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Succession of saline vegetation in Slovakia after a large-scale disturbance

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We studied the vegetation development in the Pannonian salt steppes in SW Slovakia (class *Festuco-Puccinellietea*) for eight years on permanent plots. The saline grassland was ploughed in 2002 to cultivate wheat and barley, and after two years it was left fallow. An open vegetation structure was typical for the initial stages, dominated by the obligate halophyte *Tripolium pannonicum*, accompanied by *Atriplex littoralis* and other annuals. Species richness significantly increased in the subsequent years. From the fifth year of the study, a significant increase of facultative halophytes (e.g. *Lotus tenuis*, *Tetragonolobus maritimus*, *Agrostis stolonifera*) and colonization of some expansive species (*Phragmites communis*, *Calamagrostis epigejos*) was observed and accompanied by a decrease in the cover of obligate halophytes (*T. pannonicum* and *Puccinellia distans*). *Plantago maritima* exhibited an opposite trend, and it was the only halophyte that was able to increase its population after the disturbance, due to vegetative propagation by rhizomes which increased the competitiveness of the species. The declining presence of salt-demanding species indicates a strong degradation of the saline vegetation, which might be linked to gradual desalinization of the soil. We conclude that population fluxes after adverse human disturbance and subsequent abandonment are very high, and succession of halophytic communities after such a strong disturbance is very fast, leading to deterioration of the habitat.

Introduction

Deterioration resulting from land-use change and demand for arable land is known worldwide (Assede *et al*. 2012, Nitsch *et al*. 2012), and both intensification of land-use and land abandonment decrease the number of rare habitats (Rosenthal 2010, Uematsu *et al*. 2010). Transforming the vegetation into intensive arable land directly endangers the natural vegetation, and leaving grasslands fallow leads to their gradual disappearance in the course of secondary succession (Somodi *et al*. 2004, Cremene *et al*. 2006). The same trend regarding overall grassland loss is observable in central Europe (Grulich 1987, Nováková 1997, Dajic-Stevanovic *et al*. 2008, Biró *et al*. 2013).

The direction of secondary succession in natural habitats is strongly dependent on the propagule input (Luzuriaga *et al*. 2005, Beatrijs & Olivier 2008). Spontaneous regeneration is usually effective in man-made and novel habitats, developed generally under long-term anthropogenic disturbance, such as quarries or old fields, (Lee *et al*. 2002, Rehounková & Prach 2006, Jírová *et al*. 2012) as the natural succession proceeds towards target stages and "passive" restoration is sufficient, since the adjacent stands provide propagules of target species. Natural succession also appears to function well in temperate forests (Dölle *et al*. 2008, Romagosa & Robinson 2003).

However, in rare grassland communities requiring a low intensity of permanent, more natural forms of disturbance, such as grazing, for their existence (Bakker 1981), active intervention could accelerate the recovery process (Loucougaray *et al*. 2004). If non-natural intensive disturbance (e.g. tillage, drainage) that destroys the equilibrium and the typical biological processes of the habitat takes place in grasslands, progressive succession will follow. In general, tillage of grasslands results in increased mineralization of soil organic matter, resulting in elevated losses of soil nitrogen (Davies *et al*. 2001), and leads to the death of most of the living plant biomass, which then serves as organic input to the soil (Linsler *et al*. 2013). There are numerous reports concerning the negative effects on grassland habitats caused by several forms of natural and anthropogenic disturbance, for instance, overgrazing (Török *et al*. 2008), heavy trampling (Liddle 1975, Andersen 1995) or abandonment (Matus *et al*. 2003, Jírová *et al*. 2012), but knowledge about the direct impact of tillage on grasslands occurring under specific ecological, highly-specialized conditions is lacking.

Inland saline vegetation is a specific plant community-complex in central Europe (Borhidi *et al*. 2013), where several halophytes of the salt steppes reach their northernmost occurrence in the lowlands of Slovakia (Krist 1940). Currently, halophytic vegetation in Slovakia is known only from scattered fragments. Over the course of 50 years its area has decreased to below 500 ha (Sádovský *et al*. 2004) which is about 6% of that present in the early 1960s (8300 ha), according to Osvačilová and Svobodová (1961). The main reason for the dramatic area reduction is strong intensification of agriculture in the lowland areas (amelioration, new tillage practices, pesticide application, etc.); less frequent ones are afforestation and urbanization.

