

Solonetz meadow vegetation (*Beckmannion eruciformis*) in East-Hungary – an alliance driven by moisture and salinity

Solonetzgrasland-Vegetation (*Beckmannion eruciformis*) im östlichen Ungarn – ein von Feuchtigkeit und Salinität bestimmter Verband

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Abstract

Wet meadows are transitional habitats between wetlands and dry-mesophilous grasslands; thus, they are vital in sustaining biodiversity as sources, stepping stones and green corridors of species dispersal. It is especially valid for inland alkali vegetation, where high landscape-scale patchiness is typical and rapid shifts between vegetation types occur frequently. Solonetz meadows (*Beckmannion eruciformis*) are among the best-preserved open habitats in Europe harbouring a unique flora including several endemics. Besides their importance, studies on the vegetation of solonetz meadows are scarce even though this knowledge would be vital for their effective conservation and management. Using own records and literature data, we provide a synthesis of the alliance *Beckmannion eruciformis* to characterise its associations floristically and ecologically in five regions along the river Tisza, East Hungary. We studied three associations of the alliance: (i) *Agrostio stoloniferae-Alopecuretum pratensis*, (ii) *Agrostio stoloniferae-Beckmannietum eruciformis* and (iii) *Agrostio stoloniferae-Glycerietum pedicellatae*. We found that solonetz meadow associations were separated along a moisture gradient with *Agrostio stoloniferae-Alopecuretum pratensis* at the drier end and *Agrostio stoloniferae-Glycerietum pedicellatae* at the wet end. This gradient was also justified by the distribution of the phytosociological groups. The proportion of species of *Festuco-Brometea* division was the highest in *Agrostio stoloniferae-Alopecuretum pratensis*, while the proportion of *Cypero-Phragmitetea* species was the highest in *Agrostio stoloniferae-Glycerietum pedicellatae*. Species of *Puccinellio-Salicornetea* had the highest proportion in *Agrostio stoloniferae-Beckmannietum eruciformis*, indicating the high soil salinity of this association. Our results suggest that *Agrostio stoloniferae-Alopecuretum pratensis* association plays an important role in preserving the continental flora elements of the surrounding dry grasslands. The ecological indicator values for soil moisture and salinity suggest that in case of the studied solonetz meadow associations, humidity increases with decreasing elevation, while salinity is highest at medium elevations. Our results suggest that *Agrostio stoloniferae-Beckmannietum eruciformis* is a transition towards salt marsh associations, while *Agrostio stoloniferae-Glycerietum pedicellatae* is a transition towards freshwater marshes. Our results show that preserving solonetz meadows is an important task for nature conservation as they have a crucial role in maintaining landscape-scale species and habitat diversity and act as buffer zones around wetlands.

Keywords: alkali grasslands, *Festuco-Puccinellietea*, hay-meadows, landscape-scale diversity, moisture gradient, salinity gradient

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

1. Introduction

Grassland biodiversity research became a hot topic in vegetation science; in the last few years several special features were compiled focusing on patterns and processes of grassland biodiversity in the Palearctic (BECKER et al. 2013, GALVÁNEK et al. 2012, HABEL et al. 2013, DENGLER et al. 2014). These special features focused mostly on dry and mesic grasslands, because these habitats count to the most species-rich habitats in the world at the small scale (WILSON et al. 2012). On the other hand, macrophytes became one of the core groups of water quality assessment in wetlands (EU WATER FRAME DIRECTIVE 2000, TÚRI et al. 2013). Thus, vegetation research in wetlands became more intensive in the last few decades (ENGELHARDT & RITCHIE 2001). Wet grasslands as transitional habitats between wetlands and dry-mesic grasslands gained proportionally less attention, although they harbour high number of species of adjacent habitats and play an important role in sustaining biodiversity (mesoecotones, RŰSIŇA et al. 2013), acting as diaspore sources or stepping stones and green corridors for species dispersal (JANIŠOVÁ et al. 2013).

These findings are especially valid for the inland alkali vegetation, where high landscape-scale patchiness is typical and rapid shifts between vegetation types occur frequently (KELEMEN et al. 2013, VALKÓ et al. 2014). Former studies on inland alkali vegetation dealt mostly with alkali wetlands and salt marshes (EGAN & UNGAR 2000, WANNER et al. 2014) or with dry alkaline grasslands (KELEMEN et al. 2013, VALKÓ et al. 2014). Only a few studies focused on saline meadows (but see BODROGKÖZY 1965, 1970, HEJNÝ 1960, DÍTĚ et al. 2012) and these associations are underrepresented in vegetation databases (see ELIÁŠ et al. 2013, WILLNER et al. 2013). Thus, there is an urgent need for a synthetic approach and fine-tuned studies to analyse biodiversity patterns in these type of grasslands.

Continental saline wet meadows (*Scorzonero-Juncetalia gerardii* Vicherek 1973) are among the best-preserved open habitats in Europe. They are typical of the Pannonian biogeographical region and harbour several species listed in Annex I of the Habitats Directive and endemics like *Cirsium brachycephalum*, *Limonium gmelinii* spp. *hungarica*, *Plantago schwarzenbergiana* and *Puccinellia limosa* (ELIÁŠ et al. 2013, TÖRÖK et al. 2012). Continental saline wet meadows are included in the priority habitat type “Pannonic salt steppes and salt marshes (1530)” of the Natura 2000 network. For the effective conservation and management of these meadows, knowledge on their landscape-scale and local patterns of species composition across regions is necessary.

The “Continental saline wet meadows” habitat group contains the alliances of Pannonian wet saline meadows on solonetz soils (*Beckmannion eruciformis* Soó 1933) and Pannonian wet saline meadows on solonchak soils (*Scorzonero-Juncion gerardii* (Wendelberg 1943) Vicherek 1973) (BORHIDI et al. 2012, MOLNÁR & BORHIDI 2003). In the present study we use own vegetation records and literature data to provide a synthesis of the alliance *Beckmannion eruciformis* (mentioned as ‘solonetz meadows’ hereafter), and to characterise their associations floristically and ecologically in five regions along the river Tisza, East Hungary.

