Festuca vaginata* and *F. pseudovaginata* relevés had common species, which are characteristic members of natural and semi-natural grasslands. Species typical of calcareous sandy grasslands (*Festucion vaginatae* Soó 1929) were *Arenaria serpyllifolia*, *Bromus squarrosus*, *Centaurea arenaria*, *Erysimum diffusum*, *Festuca vaginata*, *Fumana procumbens* and *Koeleria glauca*. Elements of acidophilous sandy grasslands (*Corynephorretalia* Klika 1934) (*Cerastium semidecandrum*, *Rumex acetosella* and *Veronica dillenii*) occurred in both types.

Moss-lichen synusia were only found in *F. vaginata* relevés; typical species were *Cladonia magyarica*, *C. rangiformis*, *Polytrichum piliferum* and *Tortula ruralis*. Several elements of the class *Festuco-Brometea* (general grassland species) appeared in *F. pseudovaginata* relevés, e.g., *Alyssum alyssoides*, *Asparagus officinalis*, *Erophila verna*, *Hypericum perforatum*, *Phleum phleoides*, *Poa angustifolia* and *P. bulbosa* (Supplement E1). *Carex liparicarpos*, *C. stenophylla*, *Iris arenaria* (sandy and loess grassland species – *Festucetalia vaginatae & rupicolae*), *Viola kitaibeliana* and *Thymus praecox* (*Festucetalia vaginatae & valesiaca*) occurred only in *F. pseudovaginata* grasslands; these species are also character-

istic of closed grasslands. Besides these species, fundamental separation was caused by ruderal elements of different ruderal vegetation types (*Chenopodietea*, *Chenopodietea & Secalietea*, *Secalietea*, *Aphanion*) such as *Ambrosia artemisiifolia*, *Anchusa officinalis*, *Anthemis austriaca*, *Apera spica-venti*, *Conyza canadensis*. In one of the *F. pseudovaginata* relevés, a xerophilous oak forest (*Quercetea pubescentis-petraeae* Br.-Bl. 1932) element characteristic of forests (*Lithospermum officinale*) occurred. In *F. pseudovaginata* relevés, the frequency of *Cynodon dactylon* was considerably higher (Supplement E1). Based on the results of the multivariate analyses, *F. vaginata* grasslands were separated from those dominated by *F. pseudovaginata* in both sites in case we used all species for the classification (Fig. 2). Based on the results of the Mann-Whitney U test (Table 1), the cover of *Arenaria serpyllifolia*, *Cerastium semidecandrum*, *Medicago minima* and *Poa bulbosa* was higher in *F. pseudovaginata* grasslands, whereas the cover of *Plantago arenaria* was higher in *F. vaginata* grasslands.

3.2 Soil parameters

The pH of the studied topsoil was around 8 in both sites, and the CaCO₃ content varied between 3 and 5%, which indicates a low lime content. The humus content was very low in all cases (< 1%). Based on the soil laboratory analyses and field data, soils can be classified as regosols. The soil type was different in the two vegetation types: In *Festuca vaginata*-dominated areas, it was sandy skeletal soil, whilst in case of *F. pseudovaginata*, it was brown soil, which is characteristic of sandy forests (STEFANOVITS 1992). As shown by the

