Halophytic Vegetation in the Pannonian Basin: Origin, Syntaxonomy, Threat, and Conservation

Pavol Eliáš jun, Daniel Dítě, and Zuzana Dítě

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Abstract

After the Pannonian Sea has dried up, the Pannonian Basin has become a major depression in Central Europe. The continental climate and intensive groundwater evaporation from the upper layers of the soil caused the accumulation of salts and the formation of Solonchak and Solonetz soil. A mosaic of very specific halophytic vegetation has developed on these soils. Pioneer, species-poor vegetation of annual succulents of the *Therosalicornietea* class occupy the exposed bottoms of salt marshes and inland salt lakes. Very similar vegetation of the class *Crypsietea aculeatae* is developed in periodically flooded bare shores and bottoms of salt lakes, dead oxbows, ponds, and terrain depressions. Typical vegetation of inland salt steppes is included in the class *Festuco-Puccinellietea*, while

P. Eliáš jun (✉)
Department of Environment and Biology, Slovak University of Agriculture, Nitra, Slovakia

D. Dítě · Z. Dítě
Plant Science and Biodiversity Centre, Institute of Botany, Slovak Academy of Sciences, Bratislava, Slovakia

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the class *Scorzonero-Juncetea gerardii* associates subhalophytic grassland vegetation of wet meadows and pastures. The extreme character of these habitats not allowed human to use them for agricultural purposes for hundreds of years; they have traditionally been managed as pastures for sheep or cattle. A significant human impact on these habitats began only in connection with land drainage and flood control measures about 150 years ago. After World War II, there were attempts to intensify agriculture in stands of halophytic vegetation (plowing, amelioration, fertilization) but caused only the destruction or severe damage to these habitats. Recently, however, it has begun to pay more attention to protection and recovery supporting their conservation for the future.

Keywords

Communities · Halophytes · Management · Pannonia

1 Introduction

The Pannonian Basin is a major depression gripped by the Carpathians, Dinars, and Alps. It is situated at the boundary between Central, Eastern Europe, and the Balkans (Fig. 1). Its geological origin is in the Pannonian Sea, a shallow sea that reached greatest extent during the Pliocene Epoch. This area consists of a large Neogene basin filled with thick layer of Tertiary and Quaternary both fluvial and aeolian sediments (Dítě et al. 2017). Phytogeographically, it forms a discrete unit, the Pannonian vegetation region (Fekete et al. 2016).

The Pannonian Basin has been included in a temperate continental steppic bioclimatic region, characterized by cold snowy winters and hot dry summers with occasional droughts (Dítě et al. 2017). Those climatic conditions allowed the formation of salt-affected soils. Dry and warm summer periods caused the intensive evaporation; the groundwater which is near to the soil surface and has high salt content transports the salt to the upper soil layers where it accumulates (Török et al. 2012).

Types of alkali soils and grasslands are generally determined by the vertical position of salt accumulation zone and groundwater level. Characteristic alkali soil types in the Pannonian Basin are Solonchaks and Solonetz. Solonchak soil type frequently includes a considerable sand soil fraction; the soluble salt accumulation zone is located near to the soil surface due high mean groundwater levels. The humus content is generally low, and no definite geometric soil structure (layering) is developed. In contrast, Solonetz soils are well structured and can be characterized with deeper salt accumulation zones and groundwater tables. High humus content is typical for the steppic types. The upper soil layer can be very hard (when dry) or soapy (when wet). Salt-affected soils are an essential element for the formation of halophytic flora and vegetation (Dítě et al. 2017).

Halophytes are commonly regarded as salt-tolerant plants. Although the first definitions of this group of plants occur more than 200 years ago in the late

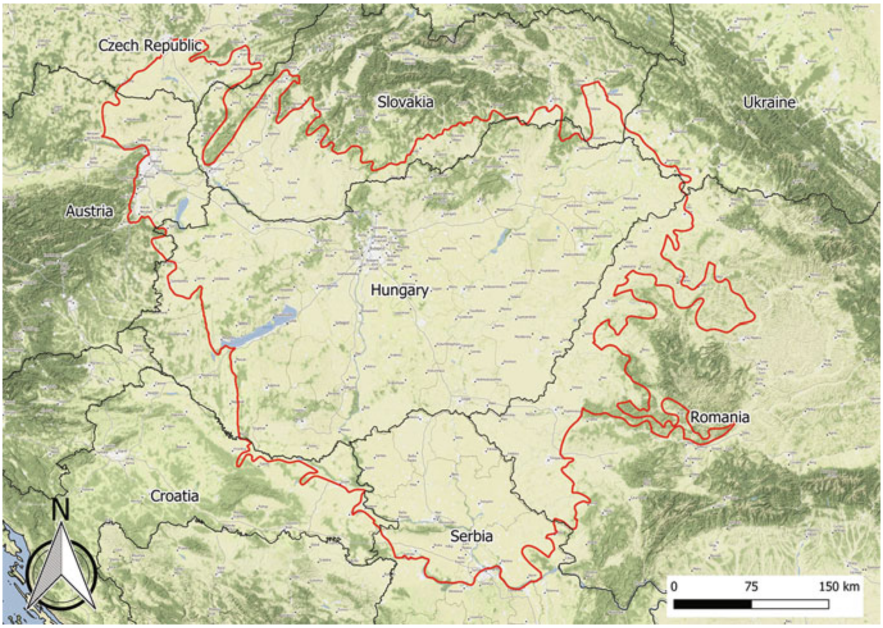

Fig. 1 The Pannonian Basin extends especially in Central Europe; their phytogeographical borders are marked red (modified according to Fekete et al. 2016)

eighteenth and mid-nineteenth centuries, they still remained ambiguous. Halophytes are frequently defined as plants, which are possible to survive and complete their life cycle in habitats with a high salt content, or, more recently, as plants that survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more (Grigore et al. 2010, 2014). According to Grigore and Toma (2017) a broader definition of halophytes, in an ecological way, would be more appropriate in an operational sense. Plants growing in saline environment should be considered halophytes, as there is always a close dependence on the salinity of the soil, although it varies at very variable levels.

Halophytes were divided traditionally to obligate and facultative or terrestric and aquatic or oligohalophytes, mezohalophytes, and euhalophytes according to the width of ecological valence. More recently, halophytes are classified into three basic groups, based on anatomical and ecological characteristics: euhalophytes (extreme halophytes), mesohalophytes, and glycophytes. Euhalophytes are species very well adapted to the presence of salts and occur in an environment with high salt concentration, mesohalophytes are species with transient anatomical adaptations between extreme halophytes and glycophytes capable of living in habitats more or less saline to not saline, while glycophytes are plants that do not tolerate the presence of salt (Grigore and Toma 2010, 2017).

Halophytic vegetation is a part of the landscape mosaic together with various non-halophytic plant communities in the Pannonian Basin. For example, salt steppes and saline lakes in the Hortobágy region (SE Hungary) are interrupted by loess steppes on the ridges, alkali or freshwater marshes, and freshwater oxbows in the depressions (Molnár and Borhidi 2003). In areas where saline soils are smaller in size, halophytic vegetation is islet-like, and it is often isolated to small fragments within field crops, artificial water channels, urban areas, etc. However, it is a unique phenomenon in any case reflecting the thousands of years of landscape development.

2 Origin and Distribution

Today, opinions that salt-affected soils and its vegetation are of anthropogenic origin, and they were developed in connection with water regime adjustments in the nineteenth century (flood control and land drainage), outdated. The ancient origin of halophytic vegetation is indirectly evidenced by previously published data of explorers and travelers (fifteenth–eighteenth century) on land use (grazing, soda sweeping), as well as published data on halophilic flora and fauna in the works of natural scientists from eighteenth century (e.g., botanists P. Kitaibel and S. Lumnitzer). These were complemented by paleoecological (mainly pollen) data in recent years (Sümegi et al. 2013). From this we know that halophyte vegetation has probably begun to form already in the Late Pleistocene. In this time, mixed cold continental steppe and tundra as well as boreal taiga vegetation elements covered this area. The mainly open forest-steppe landscape with scattered spots of alkaline habitats dating to the Pleistocene/Holocene transition was preserved in the younger periods of the Holocene as well. The last natural period of halophytic vegetation formation is presumed to happen in the Subatlantic stage of the Holocene. Evaporation and capillary rise increased under drier and warmer climate, especially next to low floodplains. The alkalization of subsoils was repeatedly enabled and promotes the formation of Solonetz-type soils (Tóth et al. 2015). According to Sümegi et al. (2013), the grassland dominated character of Hortobágy (SE Hungary) has not been fundamentally transformed by human communities for the past 5000 years. The situation was changed dramatically about before 150 years ago. The area of alkali Solonetz soils really began to expand in response to the effect of decreasing groundwater levels caused by river regulation and land drainage starting in the second half of the nineteenth century. Groundwater levels have dropped markedly (by 10–100 cm); secondary halophytic vegetation starts to develop in some regions (e.g., Hortobágy and Kiskunság in Hungary), or native halophytic vegetation was turn off to arable land and subsaline grasslands (NW Hungary, Czech Republic, Slovakia).

Based on the above data, the "Two-Phase Theory" was established in the first third of the twentieth century in Hungary and seriously confirmed in last decades for halophytic vegetation developed on Solonetz soils. This theory assumes that there had existed primary (natural) alkali habitats in prehistoric times that later expanded due to human land use (secondary alkali habitats). Primary halophytic habitats are characterized by species-rich and specific vegetation (*Artemisia* steppes predominated), alkali vegetation was developed here before the drainages, and their water regime remained basically constant in the past 150 years. On the other hand, secondary halophytic habitats are steppes on secondary developed Solonetz soils (*Achillea* steppes predominated), which formed from practically non-alkaline meadow and marsh floodplain habitats as a result of river regulations and inland flooding control. There is also the transitional type covering drained primary alkali steppes. Drainage management practices caused drop in groundwater table, which resulted in desalination. Desalination has caused a change in the type of halophyte vegetation toward the types demanding less salt content in soil (Molnár and Borhidi 2003).