2. Materials and Methods

2.1 General description and site characteristics of solonetz meadows

Solonetz meadows are typical for the Great Hungarian Plain along the Tisza River and its tributary streams in a total extension of around 72,000 hectares (MOLNÁR et al. 2008). They are typical of areas with continental climate and are characterised by a high groundwater level, by at least moderate salt

concentration in the soil, groundwater and surface water (Na_2CO_3 , NaCl , rarely K_2CO_3 and KCl ; TÖRÖK et al. 2012). Their stands are generally inundated from early spring even until midsummer (KELEMEN et al. 2013). *Beckmannion eruciformis* alliance is formed on solonetz soils. A moderate salt accumulation zone is present in the deeper horizons (usually in horizon B), and the mould content of horizon A is high. The pH near to the soil surface is almost neutral but becomes basic with increasing depth (BODROGKÖZY 1965).

In alkali landscapes, there is a clear vegetation gradient from salt marshes to alkali short grass steppes based on the elevation, where solonetz meadows are typically situated in an intermediate position between salt marshes and alkaline dry grasslands (Appendix S1a; ELIÁŠ et al. 2013, KELEMEN et al. 2013). Only up to a few metres differences are typical between the endpoints of the whole vegetation gradient (VALKÓ et al. 2014). Spatial distribution of alkali vegetation is also influenced by changes in soil characteristics; thus, the high soil heterogeneity typical for alkali landscapes results in a very complex vegetation mosaic (TÓTH & KERTÉSZ 1996, VALKÓ et al. 2014). Associations of the *Beckmannion eruciformis* alliance can form either a narrow transitional zone or larger homogenous stands between dry alkali steppes and marshes, composing a mosaic structure with other alkali associations.

Beside the natural stands, there are extensive stands of solonetz meadows which originated by anthropogenic influences initiating secondary salinisation processes (MOLNÁR & BORHIDI 2003). The natural stands of solonetz meadows are present in the Pannonian Plain since the Pleistocene with considerable extension (BARCZI et al. 2006, SÜMEGI et al. 2013). Secondary solonetz meadows of the Pannonian Plain are generally the result of the river regulations (like the Tisza and its tributary streams; 19th century) and the landscape-scale water management campaigns (drainage and watering) of the socialist era (MOLNÁR & BORHIDI 2003, TÖRÖK et al. 2012). These secondary solonetz meadows are generally less diverse, harbouring lower proportion of endemics and salt-tolerant species than pristine solonetz meadows (MOLNÁR & BORHIDI 2003). In our study we focused on pristine solonetz meadows which were not or just slightly affected by secondary salinisation (BARCZI et al. 2006).

2.2 Species pool of the solonetz meadows

Solonetz meadows usually have two herb layers. The upper herb layer is generally formed of tall-grass species like *Agrostis stolonifera*, *Alopecurus pratensis*, *Beckmannia eruciformis*, *Elymus repens* and *Glyceria fluitans* ssp. *poiformis* (BORHIDI et al. 2012, TÖRÖK et al. 2012). Characteristic species of salt marshes (*Bolboschoenus maritimus*), non-alkali meadows (*Phalaris arundinacea*) and dry alkali steppes (*Achillea collina* and *Limonium gmelini* ssp. *hungarica*) are often present in the vegetation. Several species, like *Alopecurus geniculatus*, *Eleocharis palustris*, *E. uniglumis*, *Myosurus minimus*, *Pholiurus pannonicus* and *Plantago tenuiflora* frequently occur and indicate silt accumulation processes on the soil surface. The most characteristic endemic species of solonetz meadows is *Cirsium brachycephalum*. This species listed in Annex I of the Habitats Directive can form dense stands up to several hectares (Appendix S1b).

Solonetz meadows are sensitive to the changes of water availability.

After consecutive dry years their species pool can shift towards Pannonian dry alkaline grasslands (Appendix S1c; *Festucion pseudovinae* Soó 1933) while after a longer wet period they can have salt marsh (order *Bolboschoenetalia maritimi* Hejný 1967) characteristics (MOLNÁR & BORHIDI 2003). In dry years, the cover of *Agrostis stolonifera* decreases and some dry grassland species (*Festuca pseudovina*, *Poa angustifolia*, *Scorzonera cana* and *Trifolium* spp.) can increase in cover. In dry years with some extra nutrient surplus, weedy thistle species (*Cirsium arvense* and *C. vulgare*) may invade solonetz meadows.

2.3 Studied solonetz meadow associations

The most widespread associations of the alliance *Beckmannion eruciformis* are: (i) *Agrostio stoloniferae-Alopecuretum pratensis* Soó 1933 corr. Borhidi 2003, (ii) *Agrostio stoloniferae-Beckmannietum eruciformis* Rapaics ex Soó 1930 and (iii) *Agrostio stoloniferae-Glycerietum pedicellatae* Magyar ex Soó 1933 corr. Borhidi 2003. We abbreviated these association names as *Agrostio-Alopecuretum*, *Agrostio-Beckmannietum* and *Agrostio-Glycerietum* hereafter in the text.

2.3.1 *Agrostio stoloniferae-Alopecuretum pratensis*

This widespread mesophilous solonetz meadow association is typical at the highest elevations compared to the other two solonetz meadow associations, on soils with moderate to low salt contents (TÖRÖK et al. 2012). Soil horizons A and B are generally salt-free; salts and/or CaCO_3 can accumulate only in the deeper soil layers (BODROGKÖZY 1965). The stands of this association are covered by water from early spring till early summer. Then they get dry also in the deeper soil layers. Thus, polygonal patterns of deep cracks are formed in the soil (TÖRÖK et al. 2012). This association is often positioned between Pannonian dry alkaline grasslands (*Festucion pseudovinae*) and other solonetz meadow associations (*Agrostio-Beckmannietum* or *Agrostio-Glycerietum*; BORHIDI et al. 2012). Depending on the amount of winter and spring precipitation, the stands of *Agrostio-Alopecuretum* can have either dry grassland or a salt marsh character. *Agrostio-Alopecuretum* stands are rich in species of neighbouring associations, and the species composition can be highly variable, driven by changes in site conditions and water availability (BORHIDI et al. 2012). *Agrostio-Alopecuretum* stands are usually utilised as hay meadows or pastures for cattle. In certain cases *Agrostio-Alopecuretum* stands are grazed by sheep (TÖRÖK et al. 2012).