Our study is designed to specify the characteristic features of secondary succession of a saline grassland exposed to tillage. We examined the impact of this type of disturbance and the abandonment on the species composition. We hypothesize that post-tillage succession without active management results in proliferation of rhizomatous, competitive and expansive plants to the exclusion of halophytes, where the number of species is expected to grow.

The following questions were addressed: (i) Which halophytes are the most tolerant to this type of disturbance? (ii) How long can halophytes persist on ploughed habitat? (iii) What are the consequences of tillage and what type of vegetation can develop after abandonment in the course of secondary succession on salt-affected soils?

Material and methods

Site description and history

The study site Pavel is located west of the village Zlatná na Ostrove in the Žitný ostrov region in the alluvium of the Danube river (47°46´23´´N and 18°0´2´´E, 107 m a.s.l.).

The area belongs to the Pannonian bioregion, with a moderately continental climate of relatively hot summers and cold winters. The mean annual temperature is about 10.3 °C, averaging 20 °C in July and –1.5 °C in January. The mean annual rainfall is 550 mm (Miklós & Hrnčiarová 2002), but it may vary from year to year. In 2010, when extreme rainfall was recorded in central Europe, the rainfall measured at the Zlatná na Ostrove weather station was 942 mm (Slovak Hydrometeorological Institute, Bratislava, unpubl. data). The soil type is alkaline solonetz.

The site is located next to a Natura 2000 locality, Pavelské slanisko, declared as an important site of biodiversity in the agricultural landscape with valuable and rare halophytic flora. The first botanical survey of the area was made by Krist (1940), who recorded *Artemisia santonicum*, *Camphorosma annua*, *Pholiurus pannonicus*, *Plantago tenuiflora*, *Puccinellia distans* and *Tripolium pannonicum*.

Krippelová (1965), reporting from the broader municipality area, described open salty areas with initial halophytic stands of *Puccinellion limosae* surrounded by *Festucion pseudovinae* alliances. Prior to negative disturbance, the grassland was used for grazing, which maintained the open vegetation structure typical of saline habitats. In the 1990s, the vegetation fragments were stepp-like, within a patchy mosaic of *Artemisia santonicum* and *Puccinellia distans* dominated stands, and there were large open areas of soil without plant cover. Two types of grasslands in a rather degraded, secondary stage were confirmed on the site by Zlinská (2006): halophytic (*Artemisio-Festucetum pseudovinae*) and xeric vegetation related to *Potentillo arenariae-Festucetum pseudovinae*. The current area of halophytic communities on the site is 0.5 ha. The last tillage was documented in 2002 when a local agricultural company attempted to grow barley and wheat, but it ended with a crop failure and two years later it was abandoned again. In the initial stages on the denuded soil surface we observed an open vegetation structure and salt efflorescence on the gaps with no plant cover.

Sampling design and data processing

In 2005, three years after the tillage, we established three fixed permanent plots with an area of 4 × 4 m to examine the effects of disturbance on the diversity and structure of the ploughed saline habitat. We selected the plots on the sites with the highest salt content, clearly indicated by the vegetation physiognomy and the white colour of the soil surface covered with crystallized salts. Within each plot, we recorded percentage cover of plant species in early September, when saline vegetation is optimally developed. We repeated the sampling once a year until 2012. Since the whole locality was ploughed, it was not possible to establish reference sites that have not been disturbed. Studies on the secondary succession on similar vegetation affected by controlled top soil removal for micro-restoration purposes in the same region were made by Melečková *et al*. (2013).