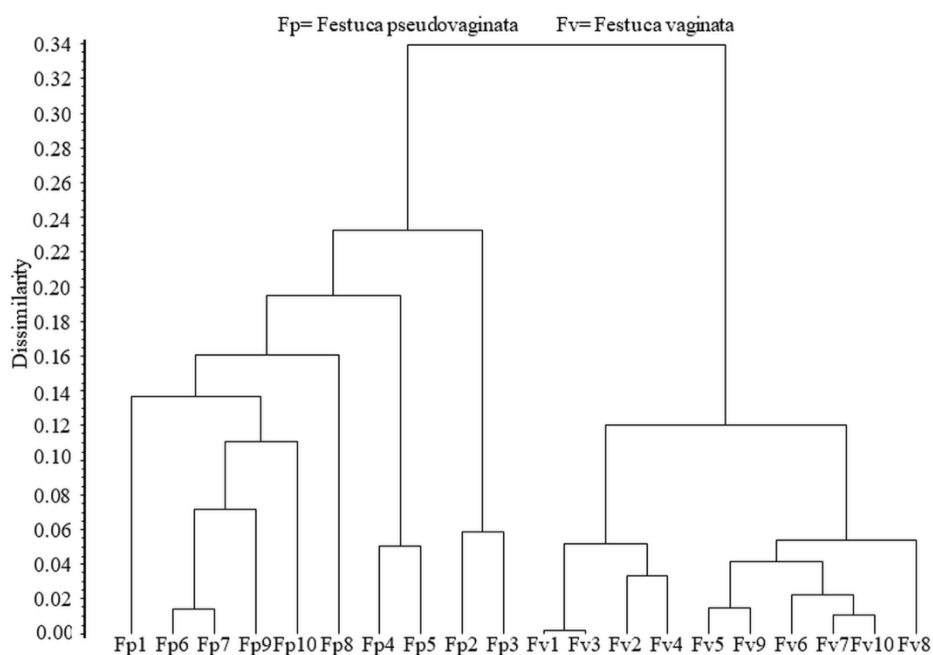


Fig. 2. Dendrogram of the studied grassland types based on species cover scores.

Abb. 2. Dendrogram der *Festuca vaginata*- und *F. pseudovaginata*-Rasen nach den Deckungswerten der beteiligten Arten.

Table 1. Results of the Mann-Whitney U test. Significant differences are marked in boldface.**Tabelle 1.** Ergebnisse des Mann-Whitney-U-Tests. Signifikante Unterschiede sind fett hervorgehoben.

	Mann-Whitney U	Sig.	Cover (%; mean±SD)	
			<i>F. pseudovaginata</i> grasslands	<i>F. vaginata</i> grasslands
<i>Arenaria serpyllifolia</i>	7.0	0.001	2.6±1.5	0.4±0.2
<i>Botriochloa ischaemum</i>	36.5	0.315	2.3±2.9	0.9±1.7
<i>Cerastium semidecandrum</i>	0.1	0.001	2.3±1.2	0.2±0.3
<i>Euphorbia seguierana</i>	48.5	0.912	1.2±1.6	0.7±0.7
<i>Medicago minima</i>	3.0	0.001	3.5±0.7	0.6±0.5
<i>Minuartia verna</i>	26.5	0.075	4.5±5.3	0.8±1.6
<i>Plantago arenaria</i>	77.5	0.035	0.8±1.1	4.8±7.7
<i>Poa bulbosa</i>	0.1	0.001	5.6±2.5	0.2±0.1
<i>Stipa borysthenica</i>	46.0	0.796	3.9±7.3	0.8±1.1

Table 2. Results of the soil laboratory analysis for Tatárszentgyörgy and Imrehegy. Means and standard deviations of the five soil samples are given for each location.**Tabelle 2.** Ergebnisse der Bodenanalysen für die beiden Untersuchungsgebiete Tatárszentgyörgy und Imrehegy. Mittelwert und Standardabweichung für jeden Rasentyp in jedem Gebiet unterschieden nach Bodenhorizonten.

	<i>Festuca pseudovaginata</i>		<i>Festuca vaginata</i>	
	Tatárszentgyörgy	Imrehegy	Tatárszentgyörgy	Imrehegy
0–15cm				
pH (KCl)	7.34±0.21	7.32±0.18	7.51±0.23	7.50±0.13
pH (H ₂ O)	8.11±0.27	7.85±0.33	8.31±0.18	8.31±0.21
humus (mg/kg)	0.23±0.16	0.84±0.81	0.05±0.07	0.09±0.06
total N (mg/kg)	184.60±102.20	105.80±29.41	528.20±427.99	584.80±688.84
Ca (%)	4.38±0.25	4.74±0.52	3.44±0.92	3.87±1.04
P ₂ O ₅ (mg/kg)	15.38±1.63	16.76±2.18	26.84±9.48	37.18±38.05
K ₂ O (mg/kg)	32.22±2.07	30.16±5.39	59.50±28.56	53.88±39.00
15–30cm				
pH (KCl)	7.74±0.19	7.70±0.25	7.79±0.21	7.77±0.24
pH (H ₂ O)	8.37±0.25	8.37±0.18	8.71±0.12	8.81±0.12
total N (mg/kg)	204.00±71.83	407.60±485.54	352.60±161.00	323.40±123.89
Ca (%)	3.83±1.00	3.72±1.38	4.01±0.81	3.92±0.93
P ₂ O ₅ (mg/kg)	18.78±6.70	33.46±29.98	17.64±3.41	25.46±7.95
K ₂ O (mg/kg)	37.58±6.73	44.86±30.58	39.90±7.56	39.16±11.46

Table 3. Results of linear mixed-effect models for testing the effects of ‘grassland type’ (fixed factor) and ‘site’ (random factor nested in ‘grassland type’). Significant differences are marked in boldface.