Dominant grass species are *Alopecurus pratensis*, *Elymus repens* and *Agrostis stolonifera*. Both consecutive dry summers and cessation of grazing in formerly grazed areas can result in an increased dominance of *Elymus repens* (BODROGKÖZY 1965). Steppe species such as *Achillea collina*, *Festuca pseudovina*, *Trifolium angulatum*, *T. retusum* and *T. striatum* may spread into dried stands. Tussocks are typical in stands with stable water regime, regular water supply and cattle grazing (BORHIDI et al. 2012). In stands where the salt accumulation is higher in the upper horizons, *Limonium gmelini* ssp. *hungarica* may appear (BODROGKÖZY 1965). In wet stands of *Agrostio-Alopecuretum* association, *Juncus* species (*Juncus effusus*, *J. conglomeratus*, *J. compressus* and *J. gerardi*) occur with high frequency and cover (BORHIDI et al. 2012).

2.3.2 *Agrostio stoloniferae-Beckmannietum eruciformis*

Agrostio-Beckmannietum association is typical of soils with moderate to high salt-content (TÖRÖK et al. 2012). This solonetz meadow association is usually in an intermediate position between *Agrostio-Alopecuretum* and *Agrostio-Glycerietum* associations. Surface layer of the soil has generally a loose structure, but in the deeper B horizon there is a thick columnar structure (BODROGKÖZY 1965). *Agrostio-Beckmannietum* has a long-lasting surface water cover from spring till early summer, and it dries out regularly during midsummer (DÍTĚ et al. 2011, 2012). *Agrostio-Beckmannietum* stands are usually not used for hay-making because their wet soil and tussocks prohibit mechanical harvest. *Agrostio-Beckmannietum* stands are generally used for cattle grazing (TÖRÖK et al. 2012).

Similarly to the other two solonetz meadow associations grass dominance is typical in *Agrostio-Beckmannietum* caused by the high cover of *Alopecurus pratensis*, *Agrostis stolonifera* and *Beckmannia eruciformis*. Halophyte species, like *Aster tripolium* ssp. *pannonicum* and *Puccinellia limosa* are typical in this association. Due to the high salt content and permanent water cover till midsummer species characteristic of salt marshes like *Bolboschoenus maritimus* often occur (BORHIDI et al. 2012).

2.3.3 *Agrostio stoloniferae-Glycerietum pedicellatae*

Agrostio-Glycerietum is typical at the lowest elevations among solonetz meadows, generally covered by water until late summer (BORHIDI et al. 2012). The soil surface dries out only in very dry summers (BODROGKÖZY 1965). The soil is eluviated without a definite column structure, and a low salt-content is typical (BODROGKÖZY 1965). This association often forms a transition between solonetz meadow and salt marsh associations. Stands of this association are often unmanaged as they cannot be mown by machinery because of the permanently wet soil. When the surroundings are grazed, cattle may feed here accidentally. Tussock formation is not typical in this association (BORHIDI et al. 2012, TÖRÖK et al. 2012). In this association the dominant grasses are *Glyceria fluitans* ssp. *poiformis* and *Agrostis stolonifera*. As subordinate species *Beckmannia eruciformis*, *Eleocharis palustris*, *Epilobium*

tetragonum and *Lycopus europaeus* are typical. Several species characteristic of salt marshes like *Bolboschoenus maritimus*, *Schoenoplectus lacustris* ssp. *lacustris* and *S. lacustris* ssp. *tabernaemontani* occurs regularly in the vegetation.

2.4 Study sites

We collected altogether 155 relevés from five regions in the Hungarian Great Plain, along the river Tisza (East Hungary, Fig. 1). We used published relevés of BODROGKÖZY (1965) from the Hortobágy region and GALLÉ & KÖRMÖCZI (2004) from the Jászság region. The location, number and source of relevés used in the paper are summarized in Table 1. We studied the following associations: (i) *Agrostio-Alopecuretum* (Fig. 2), (ii) *Agrostio-Beckmannietum* (Fig. 3) (iii) *Agrostio-Glycerietum* (Fig. 4). The nomenclature follows BORHIDI et al. (2012) for syntaxa and KIRÁLY (2009) for taxa.

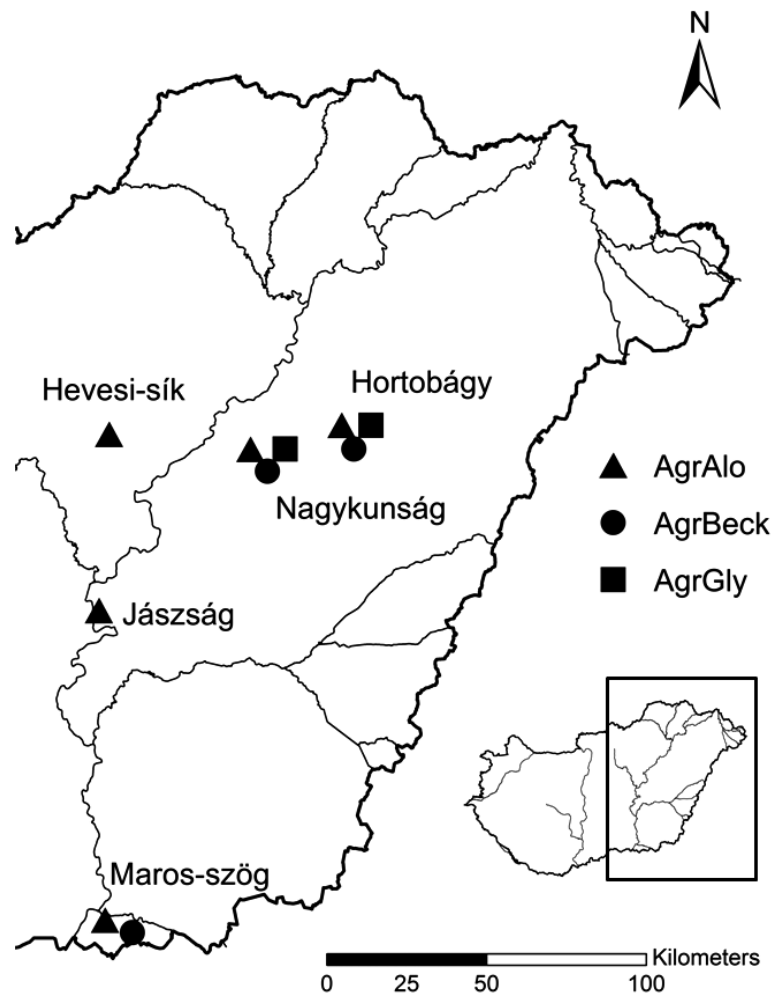


Fig. 1. Location of the study sites in East Hungary. Notations - Abbreviation of associations: AgrAlo – *Agrostio stoloniferae-Alopecuretum pratensis*, AgrBeck – *Agrostio stoloniferae-Beckmannietum eruciformis*, AgrGly – *Agrostio stoloniferae-Glycerietum pedicellatae*.