The halophytic vegetation developed in Solonchak soils is always regarded as primary due diverse halophytic flora and occurrence of many endemics species (Fehér 2018).

Recently, saline habitats cover an area of ca. 10,000 km^2 in the Carpathian Basin. The major part, up to 95%, is located in the Great Hungarian Plain (Alföld), in Central and SE Hungary (Molnár et al. 2008; Tóth et al. 2015), and also in adjacent regions: in the Pannonian plain, in the Vojvodina Province, N Serbia (1530 km^2), and in the Transylvania Province in W Romania (200 km^2) (Dajić-Stevanović et al. 2008; Dumitru et al. 2009). The second, much smaller area is the Little Hungarian Plain situated in the NW part of the basin: around the Neusiedler See in E Austria (25 km^2), in SE Moravia (today only very small fragments), and in the Podunajská nížina Lowland in SW Slovakia (80 km^2) (Sádovský et al. 2004; Chytrý 2012).

3 Syntaxonomy

The great diversity of halophytic communities in the Pannonian Basin is related to the nature of the habitat – in particular, it reflects very dynamic mosaic pattern of soil types and its microtopography caused by rainwater erosion. Salt-affected soils with high clay contents are easily prone to cracking. Rainwater precipitation of proper amount and intensity started erosion processes as early as the Late Pleistocene and manifested in the retreat of berm edges and sedimentation in the berm foregrounds although the rate of erosion is very low (some millimeters per year) under natural conditions. In addition, human influences (digging canals, wheel tracks, intensive grazing) increased the rate of microrelief development significantly (Tóth et al. 2015).

As mentioned above, halophytic habitats have covered the largest area in Hungary; hence specific terminology for microhabitats has been developed in Hungarian language (Molnár 2012). The habitat of saline vegetation comprises mosaic of four main subunits ("floors of the puszta," Figs. 2 and 3): szikpadka, vakszik, szikfok, and szikér (none has an exact English equivalent).

- "Szikpadka" ("alkali step") is an almost bare erosional slope between the higher placed *Artemisia* steppe and lower situated the vakszik habitat.
- "Vakszik" patches ("blind alkali spot") are almost bare, highly alkaline white patches or narrow zones at the foot of the szikpadka habitats, it is temporarily

Fig. 2 Characteristic zonation of halophytic vegetation reflecting microhabitat and soil salinity level (the Körös-Maros National Park, Hungary). (Photo P. Eliáš jun.)

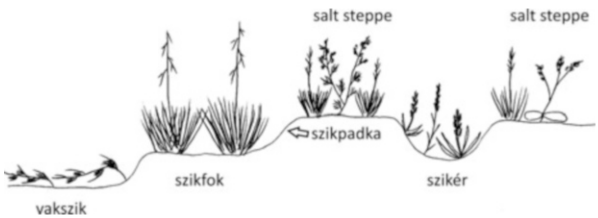

Fig. 3 Microhabitats of salt steppe: szikpadka, erosional slope of alkali steppe; vakszik, blind alkali spot, typical habitat of *Camphorosmetum annuae*; szikfok, transitional zone between vakszik habitats and alkali meadows occupied by *Puccinellietum limosae*; szikér, alkali valley, small muddy rills, habitat of *Plantagini-Pholiuretum. (drawn by P. Eliáš jun.)*

waterlogged in winter, but by the end of spring, it turns to a dry and bare habitat; it the least favorable habitat for the vegetation.

- "Szikfok" ("berm foreground") is a type of halophytic mud vegetation dominated by *Puccinellia* species; it is developed in the transitional zones of vakszik habitats and alkali meadows, usually flooded in spring and dried hard in summer.
- "Szikér" ("alkali valley") stripes are small, salt-affected, and muddy rills in the erosional troughs between szikpadka patches.

The halophytic vegetation of the Pannonian region can be characterized by several major syntaxonomic units that differ in physiognomy, life forms of dominants, and species composition (Molnár and Borhidi 2003). In the chapter, true halophytic vegetation of four classes: *Therosalicornietea* Tx. in Tx. et Oberd. 1958, *Crypsietea aculeatae* Vicherek 1973, *Festuco-Puccinellietea* Soó ex Vicherek 1973, and *Scorzonero-Juncetea gerardii* (Vicherek 1973). Golub et al. 2001 are presented (Table 1). Except the *Scorzonero-Juncetea* class, global hierarchical syntaxonomic concept of alliances, orders, and classes of the Braun-Blanquet syntaxonomy was accepted (Mucina et al. 2016). Most of plant associations follow work of Borhidi et al. (2012).

3.1 Class *Therosalicornietea* Tx. in Tx. et Oberd. 1958

Pioneer Vegetation of Annual Succulent Halophytes on Tidal Mud Flats and Edges of the Irregularly Flooded Saline Inland Waters of Eurasia

The class represents the pioneer, species-poor vegetation of annual succulents of semidesert character (e.g., *Salicornia perennans*, *Salsola soda*, *Suaeda pannonica*) on the exposed bottoms of salt marshes and inland salt lakes. They develop on extremely salty and humid soils. The communities of this class are missing in Slovakia and Croatia within the Pannonian Basin (Borhidi et al. 2012; Dajić-Stevanović et al. 2016); they are extinct in SW Moravia (Chytrý 2012).

3.1.1 Alliance *Salicornion prostratae* Géhu 1992

Pannonian Vegetation of Annual Succulent Halophytes on Solonchak Soils in Temporarily Wet Inland Salt Pans

Vegetation develops on bottoms of shallow continental alkaline lake beds. It is characteristic with the dominance of succulent euhalophytes *Salicornia perennans*, *Salsola soda*, and *Suaeda pannonica*. Soils are very salty, loamy, or clayey. Stands are species-poor; distinct dominance of one species, sporadically accompanied by other species with low cover, is typical. The formation of monodominant stands is also characteristic. Except above mentioned succulent taxa, only few halophytes are accompanied, for example, grasses *Crypsis aculeata*, *Puccinellia distans* agg. or nitrohpyte *Chenopodium chenopodioides*. Borhidi et al. (2012) mentioned the presence of some other *Chenopodiaceae* taxa (e.g., *Chenopodium glaucum*, *Atriplex prostrata*, *A. tatarica*) in stands of this alliance; however, Dítě et al. (2017) did not detect these species there. These species are more typical in the communities of the class *Crypsietea aculeatae*.

According to Dítě et al. (2017), only three associations belong to this vegetation unit: *Suadetum pannonicae*, *Salicornietum prostratae*, *Salsoletum sodae. Spergulario marginatae-Suaedetum prostratae* is extinct. Some authors (Molnár and Borhidi 2003; Borhidi et al. 2012) mentioned also other associations within alliance: *Crypsido-Suaedetum maritimae*, *Camphorosmetum annuae*, *Lepidio crassifolii-Camphorosmetum annuae*, and *Lepidietum crassifolii*. The first one probably represents only the ecotone between the communities of *Suaedetum pannonicae* and *Crypsietum aculeatae*, and it was not found during detailed analysis of salt lake beds vegetation (Dítě et al. 2017). Three other above communities belong to the class *Festuco-Puccinellietea* (Mucina 1993; Dajić-Stevanović et al. 2016; Dítě et al. 2017).

Table 1 Survey of vegetation units of halophytic vegetation in the Pannonian Basin

Class	Alliance	Association
Therosalicornietea	*Salicornion prostratae*	*Salicornietum prostratae*
		Salsoletum sodae
		Suadetum pannonicae
		Spergulario-Suaedetum prostratae
Crypsietea aculeatae	*Cypero-Spergularion salinae*	*Crypsietum aculeatae*
		Heleochloëtum schoenoidis
		Chenopodietum chenopoidis
		Atriplici-Chenopodietum crassifolii
		Cyperetum pannonici
Festuco-Puccinellietea	*Puccinellion limosae*	*Camphorosmetum annuae*
		Plantagini-Pholiuretum pannonici
		Puccinellietum limosae
		Matricario-Plantaginetum tenuiflorae
		Hordeetum hystricis
		Bassietum sedoidis
		Chenopodio-Puccinellietum limosae
		Lepidietum crassifolii
	Festucion pseudovinae	*Artemisio-Festucetum pseudovinae*
		Limonio-Artemisietum santonici
		Achilleo-Festucetum pseudovinae
		Centaureo-Festucetum pseudovinae
	Peucedano-Asterion sedifolii	*Peucedano-Asteretum sedifolii*
Scorzonero-Juncetea gerardii	*Juncion gerardii*	*Scorzonero-Juncetum gerardii*
		Agrostio-Caricetum distantis
		Caricetum divisae
		Loto-Potentilletum anserinae
	Beckmannion eruciformis	*Agrostio-Alopecuretum pratensis*
		Agrostio-Beckmannietum eruciformis
		Agrostio-Glycerietum pedicellatae
		Eleocharito-Alopecuretum geniculati
		Rorippo-Ranunculetum lateriflori

Salicornietum prostratae Soó 1947 Corr. 1967

This pioneer vegetation type is the most species-poor, usually with only single recorded species – taxonomically ambiguous *Salicornia perennans* (Fig. 4). It

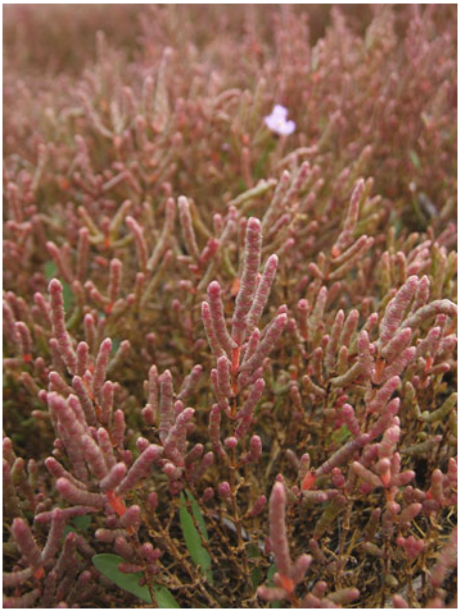

Fig. 4 In summer, *Salicornietum prostratae* stands have a characteristic reddish color. (Photo P. Eliáš jun.)

occupy sites with relatively higher water levels, while as the soil dries, *Suaeda pannonica* occurs, and at the end of the growing season, *Puccinellia distans* agg., *Spergularia media*, and *Tripolium pannonicum* are also present (Borhidi et al. 2012).