Tabelle 3. Ergebnisse des linearen Mixed-Effekt Modells zur Untersuchung von ‘Graslandtyp’ (fester Faktor) und ‘Gebiet’ (Zufallsfaktor geschachtelt in ‘Graslandtyp’). Signifikante Unterschiede sind fett hervorgehoben.

	Grassland type		Site	
	F	<i>p</i>	F	<i>p</i>
0–15 cm				
pH [KCl]	218.00	0.005	0.01	0.980
pH [H ₂ O]	6.42	0.127	1.28	0.305
humus	3.05	0.223	3.86	0.043
Ca	13.13	0.068	0.50	0.615
total nitrogen	22.77	0.041	0.51	0.608
P ₂ O ₅	65.10	0.015	0.10	0.903
K ₂ O	30.33	0.031	0.25	0.780
15–30 cm				
pH [KCl]	5.10	0.152	0.10	0.941
pH [H ₂ O]	73.00	0.013	0.40	0.709
total nitrogen	5.80	0.138	0.19	0.833
Ca	4.89	0.157	0.05	0.946
P ₂ O ₅	0.04	0.860	1.43	0.269
K ₂ O	0.78	0.469	0.02	0.979

results of the LMM, four soil properties (pH [KCl], total nitrogen, AL-P₂O₅ and AL-K₂O content) of the upper 0–15 cm layer were different in the two *Festuca*-dominated grassland types (Table 2–3) in so far as *F. vaginata*-dominated grasslands were characterised by higher values. In the 15–30 cm layer, there was a significant difference in pH [H₂O] between the two grassland types; *F. vaginata*-dominated grasslands had higher pH values (Table 2–3). The cluster analyses of the vegetation (76 species cover and cryptogam crust cover) showed that relevés from *F. pseudovaginata* and *F. vaginata* grasslands were well separated. Similarities between the plots of the *F. vaginata* group were stronger than between the plots of the *F. pseudovaginata* group. Based on the cluster analyses using the upper 0–15 cm soil layer data, *F. pseudovaginata* and *F. vaginata* grasslands were well separated (Fig. 3a). Data from the 0–15 and 15–30 cm soil layers were applied together in the cluster analyses and for the preparation of the dendrogram, where *F. pseudovaginata* and *F. vaginata* samples were not separated (Fig. 3b).

4. Discussion

Our results refine the former statement of BORHIDI et al. (2012), which suggests that the only dominant *Festuca* species of open sandy grassland vegetation is *F. vaginata*. The two types of studied *Festuca* grasslands differed considerably in their species composition. However, we found that 30% of their species pool harboured common species from the *Festucion vaginatae*, *Festucetalia vaginatae* & *valesiaca* and *rupicola* coenotaxa. *Cynodon dactylon* indicating disturbance of the habitat occurred mainly in *F. pseudovaginata* grasslands.