Soil samples (300 g each) were taken on 24 September 2009 from all three plots from the depths of 10 and 30 cm, and the following properties were analyzed: soil reaction (pH/$CaCl_2$); exchangeable cations Na, Mg, Ca, K; amount of total salt (NaCl and Na_2SO_4), total nitrogen (N_{TOT}), total organic carbon (Cox), sodium absorption ratio and (SAR) and exchangable sodium percentage (ESP). Exchangeable cations were evaluated in an acidified soil extract of barium chloride buffer (pH 8.1) and triethanolamine by flame atomic absorption spectrometry (AAS-F) at a wavelength specific to the individual cation (Richards 1954). Salt content was determined by water extraction followed by evaporation of the water extract and drying the residue at the temperature of 105 °C. Soil reaction was measured potentiometrically in a saturation extract obtained from saturated soil paste according to international standards (STN ISO 13536 2001). Total nitrogen was determined by a patented method of dynamic combustion in an oxygen atmosphere. The purpose of the soil analysis was to illustrate the specific soil chemistry of the studied halophytic vegetation (Table 1).

We indicate the changes in soil conditions indirectly by using plant-sociological data and indicators of the SE-central European flora (Borhidi 1995; *see* Trend analysis below).

The nomenclature of plant taxa follows Marhold and Hindák (1998) and the names of syntaxa follow Molnár and Borhidi (2003); names not present in this list are followed by the author's abbreviation.

Multivariate analysis

We performed multivariate analysis on the data collected during eight years. Cover values were log-transformed to decrease the strong impact of dominant species on the analysis results, because the overall floristic composition on our plots was our foremost interest. The succession rate was measured by calculating the effect of time after tillage and abandonment on the permanent plots. We tested *Time* as a consecutive independent variable between the first vegetation survey and the subsequent years. Due to the linear response of species to succession (length of the gradient in DCA 2.988 SD units) we performed a redundancy analysis RDA (Lepš & Šmilauer 2003). Plots were used as covariables, samples were standardized by norm. We performed a Monte Carlo permutation test (499 restricted permutations by time-series) under full model, blocks defined by covariables (Plots 1, 2 and 3). For gradient analyses we used the software package CANOCO for Windows 4.5 (ter Braak & Šmilauer 2002).

Trend analysis

We subjected the dataset to non-parametric Mann-Kendall test using the software Statistica 7. A non-parametric trend analysis was used to avoid problems with normality of our variables, as most of them did not follow the normal distribution. We tested the response of two traits (*Salt tolerance* and *Life cycle*) to successional time, as they are the best traits describing the changes in the species composition from the early to well-developed stages of succession after tillage and abandonment.

For *Salt tolerance*, we divided the vascular plants according to Borhidi (1995), simplifying his detailed plant sociological groups (10 grades) into three major groups (Table 2): (1) obligate halophytes, which demand higher rates of soil salinity and grow naturally in saline habitat; (2) facultative halophytes, which can withstand higher salt concentration, but have a wide optimum in moderately saline to minimally saline habitats; (3) glycophytes, usually generalists, which grow only on mesic soils unaffected by salt. The second trait was *Life cycle*, for which we classified the plants into two groups according to Király *et al*. 2009 (Table 2): (1) annuals and biennials; (2) perennials (including woody plants, since all of them grow in the herb layer). We used the same method to analyse changes in the species richness and total cover, abundance of the indicator key halophytes (*Tripolium pannonicum*, *Puccinellia distans* and *Plantago maritima*) and subhalophytes (*Lotus tenuis, Tetragonolobus maritimus* and *Agrostis stolonifera*) individually. We excluded bryophytes and algae (*Didymodon acutus* and *Nostoc communae*) from the regression analysis, since they cannot be classified according to the traits and their cover was negligible.

Results

We recorded a total of 35 plant species on the permanent plots over the eight years. Year-to-year species richness ranged from 7 to 14. While in 2005 we recorded only seven species, that

Table 1. Results of soil analyses on three permanent plots from 10 cm and 30 cm depth (samples collected on 24 September 2009).]

	Plot 1		Plot 2		Plot 3	
	10 cm	30 cm	10 cm	30 cm	10 cm	30 cm
N_{TOT} (%)	0.046	0.044	0.040	0.032	0.031	0.033
Cox (%)	0.006	0.366	0.232	0.011	0.048	0.003
K_{exch} (cmol$^+$ kg^{-1})	0.11	0.13	0.11	0.17	0.11	0.13
Na_{exch} (cmol$^+$ kg^{-1})	2.62	2.41	4.59	4.01	1.28	2.20
SAR	129.00	133.00	94.10	68.30	26.20	45.20
ESP (%)	79.70	80.30	72. 40	63.80	37.50	52.20
pH/KCl	8.90	8.90	9.28	8.32	8.83	8.40
Total salts (%)	0.378	0.283	0.428	0.168	0.268	0.180

number increased gradually during the subsequent years, until the maximum number (14) of species was reached in 2009, after which it oscillated moderately until the last year of the study. Total vegetation cover varied between 45% (2005) and 65% (2012), at which time it was constantly increasing.