Distribution: rare in several sites in Hungary, E Austria, and N Serbia.

Salsoletum sodae Slavnić 1948

The species-poor vegetation often forms monocoenoses with dominance of *Salsola soda* on shortly periodically flooded and strongly salt-affected Solonchaks. Recently, *Suaeda pannonica*, *Crypsis aculeata*, and *Puccinellia distans* agg. were the most commonly associated species here (Dítě et al. 2017); Slavnić (1948) pointed out *Atriplex littoralis*, *A. tatarica*, and *Heleochloa schoenoides* as frequent. Occurrence of these species indicated lower salt content in the soil and a higher supply of nutrients. *Salsola soda* has relatively wide ecological amplitude. It can survive even on severely damaged salt marshes, even like weeds in the alpha field (Dítě et al. 2017).

Distribution: very rare in Central Hungary (the Kiskunság National Park) and N Serbia (probably disappeared now).

Suaedetum pannonicae (Soó 1933) Wendelberger 1943

The community has very distinctive look with a strong dominance of *Suaeda pannonica*. This species often forms relatively low (mostly only 5–10 cm height) monocoenoses with up to 100% surface cover on large areas of exposed dry bottoms of salt lakes (Fig. 5). In addition, *Puccinellia distans* agg. is relatively more common here, while several other species as *Crypsis aculeata*, *Chenopodium chenopodioides*,

Fig. 5 Stand of *Suaedetum pannonicae* in the Böddi-szék salt pan (the Kiskunság National Park, Hungary). (Photo D. Dítě)

and *Salsola soda* are rare. The stands are developed on soils of Solonchak type, flooded in spring, heavily dried up, and cracked in summer, with the highest values of salinity in general (Dajić-Stevanović et al. 2016; Dítě et al. 2017).

Distribution: E Austria, N Serbia, and Hungary.

Spergulario marginatae-Suaedetum prostratae Vicherek in Moravec et al. 1995
The association was developing in shallow depressions of saline grasslands on nitrogen-richer soils, not on lake shores and bottoms. In stands, *Suaeda prostrata* dominated *Spergularia media*, *S. salina*, and *Puccinellia distans* agg. were constant. The community was relatively species-rich. The community is extinct due to disturbance of the water regime in the habitat and subsequent desalination of the soil (Vicherek 1973; Šumberová 2007a).

Distribution: the Czech Republic.

3.2 Class *Crypsietea aculeatae* Vicherek 1973

Pioneer Ephemeral Dwarf-Grass Vegetation in Periodically Flooded Saline Habitats of Submediterranean and (Sub)continental Eurasia
The communities of this unit are described from extreme saline habitats with a continental climate: periodically flooded bare shores and bottoms of salt lakes, dead

oxbows, ponds, and terrain depressions. They are found also on secondary saline habitats such as field roads and artificial depressions. They develop periodically in years with low precipitation after natural seasonal decrease in the water-table level, with the optimal stage being from late summer until the middle of October (Šumberová 2007b). The vegetation consists mainly of low, trampling-tolerant species, such as *Crypsis aculeata*, *Heleochloa schoenoides*, and *Cyperus pannonicus*. Other obligate halophytes *Spergularia media*, *S. salina*, and *Tripolium pannonicum* are also abundant. Stands are species-poor, often homogenous with abundant populations of dominant species, sporadically accompanied by other species with low cover (Šumberová 2007b; Eliáš jun. et al. 2008). Communities of this unit occupy sandy or clayey Solonchak soils where through gradual drying out during the hot summer period salt crystals accumulates in the surface. Therefore, soil salinity is generally high, but several communities can developed on slightly saline and even nonsaline soils (e.g., *Heleochloetum schoenoidis*). Due to the accumulation of humus, the soils are dark and rich in nutrients. From this reasons, occurrence of nitrophilous species of the *Chenopodiaceae* family (*Atriplex littoralis*, *A. prostrata*, *Chenopodium chenopodioides*, *Ch. glaucum*) is also characteristic (Borhidi et al. 2012; Dítě et al. 2017).

The communities of this class are present in suitable halophytic habitats throughout the Pannonian Basin except Croatia (Dajić-Stevanović et al. 2016; Dítě et al. 2017).

3.2.1 Alliance *Cypero-Spergularion salinae* Slavnić 1948

Pioneer Ephemeral Dwarf-Grass Vegetation in Periodically Flooded Saline Habitats of Subcontinental Central and Eastern Europe

The alliance includes communities dominated by annual halophilous graminoids and herbs, e.g., *Crypsis aculeata*, *Atriplex prostrata*, and *Chenopodium chenopodioides*. Stands are developed on moderately to strongly salt-affected, muddy, gravel, or sandy soils in periodically flooded sites located in littoral zones contacted with the open-water surface of salt lakes. Almost each characteristic species to the alliance can create homogenous, separate community. Sometimes they are neighboring with reed beds or another saline vegetation. If the salt content decreases (mostly by human activities), this vegetation can overlaps with communities of the *Isoëto-Nanojuncetea* class, which can be considered as an ecological vicariant occupying soils without significant soluble salt content (Borhidi et al. 2012).

Up to seven associations were included in this alliance according some authors (Molnár and Borhidi 2003; Borhidi et al. 2012; Dajić-Stevanović et al. 2016). However, a detailed study of salt lake beds vegetation confirmed presence only three of them: *Crypsietum aculeatae*, *Heleochloëtum schoenoides*, *Chenopodio chenopodioidis-Atriplicetum prostratae*, and new one – *Chenopodietum chenopodioides,* have been described (Dítě et al. 2017). Four associations have not been confirmed: *Cyperetum pannonici*, *Atriplicetum prostratae*, *Chenopodietum urbici*, and *Heleochloëtum alopecuroidis*. The first one community is very rare, and, although it has been not recently found, this may happen in the future, as several sites have been confirmed in the Pannonian Basin where the species *Cyperus pannonicus* is still growing (Dítě et al. 2013). Association *Atriplicetum prostratae* is a very species-poor community formed by the dominant *Atriplex prostrata* and one or two other species, such as *Tripolium pannonicum* or *Suaeda maritima*. Although it is traditionally mentioned from the territory of Austria, Hungary, and Serbia (Mucina 1993; Molnár and Borhidi 2003; Dajić-Stevanović et al. 2016), its existence remains questionable and requires further research. Association *Chenopodietum urbici* represent relatively species-rich ruderalized vegetation of slightly and moderately saline soils. *Chenopodium urbicum* forms stands at the edges of fields and in field inundations often together with weedy species such as *Ch. album* and *Atriplex patula*. Therefore, many authors consider the association as synanthropic vegetation (Sanda et al. 2008; Dítě et al. 2017). The association *Heleochloëtum alopecuroides* is dubious because even a single relevé of it was never published and any stands were not found on exposed saline bottoms of the Pannonian Basin (Dítě et al. 2014a).

Crypsietum aculeatae Wenzl 1934

It is a very species-poor pioneer community, where, in optimal conditions, annual grass *Crypsis aculeata* (Fig. 6) create large-scale monodominant stands. Some accompanying species of low cover are present, including both obligate halophytes (*Tripolium pannonicum*, *Salicornia perennans*, *Spergularia media*, *Suaeda pannonica*) and facultative halophytes (e.g., *Bolboschoenus maritimus*, *Chenopodium glaucum*). The occurrence of facultative halophytes as well as ruderal taxa (*Potentilla anserina*, *Xanthium strumarium*) indicates degradation of the habitat (a decrease of soil salts). The community is successively heading toward to stands of the *Isoëto-Nanojuncetea* vegetation and rapidly terminated.

The association occupies flat bare shores and salt lake bottoms. It is also found but often less typically developed, in periodically flooded terrain depressions, on saline pastures, on the edges of fields, on salt-affected soils, and in drying puddles of field roads. In spring, the habitats of the community are flooded; they dry out during

Fig. 6. The annual grass *Crypsis aculeata* dominates the community of *Crypsietum aculeateae* (Kelemen-szék pond, Hungary). (Photo P. Eliáš jun.)

Fig. 7 Initial stage of the *Heleochloëtum schoenoidis* community at the exposed bottom of the small pond in the Tvrdošovce village (SW Slovakia). (Photo P. Eliáš jun.)

summer, and the strongly salted Solonchak soil is heavily polygonally cracked. Salt efflorescence occurs.

Distribution: NE Austria, Hungary, and N Serbia; extinct in the Czech Republic (SE Moravia) and SW Slovakia.