Abb. 1. Lage der Untersuchungsgebiete in Ost-Ungarn. Abkürzungen der Assoziationen s.o.

Table 1. Summary of relevés of the solonetz meadows. Notations: * – relevés of GALLÉ & KÖRMÖCZI (2004); ** – relevés of BODROGKÖZY (1965).

Tabelle 1. Zusammenfassung der Vegetationsaufnahmen des Solonetzgraslands. Anmerkungen: * – Aufnahmen von GALLÉ & KÖRMÖCZI (2004); ** – Aufnahmen von BODROGKÖZY (1965).

Association	Region	Location	No. of relevés
<i>Agrostio-Alopecuretum</i>	Hevesi-sík	Heves	5
	Jászság	Rákóczi-falva	5*
	Nagykunság	Nagyiván	20
	Nagykunság	Egyek	10
	Hortobágy	Balmazújváros	10
	Hortobágy	Nagyhegyes	10
	Maros-szög	Szeged	9
	Hortobágy	Hortobágy	15**
<i>Agrostio-Beckmannietum</i>	Hortobágy	Balmazújváros	6
	Nagykunság	Nagyiván	20
	Nagykunság	Egyek	10
	Maros-szög	Szeged	5
	Hortobágy	Hortobágy	10**
<i>Agrostio-Glycerietum</i>	Hortobágy	Hortobágy	10**
	Nagykunság	Egyek	5
	Hortobágy	Balmazújváros	5



Fig. 2. Stand of *Agrostio stoloniferae-Alopecuretum pratensis* (Photo: Balázs Deák).

Abb. 2. Bestand des *Agrostio stoloniferae-Alopecuretum pratensis* (Foto: Balázs Deák).



Fig. 3. Stand of *Agrostio stoloniferae-Beckmannietum eruciformis* (Photo: Balázs Deák).

Abb. 3. Bestand des *Agrostio stoloniferae-Beckmannietum eruciformis* (Foto: Balázs Deák).



Fig. 4. Stand of *Agrostio stoloniferae-Glycerietum pedicellatae* (Photo: Balázs Deák).

Abb. 4. Bestand des *Agrostio stoloniferae-Glycerietum pedicellatae* (Foto: Balázs Deák).

2.5 Statistical analysis

Cover-based DCA ordination was used to explore the differences among associations in the five study regions (CANOCO 4.5; LEPŠ & ŠMILAUER 2003). To reveal landscape-scale compositional differences, we used percentage cover scores from all relevés listed in Table 1 for the DCA. Mean cover scores of all detected species are listed in Appendix S2. We used phytosociological groups and flora elements to characterise the composition of the associations (BORHIDI 1995). Flora elements were categorised based on SIMON (2000) and grouped into the following six merged groups: adventive group (adventives), cosmopolitan group (cosmopolitans), European group (circumboreal, European, Eurasian), Mediterranean group (atlantic-submediterranean, submediterranean and Balkan), continental group (continental, Pontic-Mediterranean, Pontic, Pontic-Pannonian and Turanian), and endemic group (Pannonian). Species were assigned into phytosociological groups at the division level (SIMON 2000) to the following seven categories: *Lemno-Potametea*, *Cypero-Phragmitetea*, *Molinio-Arrhenatheretea*, *Puccinellio-Salicornetea*, *Festuco-Brometea*, *Chenopodio-Scleranthetea* and Indifferent.

We compared the ecological characteristics of the solonetz meadow, salt marsh (*Bolboschoenetum maritimi* Egger 1933 *sensu latissimo*, the most similar to *Astero pannonici-Bolboschoenetum compacti* see also HROUDOVÁ et al. 2009) and freshwater marsh (*Typhetum angustifoliae* Soó 1927) associations (Appendix S1d and S1e). Cover-weighted relative ecological indicator values for soil moisture (WB) and salinity (SB) were calculated using percentage cover scores based on ELLENBERG et al. (1992) modified by BORHIDI (1995). For these analyses, we used own relevés (15 relevés per association) from a single region (Hortobágy) to eliminate the effect of the regional species pools in different landscapes (DENGLER et al. 2014). Cover-weighted WB and SB scores of the solonetz meadow and marsh associations were compared using Kruskal-Wallis and Tukey tests in SPSS 20.0 (ZAR 1999).

3. Results and Discussion

3.1 General floristic composition and influence of the regional species pool

In the DCA ordination relevés of the three associations were separated along the 1st axis (Fig. 5). The 1st DCA axis represented the moisture gradient and showed an increase towards the highest scores. Accordingly, *Agrostio-Alopecuretum* was situated at the dry end of the moisture gradient, *Agrostio-Beckmannietum* in the middle and *Agrostio-Glycerietum* was on the wet end of the moisture gradient. The moisture gradient was also indicated by the distribution of the phytosociological groups along the 1st DCA axis (Fig. 5). The proportion of *Festuco-Brometea* species typical for dry grasslands was the highest in *Agrostio-Alopecuretum* association (Fig. 5; Table 2). Conversely, the proportion of *Cypero-Phragmitetea* species characteristic for salt- and freshwater marshes was the highest in *Agrostio-Glycerietum* (Fig. 5; Table 2). At the middle of the gradient the relevés of *Agrostio-Beckmannietum* and relevés of the wetter stands of *Agrostio-Alopecuretum* were placed, where we detected a high proportion of the *Puccinellio-Salicornetea* species. These species are typical in alkali landscapes, and are characterised generally by moderate moisture requirements.

The DCA ordination showed that *Agrostio-Alopecuretum* was a heterogeneous association having stands with a dry-mesophilous character. The driest stands of *Agrostio-Alopecuretum* formed a compact group (Fig. 5) with several dry grassland species like *Festuca pseudovina*, *Limonium gmelinii*, *Poa angustifolia*, *Trifolium angulatum* and *T. striatum*. These species are typical for dry steppes (*Festucion pseudovinae* Soó 1993) and alkali-grass meadows (*Puccinellion limosae* Varga & V. Sipos ex Borhidi 2003) (TÖRÖK et al. 2012). Environmental characteristics of this association offer proper site conditions for the establishment of species characteristic to the surrounding alkaline dry grasslands; thus,

Table 2. Cover-weighted proportions of phytosociological groups in the three studied solonetz meadow associations. Abbreviation of associations: AgrAlo – *Agrostio stoloniferae-Alopecuretum pratensis*, AgrBec – *Agrostio stoloniferae-Beckmannietum eruciformis*, AgrGly – *Agrostio stoloniferae-Glycerietum pedicellatae*.