The three most abundant species at the site during the study period were obligate halophytes *Tripolium pannonicum*, *Plantago maritima* and *Puccinellia distans*. In the first three years of the study, there was a rapid decline in the cover of *Atriplex littoralis* (17% in 2005, then from 1.2% to zero in 2007).

Concerning the overall vegetation development after tillage and abandonment, redundancy analysis confirmed the environmental variable *Time* ("succ_year" in the ordination diagram) as significant ($p = 0.002$). This variable explained 32.4% of the variance in species composition ($F = 13.527$). In the ordination diagram (Fig. 1), three species groups were identified which dominated in three separate states of succession:

1. Pioneer and weedy species of open vegetation types, including the salt-demanding *Atriplex littoralis*, recorded only in the first two years.
2. Obligate halophytes (*Tripolium pannonicum*, *Puccinellia distans*, sporadically *Artemisia santonicum*) occurred during the whole study period with decreasing abundance.
3. A group of perennial species with increasing abundance after tillage and abandonment: halophytes (*Plantago maritima*), subhalophytes (e.g. *Lotus tenuis*, *Tetragonolobus maritimus*, *Odontites vulgaris*, *Agrostis stolonifera*), shrubby species *Frangula alnus*, *Rhamnus cathartica*) and tall grasses (*Deschampsia cespitosa* and in the later states *Calamagrostis epigejos* and *Elytrigia repens*). These taxa, after the decline of pioneers, annuals and obligate halophytes, precipitously occupied the plots and correlated positively with progressive succession.

The Mann-Kendall trend analysis confirmed a significant ($p < 0.05$) increase of the following variables (Table 3) in time: *Total cover*, *Species richness* (*see* also Fig. 2), *Facultative halophytes* and *Perennials* (*see* also Figs. 3 and 4), and increases in cover of the individual species *Plantago maritima*, *Lotus tenuis*, *Tetragonolobus maritimus* and *Agrostis stolonifera*, which play a key role in secondary succession (*see* also Fig. 5). On the other hand, we detected a significant decrease of *Tripolium pannonicum* (Fig. 5). The cover of perennial species during the eight years increased from 31.5% to 66.2% (Fig. 4). The decrease of annual species' cover was insig-

Table 2. Classification of species occurring on plots according to the traits *Salt tolerance* and *Life cycle*. *Life cycle* is defined and indicated as follows: ◊ = perennials and biennials, ° = annuals. Species names used in the RDA diagram (Fig. 1) are followed by their abbreviation in parentheses.

Obligate halophytes	Faculative halophytes	Glycophytes
◊ *Tripolium pannonicum* (TriPan)	◊ *Agrostis stolonifera* (AgrSto)	◊ *Cirsium arvense* (CirArv)
◊ *Pantago maritima* (PlaMar)	◊ *Lotus tenuis* (LotTen)	◊ *Calamagrostis epigejos* (CalEpi)
◊ *Puccinellia distans* (PucDis)	◊ *Tetragonolobus maritimus* (TetMar)	◊ *Frangula alnus* (FraAln)
◊ *Artemisia santonicum*	◊ *Sonchus arvensis*	◊ *Daucus carota* (DauCar)
° *Atriplex littoralis* (AtrLit)	◊ *Leontodon autumnalis*	◊ *Dechsampsia cespitosa* (DesCes)
	◊ *Phragmites australis*	◊ *Betula pendula*
	◊ *Elytrigia repens*	◊ *Ononis spinosa*
	° *Atriplex prostrata* (AtrPro)	◊ *Solidago gigantea*
	° *Tripleurospermum perforatum* (TriPer)	◊ *Rhamnus cathartica*
	° *Odontites vulgaris* (OdoVul)	◊ *Populus alba*
	° *Centaurium pulchellum*	◊ *Poa angustifolia*
	° *Melilotus marcorrhizus*	◊ *Cynodon dactylon*
	° *Polygonum aviculare*	° *Lactuca serriola* (LacSer)
		° *Anagallis arvensis*
		° *Cuscuta epithymum*