Heleochloëtum schoenoidis Ţopa 1939

The association includes open, relatively species-rich stands with dominance of *Heleochloa schoenoides* (Fig. 7) accompanied by obligate halophytes (*Tripolium pannonicum*, *Puccinellia distans* agg., *Spergularia salina*) as well as species of slightly saline, wet, and nutrient-rich soils (*Chenopodium urbicum*, *Polygonum aviculare*, *Potentilla anserina*). This plant community is very rare in the dried bottom of salt lakes (Dítě et al. 2017); it is more commonly found in shallow depressions on saline pastures, on fields, tracks and puddles on dirt roads, or on the edges of fields on slightly salt-affected soils. However, those habitats are under anthropogenic influence, especially fertilization increases the nitrogen content of the soil and the halophytes are replaced by weed species such as *Echinochloa crus-galli*, *Tripleurospermum perforatum*, or *Xanthium strumarium* (Borhidi et al. 2012).

Distribution: the Czech Republic (SE Moravia), SW Slovakia, Hungary, and N Serbia.

Chenopodietum chenopodioidis Dítě et al. 2017

For this association, pure stands of *Chenopodium chenopodioides* with cover of >90% are characteristic (Fig. 8). Species richness is low; only few species are accompanied such as *Puccinellia distans* agg., *Suaeda pannonica*, and *Salsola soda*. Absence of *Chenopodium glaucum* is also typical. The community is formed on clay, slightly to moderately saline soils with high nutrient content; therefore, it is most frequently present in disturbed, eutrophic saline habitats (e.g., field depressions) but occupy also exposed lake bottoms.

Fig. 8 Extensive stand of *Chenopodietum chenopodioidis* on the exposed lake bottom near Riđica village (Vojvodina province, N Serbia). (Photo D. Dítě)

Distribution: Central and E Hungary and N Serbia.

Chenopodio chenopodioidis-Atriplicetum prostratae Slavnić 1948 Corr. Gutermann and Mucina 1993

Stands are characterized by a predominance of two *Chenopodium* species: *Ch. glaucum* and *Ch. chenopodioides*; none of them are dominant. *Crypsis aculeata* and *Atriplex prostrata* are also frequent; *Heleochloa schoenoides*, *Bolboschoenus maritimus*, *Tripolium pannonicum*, and *Agrostis stolonifera* are less often associated (Fig. 9). Stands occur on periodically flooded banks of shallow lakes and depression on salty soils. The soils are of the Solonchak type, the salt content fluctuates, and often it is lower. The soil is muddy with a higher or high content of nutrients, especially nitrogen (Dítě et al. 2017). On large-scale localities, it usually occurs in a transition or mosaic between *Crypsietum aculeatae* and *Puccinellietum limosae* (Borhidi et al. 2012). Compared to *Chenopodietum chenopodioidis* association, the stands have higher species richness and occupy soils with slightly lower nutrient content.

Distribution: Central Hungary (Kiskunság National Park), E Austria, N Serbia, and rarely in SW Slovakia.

Cyperetum pannonici Wendelberger 1943

The community consists of low, open, and single-layered stands with a high abundance of *Cyperus pannonicus* (Fig. 10). The species composition affects the salt content of the soil. On strongly salt-affected soils, stands are species-poor and only obligate halophytes such as *Crypsis aculeata*, *Spergularia salina*, *Suaeda*

Fig. 9 *Chenopodio-Atriplicetum prostratae* stands in late summer: plants of *Chenopodium chenopodioides* are red, while *Atriplex prostrata* individuals are green (the Kiskunság National Park, Hungary). (Photo D. Dítě)

Fig. 10 *Cyperus pannonicus*, one of the rarest species of bare bottoms in Pannonia (Warmsee, E Austria). (Photo P. Eliáš jun.)

pannonica, or *Tripolium pannonicum* are present. In the case of lower salt content in soil, species-richer vegetation including facultative halophytes as well as species of *Isoëto-Nanojuncetea* is developed. The stands occur on periodically flooded banks of salt lakes and depressions; the soil is usually sandy or gravel.

Distribution: one of the rarest halophytic community in Pannonia, reported from E Austria, Hungary, N Serbia, and SW Slovakia, however, it was not confirmed currently.

3.3 Class *Festuco-Puccinellietea* Soó ex Vicherek 1973

Saline Steppes and Secondary Saline Steppic Grasslands of the Continental Regions of Europe

The class comprises typical vegetation of inland salt steppes dominated by perennials grasses; some herbaceous species are abundant, too. It is strongly influenced by the movement of groundwater (wet in spring and extremely dry in the second half of the growing season) and the differences in the salinity of the both Solonetz and Solonchak soils from moderately to strongly saline. Stands are quite open, low to medium tall; the occurrence of perennial obligate halophytes including *Artemisia santonicum* or *Plantago maritima* and species of the *Puccinellia* genus is characteristic. Therophytes such as *Bupleurum tenuissimum* or *Hordeum hystrix* are typical in the more open vegetation. Communities belonging to this class are traditionally used as pastures (Mucina 1993; Borhidi et al. 2012).

The distribution range of *Festuco-Puccinellietea* covers the Ponto-pannonian district, and some communities reach Central Asia (Dítě et al. 2014b).

3.3.1 Alliance *Puccinellion limosae* Soó 1933

Pannonian Hypersaline Open Grasslands on Solonetz Soils

Plant communities included in this alliance are open and species-poor, species of *Puccinellia* genus dominate. They are developed on strongly salt-affected soils both Solonetz and Solonchak types on typically heavy clayey and muddy substrates. Some authors devoted a separate endemics *Puccinellion peisonis* Wendelberger 1943 corr. Soó 1957 alliance (or suballiance) on the basis of Solonchak soil type and occurrence of taxonomically complicated *Puccinellia peisonis* species endemic to the Neusiedler area (Mucina 1993; Borhidi et al. 2012). The alliance is not characterized by any other diagnostic species except of *Puccinellia peisonis*, and the distribution range of some its plant communities is larger than area of Lake Neusiedl; therefore, this alliance is included in to the *Puccinellion limosae*. The association of *Puccinellietum peisonis* Franz et al. 1937 corr. Soó 1947 is considered as synonym of the *Puccinellietum limosae* association because other taxa of the *Puccinellia distans* complex grow in its stands.

The alliance included eight associations in the Pannonian Basin.

Camphorosmetum annuae Soó 1930

Initial, species-poor community, mostly only 1–4 species are present. The basic physiognomy is given by monocoenosis of the annual succulent plant *Camphorosma annua* (Fig. 11). In spring, annuals such as *Matricaria recutita*, *Plantago tenuiflora*, or *Dichodon viscidum* are typical. In late summer and autumn, only *Camphorosma annua* is present. Some perennials such as *Artemisia santonicum*, *Festuca pseudovina*, *Puccinellia distans* agg., or *Plantago maritima* can be accessed here at the edges of stands from contact communities. Cyanobacteria *Nostoc commune* may occasionally appear in the spring months (Dítě et al. 2014b).

The stands of the association are formed on Solonetz soils in slightly lowered places ("vakszik" = "blind alkali spot"). These places are wet to flood in spring and dry out strongly during the late months of vegetation season. Due to fluctuations in the groundwater level and the outflow of the microrelief, the accumulation of salts increases. Such places can be considered the most extreme for the existence of vegetation within halophytic habitats (Borhidi et al. 2012).

Fig. 11 Large-scale stands of *Camphorosmetum annuae* association in the Hortobágy National Park (E Hungary). (Photo P. Eliáš jun.)

Distribution: Central and E Hungary, N Serbia, W Romania, threatened with extinction in the NE Croatia, and SW Slovakia.

Plantagini tenuiflorae-Pholiuretum pannonici Wendelberger 1943

An inconspicuous, Pannonian endemic low-herb community is characterized by the mutual occurrence of two dominant annual species, *Plantago tenuiflora* and *Pholiurus pannonicus* (Fig. 12). Obligate halophytes *Artemisia santonicum* and *Puccinellia distans* agg. are regularly represented, often with higher abundance. Otherwise, facultative halophytes (e.g., *Polygonum aviculare*, *Carex stenophylla*, *Gypsophila muralis*) are often associated. Borhidi et al. (2012) mentioned also the occurrence of mud-preferring plants (e.g., *Alopecurus geniculatus*, *Eleocharis palustris*, *Ranunculus lateriflorus*, and *Rorippa kerneri*).

The stands are developed in "szikér" ("alkali valley") stripes – small, salt-affected, and muddy rills in the erosional troughs between "szikpadka" patches (Molnár and Borhidi 2003). This specific muddy habitat is flooded in spring and then moistened for a long time. It begins to dry only at the beginning of summer, but heavy summer rainfall can significantly prolong this process.

Distribution: Hungary, E Austria, N Serbia, W Romania, and rarely in SW Slovakia.

Fig. 12 Inconspicuous annual grass *Pholiurus pannonicus* is the dominant of the *Plantagini-Pholiuretum* community (Püspökladány, E Hungary). (Photo P. Eliáš jun.)

Puccinellietum limosae Soó 1933

The association is represented by more or less open stands dominated by taxa of *Puccinellia distans* complex (*P. distans*, *P. limosa*, *P. peisonis*). In addition, obligate halophytes such as *Artemisia santonicum*, *Plantago maritima*, *Tripolium pannonicum*, or *Spergularia media* are often present. The association covers the transitional zones between open therophytic *Camphorosma*-dominated stands and perennial salt *Festuca*-grasslands (Dítě et al. 2014b).