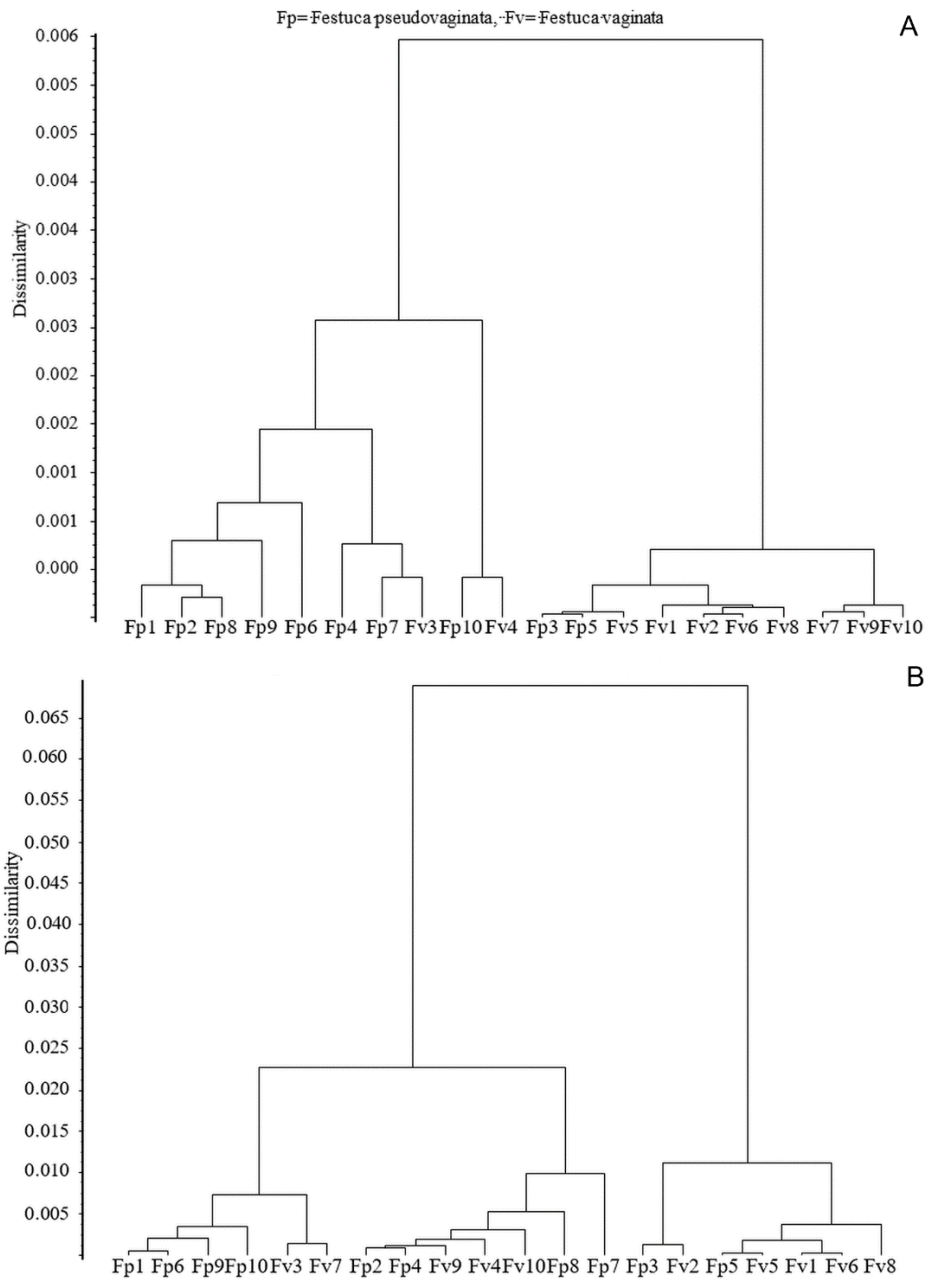


Fig. 3. Dendrogram of the studied grassland types (A) – based on soil properties measured in the upper soil layer (0–15 cm); (B) – based on the pooled soil samples of the upper (0–15 cm) and the lower (15–30 cm) layers.

Abb. 3. Dendrogram der *Festuca vaginata*- und *F. pseudovaginata*-Rasen nach (A) den Eigenschaften des Oberbodens und (B) den gemittelten Eigenschaften des Ober- und Unterbodens (0–15 cm bzw. 15–30 cm).