Tabelle 2. Nach Deckungsgrad gewichtete Anteile pflanzensoziologischer Gruppen in den drei untersuchten Solonetzgrasland-Assoziationen. Abkürzungen der Assoziationen s.o.

	AgrAlo	AgBec	AgrGly
<i>Lemno-Potametea</i>	0.0	0.1	0.3
<i>Cypero-Phragmitetea</i>	3.7	4.2	53.7
<i>Molinio-Arrhenatheretea</i>	6.6	4.1	3.9
<i>Puccinellio-Salicornetea</i>	6.6	26.7	6.5
<i>Festuco-Brometea</i>	1.6	0.0	0.0
<i>Chenopodio-Scleranthetea</i>	0.1	1.0	1.3
Indifferent	81.4	64.0	34.3

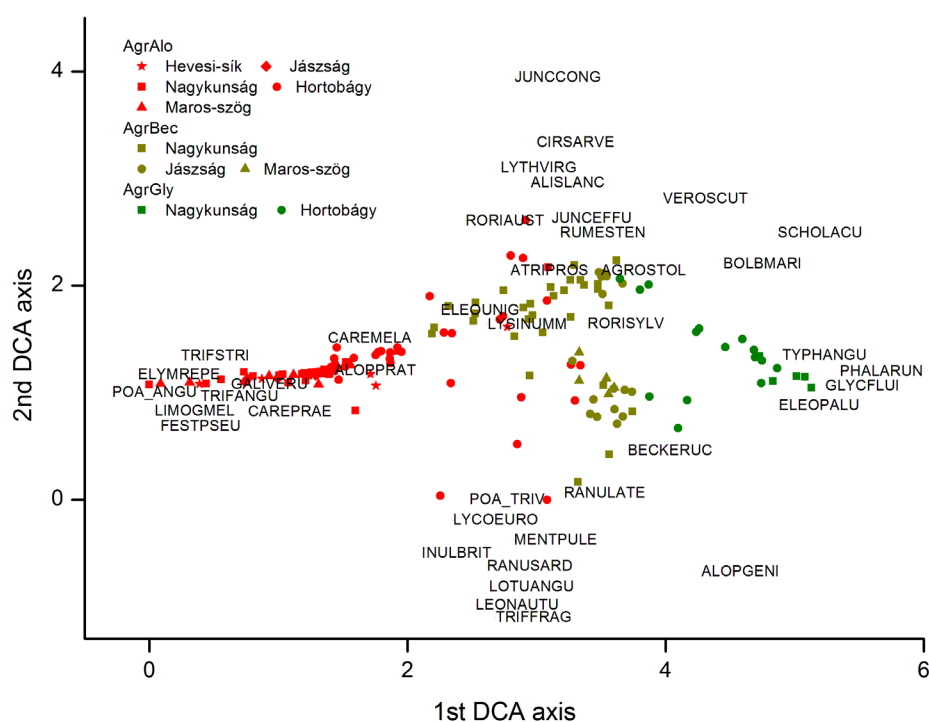


Fig. 5. DCA ordination of the solonetz meadow associations in five regions of East-Hungary based on percentage cover scores. Abbreviation of associations, see Table 2. Species are abbreviated using the first four letters of their genus and species names.

Fig. 5. DCA-Ordination der Solonetzgrasland-Assoziationen in fünf Regionen Ost-Ungarns basierend auf Prozent-Deckungswerten. Abkürzungen der Assoziationen s. Tabelle 2. Die Arten sind durch die ersten vier Buchstaben des Gattungsnamens und Artepithetons abgekürzt.

Agrostio-Alopecuretum association plays a vital role in preserving and maintaining the species pool of the surrounding dry grasslands. The analysis of flora element groups also confirmed this pattern (Table 3). We found that the proportion of the continental flora elements was high in *Agrostio-Alopecuretum* association. These continental elements, like *Festuca pseudovina*, *Lotus angustissimus*, *Scorzonera cana* and *Trifolium retusum* were mainly typical to alkaline dry grasslands. Two Pannonian endemic species, *Limonium gmelinii* and *Puccinellia limosa* were present in *Agrostio-Alopecuretum*, which are also typical species of *Festuco-Puccinellietea* class.

Elymus repens was a typical species of dry and slightly degraded *Agrostio-Alopecuretum* stands. High cover of *E. repens* typically occurs after the cessation of high intensity grazing (TÖRÖK et al. 2012). All relevés of the southern regions (Jászság and Maros-szög) were at the drier end. Some relevés of *Agrostio-Alopecuretum* were intersected with those of *Agrostio-Beckmannietum*. These stands were characterised by sufficient water supply and were only typical for the regions Hortobágy and Nagyunság. Their species pool was similar to *Agrostio-Beckmannietum*, but they had some differential species, like *Lycopus europaeus*, *Mentha pulegium* and *Poa trivialis*. As *Alopecurus pratensis* was typical for both the dry and wet stands of *Agrostio-Alopecuretum* and also for *Agrostio-Beckmannietum*, it was situated in a central position on the DCA ordination. Even though *Agrostis stolonifera* was a characteristic species of the *Agrostio-Alopecuretum* association it was typical for the wettest stands and also occurred in *Agrostio-Beckmannietum* which in general had better water supply.

Table 3. Cover-weighted proportions of Flora elements in the three studied solonetz meadow associations. Abbreviation of associations see Table 2.

Table 3. Nach Deckungsgrad gewichtete Anteile von Florenelementen in den drei untersuchten Solonetzgrasland-Assoziationen. Abkürzungen der Assoziationen s. Tabelle 2.