The community develops on flat parts of Solonetz grasslands in shallow, wide-spread depressions creating a mosaic with other halophytic communities reflecting the ecological properties of microhabitats. The soils are heavy, clayey, and strongly salinized. The habitats are damp or long-term flooded in spring, but in summer dries very hard, and the surface is polygonally cracked (Borhidi et al. 2012).

Distribution: it is found all over Pannonia.

Matricario-Plantaginetum tenuiflorae (Soó 1933) Borhidi 1996

The initial low-herb community formed by two annual salt-tolerant species: *Matricaria chamomilla* and *Plantago tenuiflora*. In addition, other annual facultative halophytic species such as *Ranunculus lateriflorus*, *Myosurus minimus* and *Dichodon viscidum* are also regularly present. Perennial obligate (*Artemisia santonicum*, *Plantago maritima*, *Puccinellia distans* agg.) as well as facultative halophytes (*Festuca pseudovina*) sporadically penetrate here from surrounding stands (Borhidi et al. 2012).

The community occupies flat depressions and strips in the stands of *Puccinellietum limosae* flooded or moistened in spring and partly drying in summer. It can also develop in secondary habitats such as plowed depressions in fields on moderately to strongly salt-affected soils.

Distribution: not well-known, it is reported from Hungary and Serbia. It was recorded rarely on a secondary habitat (field edge) in Slovakia, too.

Hordeetum hystricis Wendelberger 1950

The dominance of *Hordeum geniculatum* is a common feature of the community. If it develops in optimal conditions, this species reaches coverage of around 75–85%. Stands are more or less dense and closed. The floristic composition is diverse, and this association is considered one of the species-richest halophytic communities of Pannonia (Eliáš jun et al. 2013b). There are present several obligate halophytes (*Artemisia santonicum*, *Plantago maritima*, *Tripolium pannonicum*, *Spergularia media*) and subhalophytes (*Cynodon dactylon*, *Lotus tenuis*, *Trifolium fragiferum*), but also several mesophilic and ruderal species (*Achillea millefolium*, *Capsella bursa-pastoris*, *Elytrigia repens*). In addition, the occurrence of "trampling-resistant" species (*Lolium perenne, Polygonum aviculare*, *Sclerochloa dura*) is very characteristic (Borhidi et al. 2012).

Typical stands of the association are developed particularly on slightly and moderately salt-affected soils. The *Hordeetum hystricis* is a second-stage community of zoo-anthropogenic origin that occupies intensively grazed and trampled sites, especially around watering places, where flocks of sheep and cattle regularly gather (Fig. 13). Formation of the association is a result of nutrient enrichment of Solonetz soils initially harboring the *Puccinellietum limosae*, *Achilleo setaceae-Festucetum pseudovinae*, as well as *Artemisio santonici-Festucetum pseudovinae* associations (Eliáš jun et al. 2013b).

Distribution: E Austria, Hungary, SW Slovakia, N Serbia, and W Romania.

Bassietum sedoidis Ubrizsy 1948 Corr. Soó 1964

It is also an association of zoo-anthropogenic origin formed in the trampled roadsides or intensively grazed areas. The dominant of the stands is annual, nitrogen-, and salt-tolerant species *Bassia sedoides*. In addition, *Matricaria chamomilla*, *Hordeum geniculatum*, *Heleochloa alopecuroides*, and *Myosurus minimus* are abundant. Ruderal and weed species (*Atriplex prostrata, A. tatarica, Carduus acanthoides, Lepidium ruderale*) are often present.

Soil is strongly compacted and enriched with nitrogen. Habitat of this community is similar to *Hordeetum hystricis*, but the soil sludge fraction is slightly higher (Borhidi et al. 2012).

Distribution: referred from Hungary, Serbia, and Romania, however, Eliáš jun et al. (2013a) did not confirm it. It is possible only a ruderalized variant of the *Hordeetum hystricis*.

Fig. 13 Intensive grazing and trampling support the development of the *Hordeetum hystricis* stands near Rančevo hamlet (N Serbia). (Photo P. Eliáš jun.)

Chenopodio-Puccinellietum limosae Soó 1947

Relatively species-poor and open association with two dominants: *Puccinellia limosa* and *Chenopodium chenopodioides*. The presence of *Ch. chenopodioides* gives the community a slightly weed character. Obligate and facultative halophytes such as *Atriplex littoralis*, *Tripolium pannonicum*, *Plantago maritima*, *Suaeda prostrata*, and *Trifolium fragiferum* play a more important role. On soils with lower salt content, some species of wet meadows are present (*Carex distans*, *Triglochin palustris*); in drier places *Cynodon dactylon* penetrates into the stands. Moss level is formed on the open surfaces (Borhidi et al. 2012).

The community is developed on moderately saline, slightly muddy Solonetz soils that remain wet to damp throughout the year.

Distribution: E Hungary (the Upper Tisza region) and N Serbia, not confirmed recently (Eliáš jun et al. 2013a).

Lepidietum crassifolii Wenzl 1934

On the basis of recent research (Eliáš jun et al. 2013a; Dajić-Stevanović et al. 2016), two other associations are included within *Lepidietum crassifolii*: *Lepidio crassifolii-Puccinellietum limosae* Soó (1947) 1957 and *Lepidio crassifolii-Camphorosmetum annuae* Rapaics ex Soó (1947) 1957 because they represent a transition between *Lepidietum crassifolii* and *Puccinellietum limosae* and *Camphorosmetum annuae*, respectively.

Fig. 14 Stand of *Lepidietum crassifolii* in half of May (Zicklacke, E Austria). (Photo D. Dítě)

The community is formed mostly with a single species – *Lepidium crassifolium* (Fig. 14). It created quite dense stands, especially in the summer aspect. In addition, only a few species are more or less often present, but usually with low coverage. First of all it is *Puccinellia distans* agg. and then also *Camphorosma annua*, *Plantago maritima*, *Tripolium pannonicum*, and *Podospermum canum*. Succulent obligate halophytes (*Salsola soda*, *Spergularia media*, *Salicornia perennans*, *Suaeda pannonica*, *S. prostrata*) are sporadically present in stands developed on strongly salt-affected soils (Borhidi et al. 2012; Dajić-Stevanović et al. 2016).

The association is developed in depressions of salt steppe on strongly to moderately salinized Solonchak soils with the maximum salinity near the soil surface. Therefore, salt efflorescence can be observed regularly. The water regime is fluctuating, in the spring the stands are flooded, later they dry out, but the soil remains wet.

Distribution: E Austria, Central Hungary, and N Serbia.

3.3.2 Alliance *Festucion pseudovinae* Soó 1933

In contrast to *Puccinellion limosae*, the *Festucion pseudovinae* alliance is restricted to Solonetz soils with relatively lower salt content. Communities included in this unit represent typical continental salt steppes of primary (edaphic) origin. Their secondary area expansion may result from deforestation and drainage of the Danube and Tisza rivers' alluvia which was previously used for grazing (Molnár and Borhidi 2003). In Hungary they are called "puszta" (Borhidi et al. 2012) which is derived from the originally Slavic word "pustý" = abandoned, uninhabited.

The stands are characterized by the dominance of *Festuca pseudovina* grass; they are species-richer than the vegetation of the previous alliance. Obligate halophytes such as *Artemisia santonicum* or *Plantago maritima* occur frequently, dependent on salt content, together with facultative halophytes (*Bupleurum tenuissimum*, *Trifolium retusum*, *T. strictum*, *T. angulatum*) and species tolerating, grazing, and trampling (*Gypsophila muralis*, *Hordeum geniculatum*, *Plantago lanceolata*) are present. Endemic *Plantago schwarzenbergiana*, *Limonium gmelinii*, and *Ranunculus pedatus* are also found here (Sanda et al. 2008; Dítě et al. 2014b).

Communities of this unit occupy heavier, clayey, and moderately salt-affected Solonetz soils with lower humus content (Borhidi et al. 2012). In spring, the stands are wet, flooded only occasionally and briefly, they dry out in early summer.

Four associations are included here.

Artemisio santonici-Festucetum pseudovinae Soó 1947

The association is considered to be the primary plant community of the salt steppe (Fig. 15). The stands are species-poor, more or less dense and closed, usually with significant moss layer. In addition to two characteristic dominant species *Artemisia santonicum* and *Festuca pseudovina*, other obligatory and facultative halophytes are represented (*Dichodon viscidum*, *Plantago maritima*, *Puccinellia distans* agg., *Tripolium pannonicum*, *Podospermum canum*). Seasonality is strongly applied. In spring months, the number of species is higher, as several therophytes are present. Higher coverage of glycophytes (e.g., *Festuca rupicola*, *Poa pratensis*) together

Fig. 15 *Artemisio santonici-Festucetum pseudovinae* – the most typical plant community of salt steppe (the Hortobágy National Park, E Hungary). (Photo P. Eliáš jun.)

with the presence of ruderal species (*Elytrigia repens*) indicates degradation of the habitat and progressive desalination of the soil (Dítě et al. 2014b).

Distribution: E Austria, Hungary, NE Croatia, N Serbia, W Romania, and SW Slovakia.

***Limonio gmelini-Artemisietum santonici* (Soó 1927) Ţopa 1939**

The association has developed in flat parts of salt steppe from stands of *Artemisio-Festucetum pseudovinae* as a result of very intensive grazing. It is characteristic by a dominant co-occurrence of *Artemisia santonicum* and *Limonium gmelinii*; obligate halophytes such as *Tripolium pannonicum* and *Puccinellia limosa* are usually regularly present. *Festuca pseudovina*, however, reaches less coverage (not more than 25%) here. Other species of salt steppe such as *Bupleurum tenuissimum*, *Dichodon viscidum*, *Plantago maritima*, *Ranunculus pedatus*, and *Trifolium angulatum* are often associated. On drier, slightly saline and nutrient-rich places *Bromus mollis*, *Carex stenophylla*, and *Gypsophila muralis* may be more common (Borhidi et al. 2012; Dítě et al. 2014b).