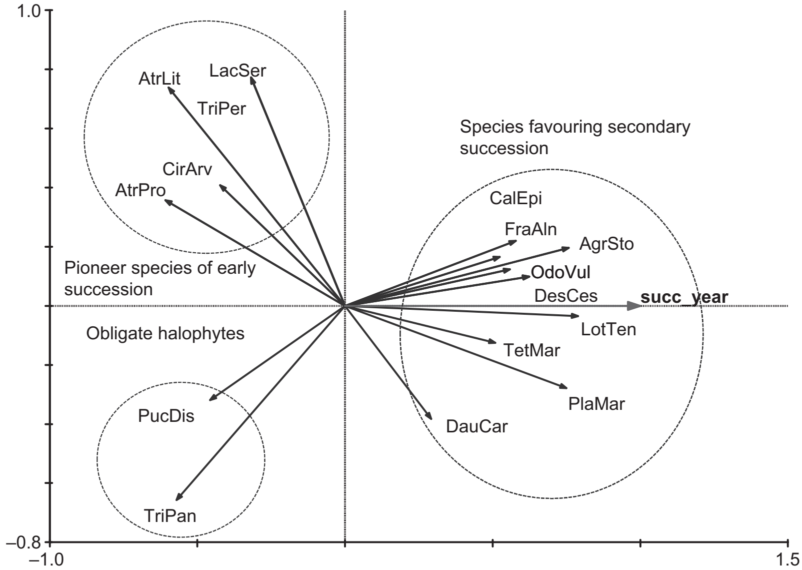

Fig. 1. RDA-ordination biplot depicting the species' responses to secondary succession ("succ_year") on the previously ploughed and abandoned plots. According to the species response, three main groups are distinguished. Species are displayed by 20% of fit range, for species abbreviations, *see* Table 1. The analysis was performed on log-transformed data.

nificant (Table 3). However, in the first year of the study, their mean cover had been 18% and in 2012 it decreased to < 2%.

To summarise, *Time* (eight-year study period) resulted in a strong increase of *Plantago maritima*, and an increasing trend of some facultative halophytes and perennials. Total cover and species richness correlated positively with *Time* (years of abandonment). Furthermore, we confirmed an evident decline of the dominating halophyte *Tripolium pannonicum*.

Table 3. Results of the trend analyses (Mann-Kendall test; τ coefficients) carried out for *Salt tolerance*, *Life cycle*, *Total cover*, *Species richness* and individual species playing a key role in secondary succession. Sample size $n = 8$. Significant trends (τ at $p < 0.05$) are set in boldface.

	τ
Salt tolerance	
Obligate halophytes	–0.255443
Facultative halophytes	**0.634916**
Glycophytes	0.234856
Life cycle	
Perennials	**0.471896**
Annuals	–0.159046
Total cover	**0.462590**
Species richness	**0.575396**
Individual species	
Tripolium pannonicum	**–0.511827**
Puccinellia distans	–0.140794
Plantago maritima	**0.719311**
Lotus tenuis	**0.682941**
Tetragonolobus maritimus	**0.432072**
Agrostis stolonifera	**0.680017**

Discussion

As predicted, species richness and total cover of ploughed and abandoned saline plots increased (Fig. 2). The trend is not surprising, as species richness and total cover increase are ordinary attributes of the secondary succession's early and mid-phases (Horn 1974, Crawley 1997). The speed of successional processes following the abandonment of grazing might change over time. A general view exists that the speed of successional dynamics decreases with time. Several case studies provided evidence that vegetation change is the quickest in the first five or ten years of vegetation development both in old fields and in abandoned pastures (Prach *et al*. 1993). In alkali-saline grasslands, the average number of species is low, usually from five to ten species per relevé (Borhidi *et al*. 2013) due to the limiting factor of higher soil salinity (Piernik 2003). In our study, the species richness increase above the average can be explained by the reduction of salt content caused by man-made disturbance,