Several subassociations of *Festucetum vaginatae* were described previously in the central sandy area of the Carpathian Basin. One of these, *Festucetosum wagneri* (PÓCS 1954), had the most similar species composition to our *F. pseudovaginata* relevés. The variability of the *Festucetum vaginatae* community is indicated by the fact that authors identified several species characteristic for a given facies, e.g., *Cynodon dactylon*, that played an important role in the vegetation dominated by *F. pseudovaginata*. *Cynodon dactylon* can spread in pastures, which can be regarded as an indicator of trampling and intensive grazing (SZENTES et al. 2011, 2012, DEÁK et al. 2014, TÖRÖK et al. 2014). In *F. vaginata* relevés, we did not find any remarkable signs of anthropogenic disturbance; the moss-lichen synusia was stable. BORHIDI et al. (2012) kept the association *Cynodonti-Festucetum pseudovinae* Soó (in Aszód 1935) 1957 when highlighting the role of grazing; moreover, he pointed out that this vegetation type was supposedly formed in meadows embedded in a forest matrix. These findings also seem to support the role of brown forest soil in differentiating the two communities. It is likely that the *F. pseudovaginata* community is still recovering after disturbance and that it has not yet reached an equilibrium status with the present disturbance regimes. It was proven by our results that *F. pseudovaginata* stands developed in former forest areas, which is confirmed by the brown soil type.

The species composition of the two grassland types was driven by environmental factors partly influenced by anthropogenic effects. *Festuca vaginata*-dominated grasslands were characterised by higher total nitrogen, potassium, phosphorous and pH values compared to *F. pseudovaginata* grasslands. This phenomenon can be explained by the lower biological activity (thickness of the root system) and the possible anthropogenic impact, such as mixing of lower, nutrient-poor layers with upper layers through digging and trampling in *F. pseudovaginata* grasslands. The higher nutrient content in the soil of *F. vaginata* grasslands can be explained by the differences in the soil types as well as lower anthropogenic impact in *F. vaginata*-dominated grasslands. Based on the classification results, we can state that the studied *Festuca* species are good indicators of the soil properties (BARTHA et al. 2004, 2008). *Festuca vaginata* was typical of soils that have a higher nitrogen and phosphorus content, while *F. pseudovaginata* was widespread on soils with a lower nutrient content. This implies a close connection between upper soil layer and vegetation. Harsh environmental conditions in *F. pseudovaginata* grasslands only allowed the formation of open grasslands; weed species did not appear in significant numbers. Based on our present examinations of *F. vaginata*- and *F. pseudovaginata*-dominated grasslands, we can state that differences in soil properties and disturbance in the vegetation were indicated by the different species compositions of the two grassland types. BAJOR et al. (2016), who studied open sandy vegetation after shrub encroachment and deforestation, found that after deforestation ephemeral species occurred, like in case of old-fields (PRACH et al. 2007, VALKÓ et al. 2016b) and spontaneously recovering grasslands (DEÁK et al. 2015, 2016, VALKÓ et al. 2017), and that these species were gradually replaced by perennials during succession (CSECSERITS et al. 2011, TÖRÖK et al. 2009) because of their better competition ability (PRACH et al. 1997). According to BAJOR et al. (2016), *F. pseudovaginata* was the most typical grass species that colonised the areas after deforestation.

Summarising our results, it seems conceivable that the observed compositional differences between the two communities may be ascribed to two main factors. The first one is linked to the different soil properties and related environmental stress. In this sense the early flowering strategy of *F. pseudovaginata* might be better understood as a strategy to avoid the fast ongoing of summer drought stress. Moreover, as indicated in previous works (CATORCI

& GATTI 2010, TROIANI et al. 2016), the land use legacy seems to play a key role in determining the current species composition. A further explanation of the differences between the two communities may be found in the different successional stages of the studied grasslands, as *F. pseudovaginata*-dominated grasslands might be considered as a dynamic stage of a forest vegetation series, while *F. vaginata* grasslands are in a climax stage. However, more studies are needed about this question.

Erweiterte deutsche Zusammenfassung

Einleitung – In den semiariden Gebieten der pannonisch-biogeographischen Region bilden offene Sandtrockenrasen auf den entsprechenden Standorten die typische Vegetation (MOLNÁR 2003). Im Stromland zwischen Donau und Theiß in Zentral-Ungarn herrschen Sandmagerrasen mit *Festuca vaginata* und *F. pseudovaginata* vor; dabei wurde *F. pseudovaginata* erst kürzlich von *F. vaginata* abgespalten (PENKSZA 2003). Inwieweit die beiden Arten auch unterschiedliche ökologische Ansprüche besitzen und unterschiedlich vergesellschaftet sind, war dementsprechend bislang nicht bekannt. Unser Ziel war daher die Untersuchung möglicher Unterschiede in (1) der Artenzusammensetzung und (2) den Bodenbedingungen zwischen Sandtrockenrasen mit dominantem Auftreten von *F. vaginata* oder *F. pseudovaginata*.