Flora elements	AgrAlo	AgBec	AgrGly
<i>Adventive group</i>			
Adventives	0.1	0.1	0.0
<i>Cosmopolitan group</i>			
Cosmopolitans	9.5	46.0	38.8
<i>European group</i>			
Circumboreal	17.2	29.6	5.2
Eurasian	61.6	14.7	6.2
European	3.3	2.1	47.8
<i>Mediterranean group</i>			
Atlantic-Submediterranean	0.3	0.0	0.0
Submediterranean	0.5	1.4	0.0
Balkan	0.8	0.0	0.0
<i>Continental group</i>			
Continental	3.9	5.0	0.8
Pontic-Mediterranean	1.3	0.3	0.0
Pontic	0.5	0.2	1.2
Pontic-Pannonian	0.0	0.4	0.0
Turanian	0.1	0.0	0.0
<i>Endemic group</i>			
Pannonian	1.0	0.2	0.0

The relevés of *Agrostio-Beckmannietum* showed a heterogeneous pattern; they were well separated from *Agrostio-Glycerietum* but had a considerable overlap with the *Agrostio-Alopecuretum* association. *Agrostis stolonifera* and *Beckmannia eruciformis* were the most typical species of this association. Both species demand moist conditions till mid-summer. Proportion of continental species was considerable here, containing *Lythrum virgatum*, *Ranunculus lateriflorus* and *Rumex stenophyllus* (Table 3). Continental flora elements typical for dry grasslands were missing except *Lotus angustissimus*. The endemic *Cirsium brachycephalum* was found exclusively in *Agrostio-Beckmannietum*. Species of *Puccinellio-Salicornetea* division had the highest proportion in *Agrostio-Beckmannietum*, because a high soil salinity is typical in this solonetz meadow association (Table 2).

Agrostio-Glycerietum formed a more homogeneous group compared to the other associations. Relevés of the two regions (Hortobágy and Nagyunság) were clearly separated. The most abundant species of *Agrostio-Glycerietum* was *Glyceria fluitans* ssp. *poiformis*. As this association was at the wet end of the moisture gradient within the *Beckmannion eruciformis* alliance, it formed a transition between the solonetz meadows and the salt marshes. This position was also confirmed by the high proportion of *Cypero-Phragmitetea* species (Table 3). Several species typical of salt and freshwater marshes were present in high cover in *Agrostio-Glycerietum*, e.g. *Bolboschoenus maritimus*, *Eleocharis palustris* and *Typha angustifolia*. Proportion of continental elements was low in *Agrostio-Glycerietum*, only *Carex melanostachya*, *Ranunculus lateriflorus* and *Rumex stenophyllus* were present with low cover and frequency (Table 2). No endemic species were found in this association.

3.2 Relative ecological indicator values for soil moisture (WB) and salinity (SB)

Soil moisture and salinity was found to be important factors affecting vegetation composition in inland saline communities (DAVY et al. 2011, WANNER et al. 2014, KELEMEN et al. 2013, ELIÁŠ et al. 2013). A recent study proved the relationship between vegetation type, soil humidity and salinity along an elevation gradient in *Festuco-Puccinellietea* associations in solonchak soils (VALKÓ et al. 2014). In their study, low humidity and medium salinity was typical at the highest-elevated *Artemisia santonici-Festucetum pseudovinae* Soó in Máthé corr. Borhidi 1996 association, while the highest humidity and medium salinity was typical at the lowest-elevated *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943 associations. The highest salinity was associated with a low humidity in *Puccinellietum limosae* Magyar ex Soó 1933 at intermediate elevations.

Our analyses of relative ecological indicator values for soil moisture showed that cover-weighted WB scores were lowest in *Agrostio-Alopecuretum* and highest in *Agrostio-Glycerietum* among the studied solonetz meadow associations (Table 4). Cover-weighted ecological indicator values for soil salinity (SB) scores were highest in *Agrostio-Beckmannietum* and lowest in *Agrostio-Glycerietum* among solonetz meadow associations (Table 4). These results suggest a similar pattern of moisture-salinity-elevation relationships in solonetz meadows, like in case of *Festuco-Puccinellietea*: humidity generally increases with decreasing elevation, while salinity is the highest at medium elevations, but this observation needs to be confirmed by further experimental measurements of soil parameters and elevation.

The relationship between cover-weighted WB and SB scores of the studied associations showed that *Agrostio-Alopecuretum* was at the driest end of the moisture gradient, followed by *Agrostio-Beckmannietum*, which slightly overlapped with *Agrostio-Alopecuretum* and *Agrostio-Glycerietum* associations (Fig. 6). *Agrostio-Glycerietum* association was character-

Table 4. Cover-weighted relative ecological indicator values for soil moisture (WB) and salinity (SB) scores of the studied solonetz meadow and marsh associations (mean±SD). Different superscripted letters indicate significant differences (Kruskal-Wallis tests, $p < 0.001$). Abbreviation of associations: AgrAlo – *Agrostio stoloniferae-Alopecuretum pratensis*, AgrBeck – *Agrostio stoloniferae-Beckmannietum eruciformis*, AgrGly – *Agrostio stoloniferae-Glycerietum pedicellatae*; Bolmar – *Bolboschoenetum maritimi sensu latissimo*; Typang – *Typhetum angustifoliae*.

Table 4. Nach Deckungsgrad gewichtete relative ökologische Zeigerwerte für Bodenfeuchte (WB) und Salinität (SB) der untersuchten Solonetzgrasland- und Marsch-Assoziationen (Mittelwert±SD). Unterschiedliche hochgestellte Buchstaben zeigen signifikante Unterschiede an (Kruskal-Wallis-Tests, $p < 0.001$). Abkürzungen der Assoziationen s.o.