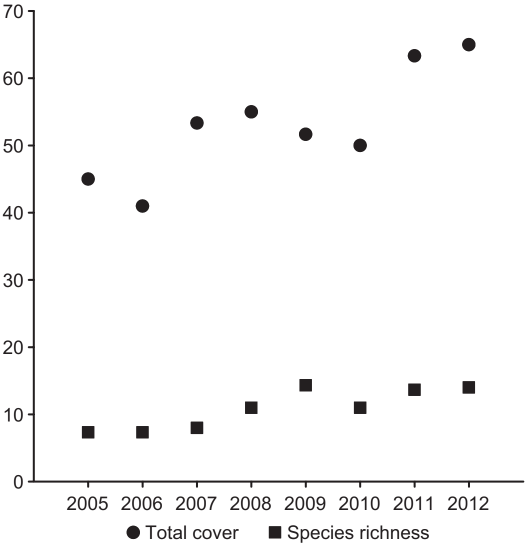

Fig. 2. Changes in *Total cover* and *Species richness* in time.

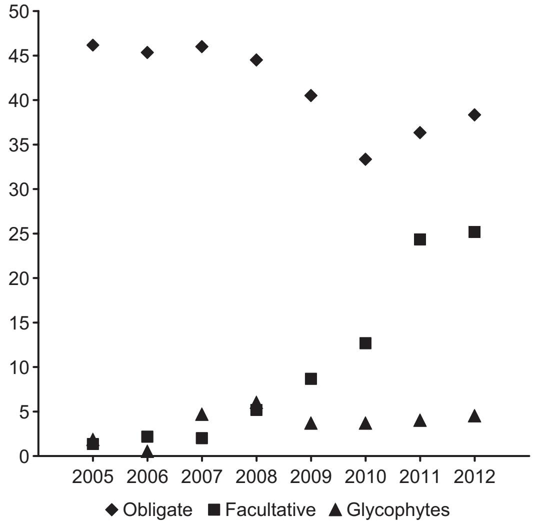

Fig. 3. *Salt tolerance*. Changes of the cover of obligate halophytes, facultative halophytes and glycophytes in time.

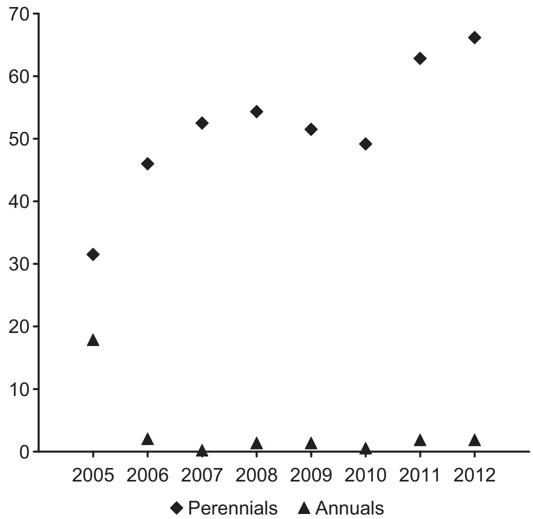

Fig. 4. *Life cycle*. Changes of the cover of annual and perennial species in time.

which supports the appearance of some mesic and ruderal species.

Tolerance of halophytes against disturbance and abandonment

Disturbance is defined as an event that destroys biomass and changes community structure and resource availability (Pickett *et al*. 1987). Initial floristic composition may strongly determine later vegetation development (Egler 1954), while later species are superior to earlier ones in exploiting resources (Connell & Slatyer 1977). On our plots, the salt-demanding therophyte *Atriplex littoralis* increased rapidly in response to denudation of the soil but its occurrence persisted only during the first two years, until perennial species began to expand. *Atriplex littoralis* is an important indicator of a pioneer stage of the secondary succession on salt-affected soils. The consequences of tillage followed by abandonment were favourable for pioneer species only for a short time; pioneers were substituted by stronger competitors in one year (Fig. 3). After the decrease of the species not favoured by abandonment, the site was notably colonized by perennial grasses, subhalophytes and light-demanding shrubby species (Fig. 1). Those, with the exception of *Plantago maritima*, are rather mesic species, some of them expansive ones, tolerating a moderate salt content. Had the site not been abandoned after ploughing, we assume that under grazing pioneers, annuals and obligate halophytes would have persisted on the plots for a longer time, as observed by Loucougaray *et al*. (2004) in the salt marshes of western Europe.