Material und Methoden – Die beiden Untersuchungsgebiete, Tatárszentgyörgy und Imrehegy, liegen in der pannonisch-biogeographischen Region in Zentral-Ungarn. In beiden Gebieten wurden im Mai 2009 Bestände mit dominanten Vorkommen von *Festuca vaginata* und *F. pseudovaginata* untersucht. Pro Gebiet und Vegetationstyp wurden fünf 2 × 2 m-Vegetationsaufnahmen (insgesamt 20 Aufnahmen) nach der Methode von BRAUN-BLANQUET (1951) erstellt. In jeder Aufnahmefläche wurden aus dem Oberboden (Bodentiefe 0–15 cm) und Unterboden (15–30 cm) Proben entnommen und die folgenden Parameter wurden darin gemessen: pH-Wert in KCl und H₂O sowie die Gehalte an Humus, Gesamtstickstoff, Phosphat, Kalzium und Kalium. In den statistischen Analysen wurden die beiden Vegetationstypen als Faktor ‘Graslandtyp’ (*F. pseudovaginata*- vs. *F. vaginata*-Rasen) und die beiden Gebiete als Faktor ‘Gebiet’ (Tatárszentgyörgy vs. Imrehegy) definiert. Mit linearen gemischten Modellen (LMM; ZUUR et al. 2009) wurden dann die Effekte des ‘Graslandtyps’ (als fester Faktor) und ‘Gebiets’ (als Zufallsfaktor verschachtelt in ‘Graslandtyp’) auf die Bodenbedingungen untersucht. Unterschiede in der Deckung der häufigsten Arten (mit >5 % Deckung) zwischen den beiden Graslandtypen wurden mit Mann-Whitney-U-Tests untersucht. Mithilfe von hierarchischer agglomerativer Clusteranalyse wurden die Aufnahmeflächen nach deren Artenkombination (inkl. Deckungsgraden) und Bodeneigenschaften in Dendrogrammen angeordnet. Alle Analysen wurden mit SPSS 20.0 durchgeführt.

Ergebnisse – Insgesamt (in allen 20 Aufnahmen) konnten wir 76 Gefäßpflanzenarten nachweisen, davon 23 Arten in beiden Rasentypen, vier Arten nur in *Festuca vaginata*-Rasen und 49 Arten nur im *F. pseudovaginata*-Rasen. Die beiden Rasentypen unterschieden sich in ihrem Artenreichtum deutlich. Mit $19,6 \pm 1,1$ Arten pro Aufnahmefläche (Mittelwert und Standardabweichung) in Tatárszentgyörgy bzw. $25,2 \pm 4,0$ Arten in Imrehegy waren die *F. pseudovaginata*-Rasen artenreicher als die *F. vaginata*-Rasen welche in Tatárszentgyörgy $10,0 \pm 3,4$ Arten und in Imrehegy $11,4 \pm 1,3$ Arten aufwiesen. Die Clusteranalyse mit allen Arten trennte die *F. vaginata*- und *F. pseudovaginata*-Rasen in beiden Gebieten voneinander (Abb. 2). In den *F. pseudovaginata*-Rasen erreichten *Arenaria serpyllifolia*, *Cerastium semidecandrum*, *Medicago minima* und *Poa bulbosa* eine signifikant höhere Deckung, während in den *F. vaginata*-Rasen nur *Plantago arenaria* eine hohe Deckung zeigte (Tab. 1). Beide Rasentypen unterschieden sich auch in ihren Bodenbedingungen. Der pH (KCl)-Wert und die Gehalte an Gesamtstickstoff, Phosphat und Kalium lagen im Oberboden der *F. vaginata*-Rasen höher (Tab. 2–3). Im Unterboden lag dagegen in den *F. vaginata*-Rasen nur der pH (H₂O)-Wert höher. Zudem unterschieden sich die beiden Vegetationstypen in ihrem Bodentyp. In *F. vaginata*-Rasen war dies ein sandiger Skelettboden und in den *F. pseudovaginata*-Rasen eine Braunerde (welche im Gebiet eher für Wälder auf Sandböden typisch ist) (STEFANOVITS 1992).