	AgrAlo	AgrBec	AgrGly	Bolmar	Typang
Cover-weighted WB scores	6.82±0.45 ^a	7.64±0.48 ^{ab}	8.17±0.51 ^b	9.83±0.24 ^c	9.89±0.24 ^c
Cover-weighted SB scores	1.39±0.48 ^{ab}	3.17±1.60 ^c	1.09±0.51 ^a	2.06±0.63 ^{bc}	1.09±0.36 ^a

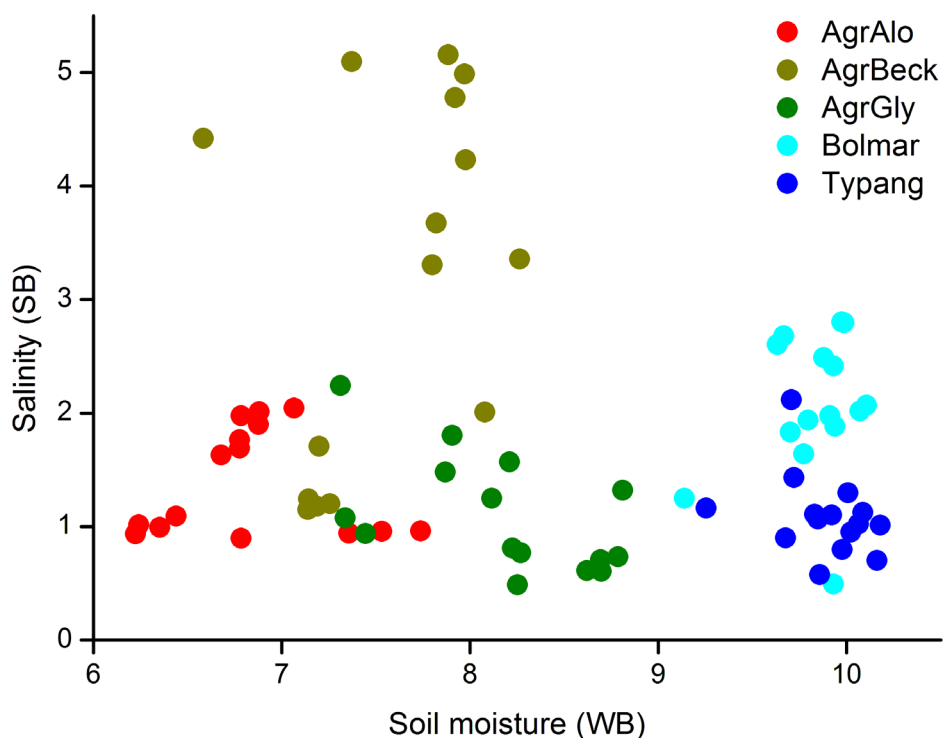


Fig. 6. Relationships between cover-weighted ecological indicator values for soil humidity (WB) and salinity (SB) in solonetz meadows, salt marshes and freshwater marshes in the Hortobágy region. Abbreviation of associations see Table 4.

Fig. 6. Beziehungen zwischen nach Deckungsgrad gewichteten ökologischen Zeigerwerten für Bodenfeuchte (WB) und Salinität (SB) im Solonetzgrasland, in Salzmarschen und in Süßwassermarschen in der Hortobágy-Region. Abkürzungen der Assoziationen s. Tabelle 4.

ised by the highest cover-weighted WB scores among solonetz meadows. Salt and freshwater marshes were at the wet end of the gradient with higher cover of hygrophite species compared to the solonetz meadows. Species typical for dry and semi-humid habitats (WB 2–5; *Artemisia santonicum*, *Pholiurus pannonicus* and *Polygonum aviculare*) were only present with low frequency and cover scores in all the studied associations. Species typical in fresh soils (WB 6) included *Alopecurus pratensis*, which had the highest cover in *Agrostio-Alopecuretum*, resulting in the shift of this association towards to the driest end of the moisture gradient. *Agrostis stolonifera* and *Beckmannia eruciformis* had the highest cover scores from the group of plants of moist soils (WB 7–8), especially in *Agrostio-Beckmannietum* and *Agrostio-Glycerietum*. Species characteristic to wet and frequently flooded soils (WB 9–10) had low cover scores in *Agrostio-Alopecuretum* and *Agrostio-Beckmannietum*. These species included *Bolboschoenus maritimus*, *Glyceria fluitans* ssp. *poiformis* and *Typha angustifolia* with a considerable cover in *Agrostio-Glycerietum* and in marsh associations, which suggests the similarity of their species pool and environmental conditions. Aquatic plants (WB 11–12) were present with low cover scores in *Agrostio-Glycerietum* (*Lemna minor* and *Ranunculus aquatilis*) and they were missing from the other two solonetz meadows associations.

We found that *Agrostio-Beckmannietum* was characterised by the highest cover of salt-tolerant species (Fig. 6, Table 4, see also DÍTĚ et al. 2012). The proportion of salt-tolerant species was the lowest in *Typhetum angustifoliae* marshes. Our results suggest that *Agrostio-Beckmannietum* might be a transition towards salt marsh associations (represented by *Bolboschoenetum maritimi sensu latissimo* in our study), while *Agrostio-Glycerietum* is a transition towards freshwater marshes (represented by *Typhetum angustifoliae* in our study) regarding SB and WB scores. The ratio of the group of species of non-alkaline soils (SB 0–1) was considerably lower in *Agrostio-Beckmannietum* and *Bolboschoenetum maritimi sensu latissimo* associations, which suggests the higher salt content of their soils. Cover of species of soils with low to medium salt content (SB 2–5) showed no clear trends in the studied associations. The group of species of soils with middle to high salt content (SB 6) had high cover scores in *Agrostio-Beckmannietum*, and it was mainly consisted of *Beckmannia eruciformis*. Polyhalin and euhalin species (SB 7–8; *Aster tripolium* and *Pholiurus pannonicus*) were present only in *Agrostio-Beckmannietum*.

4. Conclusions

We found that the three studied solonetz meadow associations were separated both in species composition and ecological indicator values along the moisture and salinity gradients. The association of *Agrostio-Alopecuretum* was characterised by low moisture and salinity, *Agrostio-Beckmannietum* by medium moisture but high salinity, and *Agrostio-Glycerietum* by high moisture and low salinity values. The ratio of the dry grassland species typical for the Pannonian alkaline dry grasslands (*Festuca pseudovina*, *Lotus angustissimus*, *Scorzonera cana*, *Trifolium angulatum* and *T. retusum*) was the highest in *Agrostio-Alopecuretum*. The proportion of the salt-tolerant species (like *Aster tripolium* and *Pholiurus pannonicus*) was the highest in *Agrostio-Beckmannietum*, due to the higher salt content of the soil compared to the other studied associations. *Agrostio-Glycerietum* was characterized by the low cover of salt-tolerant and alkaline dry grassland species and the high cover of

Cypero-Phragmitetea species. Pannonian endemic species (*Cirsium brachycephalum*, *Limonium gmelinii* and *Puccinellia limosa*) occurred only in *Agrostio-Alopecuretum* and *Agrostio-Beckmannietum* associations.