Several phenomena not conforming to the general trend must be discussed. The reason that the decrease of obligate halophytes is not signifi-

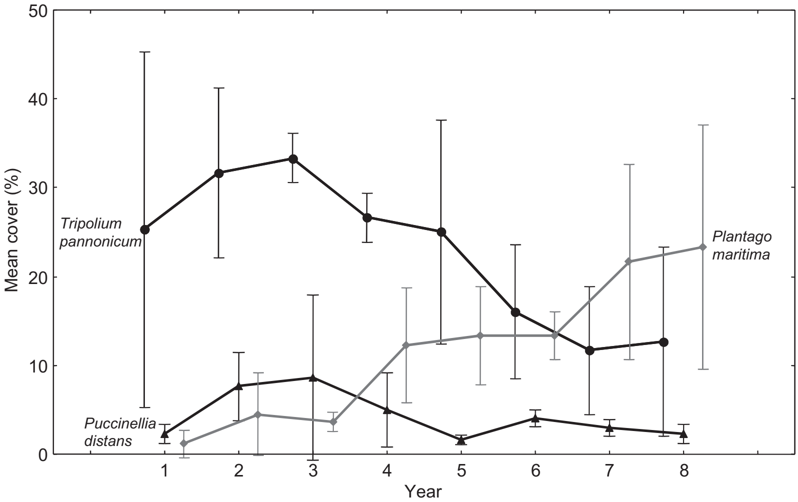

Fig. 5. Temporal changes in the mean cover of individual dominating obligate halophytes (± SD).

cant (Table 3 and Fig. 3) is the individual trajectory of *Plantago maritima*. Concerning particular species' reaction to the time of the occurrence and persistence in the succession, *P. maritima* differs from the other obligatory halophytes, *Puccinellia distans* and *Tripolium pannonicum* (Fig. 5). *Plantago maritima* appears in the succession after the early phase, and its increase is notable only from the third year on, and later it becomes the most dominant halophyte species. Due to the reduced competition caused by soil denudation, this deep-rooting species (Muraközy *et al*. 2003) can grow even on strongly degraded saline soil and may also regenerate from shoots (Makowczyńska *et al*. 2009). Our study also confirmed plants' ability to colonize the gaps after soil disturbance of the saline habitat. Rhizomes are a key factor of high competitiveness in abandoned grasslands, because they provide multiple advantages: low-risk vegetative propagation, nutrient storage and nutrient re-allocation (Rosenthal 2010). The dominance of *P. maritima* will probably decrease in the advanced stages of succession, since it is a weak competitor (Dormann *et al*. 2000a, 2000b).

A rapid decrease of other obligate halophytes (*Puccinellia distans*, *Tripolium pannonicum*) can be explained by the same fact, as the ploughed areas of salt-affected soils are occupied by more competitive halophytes. It is a contradictory finding that *P. distans*, known as a typical species on disturbed, secondary habitats like roadsides where salting during winter is applied (Lembicz 1998), did not increase on the plots. The two species tend to have mono-dominant stands on field depressions of clayey saline soils ploughed regularly (Dítě *et al*. 2009), although the species' expansive tendency was not observed on the study site (Fig. 5). Another explanation might be that *P. distans* and *T. pannonicum* are more moisture-demanding (Borhidi 1995, Knežević *et al*. 2008) and the assumed drying out of the disturbed habitat may negatively affect their persistence. However, taking into account the significant expansion of some facultative halophytes with similar moisture demands (Table 3 and Fig. 3), e.g. *Agrostis stolonifera*, it can be concluded that the decrease in alkalinity and salinity of the soil had already begun. Typical species of saline sodic soils gradually decline, as they are strongly dependent on high salinity and alkalinity (Tóth & Kuti 1999, Szabó & Tóth 2011).