Diskussion – Die von *Festuca vaginata* und *F. pseudovaginata* aufgebauten Rasen unterschieden sich in ihrer Artenzusammensetzung erheblich; dieser Unterschied dürfte v. a. an unterschiedlichen Umweltbedingungen liegen aber auch an unterschiedlichen anthropogenen Einflüssen. Die Böden der *F. vaginata*-Rasen wiesen insgesamt höhere Konzentrationen an Gesamt-Stickstoff, Kalium und Phosphor sowie höhere pH-Werte auf. Dies kann durch die geringere Durchwurzelung der Böden der *F. vaginata*-Rasen und den damit verbundenen geringeren Nährstoffentzug erklärt werden. Auch könnte die unterschiedliche Landnutzung der Bestände die unterschiedlichen Bodenbedingungen erklären. So war durch die militärische Nutzung der Flächen der *F. pseudovaginata*-Rasen offenbar nährstoffarmer Boden aus tieferen Schichten in den Oberboden eingearbeitet worden. In den *F. vaginata*-Beständen waren dagegen keine auffälligen Spuren solcher anthropogenen Störungsereignisse vorhanden. Auch erlauben die in den *F. pseudovaginata*-Rasen anscheinend extremeren Umweltbedingungen offenbar nur die Ausbildung einer sehr offenen Vegetation, ohne dass Unkräuter stärker in Erscheinung treten. Daher konstituieren wir, dass unterschiedliche Bodenbedingungen und Störungsintensitäten durch eine unterschiedliche frühere Landnutzung die Ausbildung der beiden Rasentypen bedingen. Die in den *F. pseudovaginata*-Rasen schlechteren Nährstoffbedingungen könnten dabei auch zu einem stärkeren Umweltstress in den *F. pseudovaginata*-Rasen führen. In diesem Sinn könnte man die frühere Blüte von *F. pseudovaginata* als eine Strategie zur Vermeidung von zu viel Stress interpretieren, indem die Pflanzen durch frühes Blühen wohl dem sommerlichen Trockenstress etwas ausweichen können. Zusätzlich könnte eine frühere Landnutzung für die unterschiedliche Artenzusammensetzung der Bestände eine Rolle spielen (CATORCI & GATTI 2010, TROIANI et al. 2016). Eine weitere Erklärung der Unterschiede zwischen den beiden Gesellschaften könnte darin liegen, dass es sich evtl. um unterschiedliche Sukzessionsstadien handelt. Die *F. pseudovaginata*-Rasen wachsen auf potentiellen Waldstandorten und würden sich bei ausbleibender Nutzung langfristig wohl wieder bewalden, während sich die *F. vaginata*-Rasen eher im Klimax befinden, also vermutlich natürlich offen sind. Insgesamt sollten zur Frage der potentiellen natürlichen Vegetation auf den Flächen jedoch genauere Studien stattfinden.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Synthetic data of *Festuca vaginata* and *Festuca pseudovaginata* dominated relevés.

Anhang E1. Vegetation der *Festuca vaginata*- und *F. pseudovaginata*-Rasen.

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Supplement E1. Synthetic data of *Festuca vaginata* and *Festuca pseudovaginata* dominated relevés. Notations: A–D: Minimum and maximum percentage cover, C: Constancy.

Anhang E1. Vegetation der *Festuca vaginata*- und *F. pseudovaginata*-Rasen. A–D: Minimale und maximale Prozentdeckung in den Aufnahmen, C: Stetigkeit.