Our results suggest that preserving solonetz meadows is an important task for nature conservation as they have a crucial role in maintaining landscape-scale species and habitat diversity and act as buffer zones around salt marshes. We found that solonetz meadows harbour several continental and endemic species (MOLNÁR & BORHIDI 2003, TÖRÖK et al. 2012). Our results show that soil moisture considerably affects the species pool and the spatial distribution of these associations. Thus, for their conservation it is crucial to preserve or ensure the natural water regime typical for alkali landscapes (TÖRÖK et al. 2012). Regional decrease of groundwater level by river regulations or drainage especially threaten *Agrostio-Alopecuretum* and *Agrostio-Beckmannietum* associations. Our results also suggest that due to decreased water availability, the cover of *Elymus repens*, a ruderal competitor, can increase. In such cases, especially adjacent to degraded grassland stands or arable lands, the invasion of weedy species can be foreseen (TÖRÖK et al. 2010). Soil salt content is also expected to decrease due to the decrease in groundwater level (MOLNÁR & BORHIDI 2003, TÓTH & KERTÉSZ 1996), resulting in a decline of salt-tolerant continental elements typical for alkali landscapes in the future. Besides sustaining adequate water regime, for the maintenance of biodiversity in solonetz meadows, traditional land-use by grazing or mowing is essential, like in several other open grassland systems (DENGLER et al. 2012, ROSENTHAL et al. 2012, SCHWABE et al. 2013, TÖRÖK et al. 2012).

Erweiterte deutsche Zusammenfassung

Einleitung – Feuchtwiesen sind Übergangshabitats zwischen Biotopen nasser Standorte und mesophilen bis trockenen Grasländern. Sie sind daher wesentlich zur Erhaltung der Biodiversität als Sprünge, Trittsteine und grüne Korridore für die Ausbreitung von Arten. Dies gilt insbesondere für binnenländische Alkali-Vegetation, die auf der Landschaftsebene sehr lückenhaft verbreitet ist und bei denen rasche Wechsel zwischen den Vegetationstypen vorkommen. Solonetz-Grasland (*Beckmannion eruciformis*) gehört zu den am besten geschützten Offenland-Habitaten in Europa, und es beherbergt eine einzigartige Flora und Fauna einschließlich zahlreicher Endemiten.

Material und Methoden – Unter Verwendung von eigenen Aufnahmen und Literaturdaten (Tab. 1) legen wir eine Synthese des Verbandes *Beckmannion eruciformis* vor, um seine Assoziationen floristisch und ökologisch in fünf Regionen entlang des Flusses Tisza (Theiß) in Ost-Ungarn zu charakterisieren. Wir untersuchten drei Assoziationen des Verbandes: (1) *Agrostio stoloniferae-Alopecuretum pratensis*, (2) *Agrostio stoloniferae-Beckmannietum eruciformis* und (3) *Agrostio stoloniferae-Glycerietum pedicellatae*, ab hier als *Agrostio-Alopecuretum*, *Agrostio-Beckmannietum* und *Agrostio-Glycerietum* bezeichnet. Pflanzensoziologische Gruppen und Florenelemente wurden verwendet, um die Artenzusammensetzung der Assoziationen zu charakterisieren. Die ökologischen Charakteristika der Solonetzgrasland-Assoziationen, Salzmarschen (*Bolboschoenetum maritimi*) und Süßwassermarschen (*Typhetum angustifoliae*) wurden anhand Deckungsgrad-gewichteter ökologischer Zeigerwerte für Feuchtigkeit und Salinität verglichen.

Ergebnisse und Diskussion – Die Solonetzgrasland-Assoziationen waren entlang eines Feuchtigkeitsgradienten mit dem *Agrostio-Alopecuretum* am trockenen Ende und dem *Agrostio-Glycerietum* am nassen Ende getrennt (Abb. 5). Dieser Gradient wurde auch durch die Verbreitung der pflanzensoziologischen Gruppen bestätigt (Tab. 2). Der Anteil kontinentaler Florenelemente und von *Festuco-Brometea*-Arten war im *Agrostio-Alopecuretum* am höchsten (Tab. 3). Diese Tatsache legt nahe, dass diese Assoziation eine bedeutende Rolle für die Erhaltung der Florenelemente der umgebenden trocke-

nen Grasländer spielt. Der Anteil der *Cypero-Phragmitea*-Arten war im *Agrostio-Glycerietum* am höchsten (Tab. 3). Arten der *Puccinellio-Salicornetea* hatten den höchsten Anteil im *Agrostio-Beckmannietum* (Tab. 3), was auf den hohen Salzgehalt im Boden dieser Assoziation hindeutet. Die ökologischen Indikatorwerte für Bodenfeuchte und Salzgehalt legen nahe, dass im Fall der untersuchten Solonetzgrasland-Assoziationen die Feuchtigkeit mit sinkender Höhe steigt, während die Salinität in mittlerer Geländehöhe am höchsten ist (Tab. 4, Abb. 6). Unsere Ergebnisse weisen darauf hin, dass das *Agrostio-Beckmannietum* ein Übergang zu Salzmarsch-Assoziationen ist, während das *Agrostio-Glycerietum* einen Übergang zu Süßwassermarschen darstellt (Abb. 6).

Schlussfolgerungen – Unsere Ergebnisse zeigen, dass der Schutz von Solonetzgrasland eine wichtige Aufgabe des Naturschutzes ist, da sie eine entscheidende Rolle im Erhalt der Arten- und Habitat-Diversität auf der Landschaftsebene haben und als Pufferzonen um Feuchtgebiete herum wirken. Wir fanden, dass die drei untersuchten Solonetzgrasland-Assoziationen sowohl in ihrer Artenzusammensetzung wie auch in ihren ökologischen Zeigerwerten entlang des Feuchtigkeits- und Salzgehalts-Gradienten getrennt waren. Demzufolge ist es entscheidend für den Erhalt des Solonetzgraslands, die natürlichen Wasserregime und Bodensalzgehalte zu gewährleisten.

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Supplements and Appendices

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.

Appendix S1. Photos of typical associations of alkali landscapes.

Anhang S1. Fotos typischer Assoziationen der Alkali-Landschaften.

Appendix S2. Relative ecological indicator values for soil moisture (WB) and salinity (SB) and mean cover scores of detected species in the solonetz meadows.

Anhang S2. Relative ökologische Zeigerwerte (Feuchtezahl WB, Salzzahl SB) und mittlere Deckungswerte von im Solonetzgrasland gefundenen Arten.

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