Distribution: S and SE Hungary, W Romania, and N Serbia (Vojvodina province). Dajić-Stevanović et al. (2016) did not confirm it in Southeastern Europe. Occurrence in Slovakia is considered confusion with the *Artemisio-Festucetum pseudovinae* association (Dítě et al. 2014b).

***Achilleo setaceae-Festucetum pseudovinae* Soó 1947**

The community is characterized by more or less closed, species-rich vegetation with the dominance of *Festuca pseudovina* and constant presence of several *Achillea* species (*A. collina*, *A. millefolium*, *A. pannonica*, *A. setacea*). Typical grassland glycophytes such as *Alopecurus pratensis*, *Bromus hordeaceus*, *Poa bulbosa*, and *P. pratensis* are common, and proportion of halophytes is lower. Obligatory halophytes are present very rare (e.g., *Plantago maritima*); but subhalophytes are often found (e.g., *Bupleurum tenuissimum*, *Lotus tenuis*, *Podospermum canum*). There is also typical occurrence of several salt-tolerant clover species (*Trifolium angulatum*, *T. bonannii*, *T. micranthum*, *T. strictum*, *T. retusum*).

The association is considered to be a secondary plant community established on less salinized soils turned from other primary salt communities due leaching of salts from soil and dried-out fresh floodplain meadows (Molnár and Borhidi 2003).

Distribution: E Austria, SW and SE Slovakia, Hungary, W Romania, and N Serbia.

***Centaureo pannonicae-Festucetum pseudovinae* Klika et Vlach 1937**

The community is physiognomically very similar to the previous one. *Festuca pseudovina* predominates, several halophytes (*Artemisia santonicum*, *Tripolium pannonicum*, *Plantago maritima*) and subhalophytes (*Bupleurum tenuissimum*, *Lotus tenuis*, *Taraxacum bessarabicum*) are present frequently. Meadow species of dry (*Asperula cynanchica*, *Galatella linosyris*, *Jacea pannonica*, *Galium verum*) and mesophilic habitats (*Dactylis glomerata*, *Daucus carota*, *Poa compressa*) are also common (Fig. 16). Seasonality is not significantly applied in this case; therophytes

Fig. 16 The community *Centaureo-Festucetum pseudovinae* represents the transition of halophytic vegetation toward the dry to mesophilic grasslands (Veľké Raškovce, SE Slovakia). (Photo P. Eliáš jun.)

are rare. The species composition depends on the salinity of the soil. Penetration of grassland species into the stands indicates lower soil salt content; presence of ruderal species indicates degradation due to intensive grazing (Dítě et al. 2014b).

The association develops on flat parts of secondary salt grasslands and their peripheral zones, on Solonchaks with lower salt content. It often follows stands of the *Achilleo-Festucetum pseudovinae* and represents the transition of halophytic vegetation toward the dry to mesophilic grasslands of the *Molinio-Arrhenatheretea* class.

Distribution: E Austria, SW and SE Slovakia, Hungary, and N Serbia.

3.3.3 Alliance *Peucedano officinalis-Asterion sedifolii* Borhidi 1996

Pannonian Tall-Forb Rich Subsaline Meadows on Calcareous Loess Soils

The alliance includes secondary tall-herb, species-rich plant community occupying the clearings of salt steppe oak woodlands (*Festuco-Quercetum robori*) as well as slightly saline and wet sites in secondary *Achilleo-Festucetum* steppe. This vegetation was formed from fresh floodplain meadows that had turned steppe-like and alkaline due to human intervention in the water regime (Molnár and Borhidi 2003).

Vegetation of this alliance occupies semidry and semi-humid slightly salinized Solonetz soils. In stands, mixture of subhalophytic, subxerophytic, and grassland tall herbs is present.

Only a single association is present in the Pannonia.

Peucedano-Asteretum sedifolii Soó 1947 Corr. Borhidi 1996
The community is regarded as Pannonian subendemic association and one of the most characteristic plant associations of the Great Hungarian Plain forest steppe. It is characterized by the fluctuating water surface of the Tisza Valley with its extreme water balance, where forests, saline grasslands, and swamps develop depending on local conditions. Stands of the community are species-rich, dominated by two perennial species *Peucedanum officinale* and *Galatella punctata*. Halophytes and subhalophytes such as *Artemisia pontica*, *A. santonicum*, *Limonium gmelinii*, *Iris spuria*, *Podospermum canum*, and *Ranunculus pedatus* are relatively common in stands developed on relatively more humid soils with a higher salt content. In contrary, *Elytrigia intermedia*, *E. repens*, *Festuca rupicola*, *Filipendula vulgaris*, *Fragaria viridis*, *Galatella linosyris*, and *Galium verum* are accompanied at dryer sites with lower salinity and higher loess content in soil (Borhidi et al. 2012).

Distribution: NW, S, and SE Hungary, N Serbia, and W Romania.

3.4 Class *Scorzonero-Juncetea gerardii* (Vicherek 1973) Golub et al. 2001

Vegetation of continental wet salty meadows on Solonchak soils
In contrast to Mucina et al. (2016), we decided to accept the *Scorzonero-Juncetea gerardii* class in vegetation survey of Pannonia. First, incorporating the *Scorzonero-Juncion gerardii* vegetation into the *Festuco-Puccinellietea* class, this unit would be very heterogeneous. Second, although some communities of the above classes may be physiognomically much related and often create mosaics and transitions, the fundamental ecological difference between them is the water regime. In the case of the *Festuco-Puccinellietea* class, water regime fluctuates strongly during the year, with the vegetation being flooded in spring and the groundwater level decreasing significantly during the growing season. On the other hand, the dynamics of the water regime of the *Scorzonero-Juncetea gerardii* class are more stable, and habitats are generally waterlogged throughout the year. Soil salinity is closely related to the water regime, so salt content in soil is on average higher for the *Festuco-Puccinellietea*. This also implies different groups of diagnostic species of individual classes.

The class associates subhalophytic grassland vegetation of wet meadows and pastures. Perennial species such as *Agrostis stolonifera*, *Juncus gerardii*, and *Carex distans* are dominant in those communities. Halophytes (e.g., *Plantago maritima*, *Taraxacum bessarabicum*, *Tripolium pannonicum*) are frequently accompanied. Because the concentration of soluble salts in Solonchak soil is low to moderately high, species requiring a high salt content in the soil represented in the stands of *Crypsietea aculeatae* or *Festuco-Puccinellietea* are rare. Periodically, but not dominant, there are also species of disturbed, nutrient-rich habitats (*Potentilla anserina*, *Cirsium brachycephalum*) and species of stagnant and weakly salt marshes (*Bolboschoenus maritimus* agg., *Eleocharis palustris* agg.). Stands are of secondary origin in many cases; they have developed at seminatural sites in rivers alluvia and on the banks of lakes, often in previously deforested areas. Anthropo-zoogenic factors – mowing and extensive grazing – play an important role in their dynamics (Melečková et al. 2014).

The communities of this class are distributed in the Eastern Europe and Central Asia forest-steppe zone. Vegetation is analogical to class *Juncetea maritimi* Br. ex Tüxen and Oberdorfer 1958 representing the maritime salt marshes of Western Europe (Golub et al. 2003).

3.4.1 Alliance *Juncion gerardii* Wendelberger 1943

Wet Subsaline Regularly Inundated Meadows and Pastures of Southeastern Central Europe

The alliance associates halophytic and subhalophytic communities of warm lowland areas, which have several common species with wet meadows and pastures. Their appearance is reminiscent of the salt marshes of the coastal vegetation of *Juncion maritimi* Br.-Bl. ex Horvatić 1934. However, they differ considerably because species with a continental distribution predominate in the *Juncion gerardii* alliance and Atlantic species are rare (*Carex extensa*, *Juncus maritimus*) or absent (Borhidi et al. 2012).

The stands are usually two- or three-layered, dominated by hemicryptophytes such as tussocks grasses and sedges (e.g., *Agrostis stolonifera*, *Carex distans*) and other, creeping and rhizomatous herb species, respectively (e.g., *Potentilla anserina*, *Ranunculus repens*, *Teucrium scordium*). In the zonation of the primary halophytic communities, the stands of *Juncion gerardii* are located between the salt marshes of the *Phragmito-Magnocaricetea* class and the salt steppe communities of the *Festuco-Puccinellietea* (Melečková et al. 2014).

The soils are more or less saline Solonchak with sandy-clay or less often clay fraction. Therefore, during the summer drying and evaporation, the content of soluble salts is concentrated near the surface. After high spring water level, soils are often covered with mud.

Four associations are distinguished in Pannonia (Borhidi et al. 2012).

Scorzonero parviflorae-Juncetum gerardii Wendelberger 1943

The specific community with a transitional character between salt marsh vegetation and wet meadows stands. The vegetation cover is more or less open, species-poor; the stand is relatively low in height, sometimes with two- to three layers (Fig. 17). *Juncus gerardii* is the dominant species, *Scorzonera parviflora* co-dominate. In addition, *Agrostis stolonifera*, *Bolboschoenus maritimus* agg., *Eleocharis palustris*, *Trifolium fragiferum*, *Triglochin maritima* and *Tripolium pannonicum* are accompanied depending on the content of soluble salts, nitrogen, and moisture. The bryophytes layer is usually developed (Borhidi et al. 2012).

The stands are developed on soils of the Solonchak type, significantly loamy to clay, without salt efflorescence; a thin layer of mud is on the surface.