Species	<i>Festuca pseudovaginata</i>		<i>Festuca vaginata</i>	
	A–D	C	A–D	C
Festucion vaginatae				
<i>Alkanna tinctoria</i>	3	I	0.5	I
<i>Bromus tectorum</i>	3–5	II		
<i>Cenchrus incertus</i>	5	I		
<i>Centaurea arenaria</i>	2–3	I	1–2	II
<i>Festuca pseudovaginata</i>	10–25	V		
<i>Festuca vaginata</i>	1	I	10–65	V
<i>Koeleria glauca</i>	2–10	V		
<i>Plantago arenaria</i>	1–3	II	1–25	V
<i>Polygonum arenarium</i>	0.5–3	I		
<i>Secale sylvestre</i>	1–15	I		
<i>Silene conica</i>	2		0.5	I
<i>Stipa borysthena</i>	1–20	II	1–3	II
<i>Tribulus terrestris</i>	1	I		
Festucetalia vaginatae & valesiaca				
<i>Arenaria serpyllifolia</i>	2–5	V	1	II
<i>Bromus squarrosus</i>	2–10	III	0.5	III
<i>Erysimum diffusum</i>	1–2	II	1	I
<i>Fumana procumbens</i>	2	I	1	II
<i>Veronica praecox</i>	1	I		
<i>Viola kitaibeliana</i>	1–3	II		
Festucion vaginatae & rupicolae				
<i>Carex liparicarpus</i>	3–5	III		
<i>Carex stenophylla</i>	2–5	III		
<i>Iris arenaria</i>	2–3	I		
Festucetalia valesiaca & vaginatae				
<i>Euphorbia cyparissias</i>	2–5	III		
<i>Euphorbia seguierana</i>	2–4	II	1–2	III
<i>Minuartia glomerata</i>	2–4	I		
<i>Minuartia verna</i>	1–15	III	1	II
<i>Silene otites</i>	1	I	1–20	III
Festucetalia valesiaca				
<i>Astragalus onobrychis</i>	2–3	I		
<i>Myosotis stricta</i>	2–5	II		
<i>Stipa capillata</i>	3	I		
<i>Thymus glabrescens</i>	3–5	II		
Festuco rupicolae & vaginatae				
<i>Linum hirsutum</i>	2	I		
Festuco–Brometea				
<i>Acinos arvensis</i>	1	II	0.5	I
<i>Alyssum alyssoides</i>	1–2	II		
<i>Asparagus officinalis</i>	2	I		
<i>Asperula cynanchica</i>	1	I		
<i>Botriochloa ischaemum</i>	2–8	III	2–5	II
<i>Erophila verna</i>	1	I		
<i>Eryngium campestre</i>	2–5	I		
<i>Holosteum umbellatum</i>	1–2	III	1	II
<i>Hypericum perforatum</i>	2	I		

Species	<i>Festuca pseudovaginata</i>		<i>Festuca vaginata</i>	
	type		type	
	<i>A-D</i>	<i>C</i>	<i>A-D</i>	<i>C</i>
<i>Medicago minima</i>	1-8	V	1	III
<i>Ononis spinosa</i>	5-8	II		
<i>Phleum phleoides</i>	2-3	I		
<i>Poa angustifolia</i>	1	I		
<i>Poa bulbosa</i>	3-10	V	1	I
<i>Potentilla arenaria</i>	2-5	III	2-15	II
<i>Saxifraga tridactylites</i>	2-3	I		
<i>Scabiosa ochroleuca</i>	2	I		
<i>Trifolium campestre</i>	1	I		
<i>Veronica spicata</i>	1-3	III		
Cynodonto-Festucion				
<i>Cynodon dactylon</i>	2-20	V		
Chenopodietea, Chenopodietea & Secalietea				
<i>Ambrosia artemisiifolia</i>	2	I		
<i>Anchusa officinalis</i>	2	I		
<i>Conyza canadensis</i>	0.5	I		
<i>Echium vulgare</i>	3	I		
<i>Erodium cicutarium</i>	3	I		
<i>Salsola kali</i>	1-3	III		
<i>Setaria viridis</i>	3-5	I		
<i>Tragus racemosus</i>	15-20	I		
Aphanion				
<i>Apera spica-venti</i>	1-5	I		
Arrhenatheretea				
<i>Plantago lanceolata</i>	1-2	II		
Secalietea				
<i>Anthemis austriaca</i>	1	I		
<i>Crepis rhoeadifolia</i>	2-3	II	1	I
<i>Crepis tectorum</i>	1	I		
Corynephorretalia				
<i>Cerastium semidecandrum</i>	1-5	V	0.5-1	II
<i>Rumex acetosella</i>			1	II
<i>Thymus serpyllum</i>			0.5-1	II
<i>Veronica dillenii</i>	1	I		
Quercetea pubescentis-petraeae				
<i>Lithospermum officinale</i>	1	I		
Moss-lichen synusium			2-50	V
Polygonion avicularis				
<i>Polygonum aviculare</i> agg.			0.5-1	II