Fig. 17 Stand of *Scorzonero-Juncetum gerardii* association near Apetlon (E Austria). (Photo D. Dítě)

Distribution: SE Moravia, E Austria, Hungary, N Serbia, and W Romania, extinct in SW Slovakia.

Agrostio stoloniferae-Caricetum distantis Soó 1939

This community is in fact very heterogeneous due to the wide ecological variability such water regime, nutrients, and salinity. Common feature is the dominance of rhizomatous grass *Agrostis stolonifera* and tussock sedge *Carex distans.* The stands are usually developed in three layers. First layer represents low, occasionally carpet-like stand dominated by *Agrostis stolonifera*, other halophytic or subhalophytic hemicryptophytes (*Lotus tenuis, Potentilla anserina, Plantago maritima, Taraxacum bessarabicum*, *Trifolium fragiferum*) are frequently present. The middle layer consists of *Carex distans*, *Achillea aspleniifolia*, *Jacea pratensis*, and *Tripolium pannonicum*. Tall perennial herbs such as *Althaea officinalis*, *Cirsium brachycephalum*, and *Phragmites australis* represent the third layer.

The very broad ecological amplitude of the association allows the penetration of many species from different wetland and meadow communities (e.g., *Caricion gracilis*, *Molinion*, *Festucion pseudovinae*). This causes several syntaxonomic concepts of such stands. Some authors (Mucina 1993; Borhidi et al. 2012) distinguish two separate associations: *Agrostio stoloniferae-Caricetum distantis* developing on Solonetz soils and *Taraxaco bessarabici-Caricetum distantis* Wendelberger 1943 which occupy Solonchak soils. In contrast, other authors consider this vegetation to be analogous (Vicherek 1973; Melečková et al. 2014) or represent only two geographical variants of one community (Bagi et al. 2011). In this survey, *Taraxaco-Caricetum distantis* is considered as a synonym of *Agrostio-Caricetum distantis.*

Distribution: E Austria, SW and SE Slovakia, Hungary, N Serbia, and Romania.

Caricetum divisae Slavnić 1948

The community has formed relatively dense, two-layered stands (Fig. 18). *Carex divisa* is a major component of the upper layer. Mesophilic hemicryptophytes such as *Leontodon autumnalis*, *Lolium perenne*, *Poa annua*, *Potentilla anserina*,

Fig. 18 Dense stands of *Caricetum divisae* are very characteristic (Horgoš, N Serbia). (Photo P. Eliáš jun.)

Trifolium repens, and subhalophytes (*Agrostis stolonifera*, *Juncus gerardii*, *Lotus tenuis*, *Taraxacum bessarabicum*) are predominant in the lower layer.

The association occupies habitats with fluctuating water regime – the bottoms of dried pools, marshy micro-depressions of pastures, and it also occurs in secondary wet ditches of warm lowland areas. Compared to previous communities of the *Scorzonero-Juncion*, these stands are bound to stronger groundwater dynamics during the year, flooded in the spring and partially overdrying in summer. The soil, usually slightly salinized Solonchak, is sandy-loamy or clayey-loamy, compacted, slightly humous, sufficiently supplied with nitrogen due to intensive grazing (Melečková et al. 2014; Dajić-Stevanović et al. 2016).

Distribution: N Serbia, SW Slovakia, Central and SE Hungary, and W Romania.

Loto tenuis-Potentilletum anserinae Vicherek 1973

It is relatively species-rich association. In stands, several subhalophytes co-dominated, especially *Lotus tenuis*, *Agrostis stolonifera*, *Potentilla anserina*, *Ranunculus repens*, *Taraxacum bessarabicum*, and *Trifolium fragiferum*. In addition to salt-tolerant plants, species of mesophilic lawns (*Lolium perenne*, *Odontites vernus*, *Pastinaca sativa*), alternately wet soils (*Festuca arundinacea*, *F. pratensis*, *Inula britannica*), and ruderal habitats (*Cirsium arvense*, *Taraxacum* sect. *Ruderalia*) are also abundant. The moss layer is not significantly developed. The stands are usually found around mineral rich springs, in periodically waterlogged floodplains, terrain depressions, and on the banks of village ponds (Novák and Šumberová 2007). It represents a degraded version of wet salt meadows (Borhidi et al. 2012).

The community is developed on slightly salinizes Solonchak soils with muddy, nutrient-rich surface as a result of grazing. The soils are damp, often shallowly flooded in spring, but dry out during summer (Novák and Šumberová 2007).

Distribution: E Austria, the Czech Republic, and SW Slovakia. Borhidi et al. (2012) believes that it occurs also in central Hungary (Mezőföld, Kiskunság).

3.4.2 Alliance *Beckmannion eruciformis* Soó 1933

Wet Subsaline Regularly Inundated Meadows on Heavy Clayey Soils of the Pannonian Basin

The alliance includes periodically flooded natural as well as secondary grasslands developed on slightly saline Solonetz soils. Their stands are generally inundated from early spring even until midsummer. The associations of *Beckmannion* can form either a narrow transitional zone or larger homogenous stands between dry alkali steppes and marshes (Deák et al. 2014). Floristic composition of the stands developing on less salinized soils is comparable to the vegetation of flooded wet meadows of the *Cnidion* alliance (class *Molinio-Arrhenatheretea*). In contrast, vegetation occupying heavily salt-affected soil is similar to communities of *Puccinellion limosae* (Borhidi et al. 2012).

The communities usually have two herb layers. The upper layer is generally formed of tallgrass species like *Agrostis stolonifera*, *Alopecurus pratensis*, *Beckmannia eruciformis*, *Elytrigia repens*, and *Glyceria fluitans*. The lower layer is colonized by species indicating silt accumulation processes on the soil surface (*Alopecurus geniculatus*, *Eleocharis palustris*, *E. uniglumis*, *Myosurus minimus*). Two endemic species *Rorippa sylvestris* subsp. *kerneri* and *Cirsium brachycephalum* are typical here (Török et al. 2012).

The alliance represents Pannonian endemic vegetation distributed in large areas of the Great Hungarian Plain including the territories of S and SE Hungary, N Serbia, and W Romania (Borhidi et al. 2012). It was mistakenly mentioned also from SE Slovakia (Dítě et al. 2012).

Five associations are included here.

Agrostio stoloniferae-Alopecuretum pratensis Soó 1933 Corr. Borhidi 2003

Stands are rich in species and rather heterogeneous (Fig. 19); they develop in sites with low moisture and salinity (Borhidi et al. 2012). The dominant species are tall grasses *Alopecurus pratensis*, *Elytrigia repens*, and *Agrostis stolonifera*. Furthermore, loess as well as salt steppe species such as *Achillea collina*, *Festuca pseudovina*, *Ranunculus pedatus*, *Trifolium angulatum*, *T. retusum*, and *T. striatum* may spread into dried places. In contrary, rushes (*Juncus effusus*, *J. conglomeratus*, *J. compressus*, and *J. gerardii*) indicate wet stands (Török et al. 2012).

This is the driest type of Solonetz meadows developed on the least alkali soils. Stands of this association are slightly flooded in spring and dry out in early summer. Soil surface is polygonally cracked (Deák et al. 2014).

Distribution: S and SE Hungary, N Serbia, and W Romania.

Fig. 19 Solonetz meadows of *Agrostio-Alopecuretum pratensis* are developed on the least salt-affected soils (the Hortobágy National Park, Hungary). (Photo P. Eliáš jun.)

Agrostio stoloniferae-Beckmannietum eruciformis Rapaics ex Soó 1930 Corr. Borhidi 2010

The association occupies patches with medium moisture but high salinity (Deák et al. 2014). It is characteristic by the high cover of tall grasses *Alopecurus pratensis*, *Agrostis stolonifera*, and *Beckmannia eruciformis*. Moreover, species of wet meadows such as *Cirsium brachycephalum* (Fig. 20), *Lythrum virgatum*, *Ranunculus lateriflorus*, and *Rumex stenophyllus* are very frequent in stands. Because it develops on relatively strongly salt-affected soils, sporadic occurrence of obligate halophytes like *Pholiurus pannonicus*, *Puccinellia distans* agg., and *Tripolium pannonicum* is typical (Dítě et al. 2012; Deák et al. 2014, 2019).

The community occupies Solonetz soils with significantly higher salt-content comparing to other *Beckmannion* associations; surface layer has generally a loose structure (Török et al. 2012; Deák et al. 2014). The water regime is dynamic, stands are flooded from spring till early summer, and it dries out regularly during midsummer (Dítě et al. 2012).

Distribution: E Hungary, N Serbia, and W Romania.

Agrostis stolonifera-Glycerietum pedicellatae Magyar ex Soó 1933 Corr. Borhidi 2003

The association represents the wettest alkali meadow community; it showed common characteristic with sedge meadows and alkali and non-alkali marshes. Similarly to the above two associations, tall grass species are dominant, namely, *Glyceria*

Fig. 20 The Pannonian endemic *Cirsium brachycephalum* is common in the stands of the *Agrostio-Beckmannietum eruciformis* association (the Hortobágy National Park, Hungary). (Photo P. Eliáš jun.)

fluitans and *Agrostis stolonifera*. Even species like *Beckmannia eruciformis*, *Eleocharis* spp., *Epilobium tetragonum*, and *Lycopus europaeus* are significantly represented. The higher soil salinity is indicated by occurrence of some sub-halophytes such as *Dichodon viscidum*, *Ranunculus lateriflorus*, *Rorippa sylvestris* subsp. *kerneri*, and *Tetragonolobus maritimus*. Marsh species (*Bolboschoenus maritimus*, *Schoenoplectus lacustris*, *S. tabernaemontani*, *Typha angustifolia*, *T. latifolia*) occurs regularly in the vegetation. Aquatic plants (*Lemna minor* and *Ranunculus aquatilis*) are sporadically present.

The soil is eluviated, and salt content is very low. Permanent waterlogging is typical; the soil surface dries out only in extreme dry summers (Deák et al. 2019).

Distribution: Hungary, N Serbia, and W Romania.

Eleocharito palustris-Alopecuretum geniculati (Ujvárosi 1937) Soó 1947

The community has a close relationship to vegetation of salt steppe, especially to the association *Plantagini-Pholiuretum*. However, it represents a wetter and less salinized type. It is a relatively species-poor community; dominant species are *Alopecurus geniculatus* and *Eleocharis palustris*. Moreover, differential species *Juncus gerardii* and *Eleocharis uniglumis* are usually present. Otherwise, the floristic composition of the association is very similar to that of *Agrostio-Alopecuretum pratensis* (Borhidi et al. 2012; Deák et al. 2014, 2019).

The community is developed in erosive grooves and small depressions on slightly salinized Solonetz soils with significant part of fine-grained soil substrate and mud.

Stands are flooded and wet throughout the growing season and dry out only exceptionally (Borhidi et al. 2012).

Distribution: Hungary, N Serbia, and W Romania.

Rorippo-Ranunculetum lateriflori (Soó 1947) Borhidi 1996

The association occupies deeper depressions and bays of swamp character in flat stand of *Agrostio-Beckmannietum*. Those microhabitats are exposed to seasonal flooding, and they remain flooded with shallow water level even in summer. Here, *Ranunculus lateriflorus* and *Beckmannia eruciformis* are dominant species, *Rorippa sylvestris* subsp. *kerneri*, *Agrostis stolonifera*, *Eleocharis palustris*, and *Lysimachia nummularia* are regularly represented. As important differential species, the sludge-indicating *Nanocyperion* species such as *Ranunculus aquatilis*, *Elatine alsinastrum*, and *Peplis portula* appear, too (Borhidi et al. 2012).

Distribution: rare in Hungary and N Serbia.

4 Threats of Salt Vegetation: Past and Present

4.1 From Mammoths Toward to Intensively Cultivated Fields

Pannonian steppe and meadow vegetation on salt-affected soils were maintained by large wild herbivores from Pleistocene to Early Holocene. After their disappearance, their role was taken over by domesticated animals such as cattle, sheep, and horses. Up to the mid-nineteenth century, nomadic lifestyles and extensive animal farming were the main form of human impact on the salt steppes and meadows (Sümegi et al. 1998, 2013; Šefferová-Stanová et al. 2008). The nomadic way of grazing in alkaline habitats has occurred since the Middle Ages and has been preserved until the end of World War II. Traditionally, only a negligible part of the meadows was mowed for hay production (Török et al. 2012; Fehér 2018).

A significant change of salt steppe and meadows occurred in connection with large-scale land drainage and the regulation of large rivers. These activities began at the end of eighteenth and ended only at the end of the twentieth century. The lowering of the water table leads to a gradual loss of salinity as the salts are slowly leached out from the soil, leading to the disappearance of salt-tolerant plant communities (Šefferová-Stanová et al. 2008). After World War II, there was also a downward trend in the number of grazing animals and a corresponding reduction in herding. This situation occurred not only in countries where power was gained by the Communists (former Yugoslavia and Czechoslovakia, Hungary, Romania) but also in Austria (Körner et al. 1999). However, collectivization and the pursuit of food sovereignty have led the Communist countries to use halophytic habitats for intensive agricultural production. The worst activity was the plowing of salt steppes and the effort to use them as arable land associated with application of fertilizers and pesticides (Fig. 21). For example, halophytic vegetation occupied approximately 8300 ha in SW Slovakia in the 1950s, until now only the remains on the area of approximately 500 ha have been preserved (Sádovský et al. 2004). Where the plowing of large areas of salt habitats was not an option, the poor fertility of pastures was improved by draining water, melioration, use

Fig. 21 Drainage and plowing are one of the most destructive interventions in halophytic habitats (Grăniceri, Romania). (Photo P. Eliáš jun.)

of fertilizers, commercial seeding, and by application of pesticides. Intensive animal farming where the livestock was kept in stables required sufficient forage also for winter season. Therefore, formerly grazed alkali meadows were transformed to hay meadows. Removal of grazing and introduction of mowing caused a more homogeneous vegetation structure of stands and species adapted to regular trampling and grazing became rare or vanished (Török et al. 2011).

At the end of the 1990s, after the collapse of the Eastern Bloc, it was envisaged to return to the original use of salt steppe and meadows by nomadic shepherds. But the opposite was true; imports of cheaper agricultural products and insufficient funding for new landowners have led to a 50–70% reduction in livestock numbers and a large abandonment of seminatural pastures and meadows (Isselstein et al. 2005). The accumulation of litter, the penetration of ruderal (*Dipsacus fullonum*, *Elytrigia repens*), and invasive species (*Amorpha fruticosa*, *Elaeagnus angustifolia*, *Hordeum jubatum*, *Solidago gigantea*) have been typical of such sites. This process is more pronounced in areas where habitat fragmentation has occurred and small remnants of saline habitats are surrounded by arable land.

4.2 Human Activities and Succession of Halophytic Vegetation

Intensive human activity over the last 150 years has caused irreversible changes in the character of the halophytic habitat. The drainage of the land has led to the development of secondary communities of alkali grasslands (e.g., *Achilleo-Festucetum*). Furthermore, decline of soil salt content has led to successive changes in vegetation of primary Solonetz salt steppe toward communities occupying less salinized soils. So the *Camphorosmetum annuae*, *Plantagini-Pholiuretum pannonici*, *Hordeetum hystricis*, and *Puccinellietum limosae* stands are transformed into *Artemisio-Festucetum* vegetation and *Artemisio-Festucetum* to *Achilleo setaceae-Festucetum pseudovinae*, or *Peucedano-Asteretum* stands (Molnár and Borhidi 2003; Dítě et al. 2014a, b). Similarly, the irreversible transition of pioneer halophytic communities of the alliance *Cypero-Spergularion salinae* into communities of *Isoëto-Nanojuncetea* was recorded (Šefferová-Stanová et al. 2008). In the vegetation of tall alkali grasslands of the alliance *Beckmannion,* cover of ruderal *Elytrigia repens* can increase due to decreased water availability (Deák et al. 2014, 2019).

5 Conservation and Management

Pannonian saline grasslands are the habitat of several rare and endemic species. For this reason, they were included in the habitats of European conservation interests within the Natura 2000 network under Council Directive 92/43/EEC 1992. Pannonian saline habitats are classified within units *1310 *Salicornia* and other annuals colonizing mud and sand, *1340 Inland salt meadows, and *1530 Pannonic salt steppes and salt marshes (Dajić-Stevanović et al. 2016).

Primary Solonetz alkali vegetation of *Festuco-Puccinellietea* was found relatively resistant to processes of vegetation succession. On the other hand, salt marshes (*Thero-Salicornietea, Crypsidetea aculeatae*) were more dynamic, while alkali mud communities of *Scorzonero-Juncetea gerardii* were the most dynamic, transforming easily into each other (Molnár and Borhidi 2003). This is related to the dynamics of the salt content in the soil, where the influence of human activity leads to the leaching of it. However, management of salt grasslands and meadows is equally important. These communities have adapted to relatively intensive grazing a few thousand years ago, and therefore grazing of sheep and cattle remains an essential management measure and traditional forms of land use for these habitats today (Fig. 22). Mowing is only considered an emergency response, as it will cause homogenization of the stands and the disappearance of some important plant species. In addition, heavy mechanisms damage the soil structure and adversely affect wild animals (e.g., bird nesting).

Recently, recovery management has been tested. One of the most difficult tasks is to restore the water regime. Extensive measures covering almost 10,000 hectares were carried out in the Hortobágy National Park in Hungary, where irrigation systems for grassland and rice fields were built in the 1950s and 1960s. The project resulted in the cessation of fragmentation of salt grassland and restoration of natural mosaic of dry salt steppe vegetation and salt marshes. Furthermore, abandoned fields on salt-affected soils have been successful conversed to seminatural stands by using low diversity seed mixtures of local provenance (Šefferová-Stanová et al. 2008). Surface disruption experiments have also been tested in Slovakia, but only surviving of competitively weak species (*Camphorosma annua*, *Crypsis aculeata*, *Heleochloa*

Fig. 22 Grazing of domesticated animals is one of the best management measures to preserve halophytic vegetation (the Kiskunság National Park, Hungary). (Photo P. Eliáš jun.)

schoenoides) have supported, while communities have failed to recover (Melečková et al. 2013).

Although the recovery of salt steppes and marshes is costly and long-term, positive results indicate that this pathway for the management of degraded salt habitats can help to preserve them for a future.

6 Conclusion

The unique halophytic vegetation developed in the Pannonian Basin as early as the Pleistocene period in connection with the development of Solonetz and Solonchak soils. More than 30 associations belonging to 7 alliances and 4 classes have been described on moisture and salinity gradients. And although phytosociological research has been going on for over a hundred years, the overall view of the vegetation of salt steppe, meadows, and marshes is not uniform and requires further research.

Due to the extreme conditions and unsuitability for crop cultivation, a unique symbiosis has arisen between humans, their domesticated animals, and these habitats, based on traditional pastoral land use. This situation was eroded some 150 years ago due to drainage interventions designed to reduce flooding and later also due to the agriculture intensification. Many sites have been destroyed or severely damaged. Recently, however, it has begun to pay more attention to protection and recovery supporting their conservation for the future.

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