The open niches of disturbed habitats were occupied by several occasional species which later disappeared (e.g. *Poa angustifolia*, *Leontodon autumnalis*, *Melilotus macrorrhizus*). Their short duration on the site was not caused by the pressure of the other species as in case of the above-mentioned halophytes having a key role in the succession, but it rather signals the high disturbance level of the saline grassland. They probably came from neighbouring non-saline stands in the years with higher precipitation (e.g. in 2010), when sodium could leach out or move into the deeper soil layers (Armstrong *et al*. 1996). Heavily disturbed habitats are generally subjected to invasion by alien species (Chytrý *et al*. 2008, Pyšek *et al*. 2009, Bomanowska & Adamowski 2012). In our study, however, only one invasive species, *Solidago gigantea* (Medvecká *et al*. 2012) appeared so far in the eighth year after the abandonment, although the species is abundant in the adjacent stands. This can be explained by the fact that inland saline habitats are generally resistant to invasive alien species (Bagi *et al*. 2011). However, we expect that aliens will increase if there is no further management.

The tillage-affected habitats provided free gaps and an opportunity for colonising low-competitive species, supposedly ideal conditions for certain halophytes which could withstand this type of disturbance when the soil is at least moderately saline. In spite of the soil disturbance, we did not detect any other halophytic therophytes (*Pholiurus pannonicus* or *Plantago tenuiflora*) typical of disturbed, trampled, saline habitats, recently found in other ploughed areas in the region (e.g. *P. pannonicus*; Eliáš *et al*. 2010).

Because in the first years we observed on the plots halophytic species like *Tripolium pannonicum*, *Puccinellia distans*, *Plantago maritima* and sporadically *Artemisia santonicum*, it might be considered that ploughing did not completely ameliorate the saline habitat. At the beginning of the study period, the denuded soil surface was covered by crystallized salts. However, the subsequent increase of subhalophytes and generalists after several years indicates that accelerated secondary succession is occurring.

Consequences of ploughing and vegetation development in the secondary succession on salt-affected soils

Emery (2012) considers ploughing in conventional agriculture as a low-intensity disturbance which results only in moderate succession, where species can survive in the soil and quickly colonize areas after the disturbance. Our results did not support that, and they imply that after initial stages the vegetation development of the damaged site caused negative changes (degradation, expansion of generalists and decline of specialists typical to the saline habitat).

The average pH of the studied plots was high (8.5) but, on the other hand, it is an interesting finding that in spite of the still higher values of salinity SAR and ESP (Table 1) the halophytic communities did not return, and only certain halophytes occurred. In the undisturbed saline vegetation's soil profile, there are processes resulting in formation of a compact layer enriched in clay with high peptization and its translocation creates a sintered structure lacking soil air. Such conditions are obviously the most favourable for halophytes (Lai *et al*. 2012). Ploughed saline soil has this impervious clayey layer disturbed, thereby the respiratory activity is considerably improved. In addition, the soil becomes enriched in macro-elements and, through application of fertilizers, nutrients in particular, necessary for crops. Such conditions promote weeds and other competitive species thereby reducing the survival chances of original salt-demanding vegetation. Inversion of soil layers can result in subsequent leaching of salts as well. Lower soil salinity then favours the increase of glycophytes (Bakker 1985).

It may be of interest to note that a moderate proportion of salt-affected soils in Slovakia were used as arable land: 25% of sodic solonetz soils, and 90% of saline solonchak soils were transformed for intensive agricultural purposes, usually for growing wheat, barley, corn, alfalfa or beet (Hraško 1971). However, the yields of those fields were extremely low, so they were frequently abandoned. Attempts to utilise saline grasslands did not provide considerable success due to the extremely unfavourable soil properties (Krippelová 1965), but the forced uncontrolled continuous ploughing has caused homogenization and gradual destruction of the rare saline vegetation.

Conclusions

After ploughing, halophytes persisted for some time on the abandoned site, but the disruption was so strong that no halophytic communities established themselves even during eight years of succession. Moreover, removal of land from active optimal use (e.g. grazing) triggered a progressive secondary succession which, without further management, continues with degradation. The recent stands of the study site are not classifiable into any type of halophytic plant community from the phytosociological point of view (Dítě *et al*. 2010): they have regenerated into fragments with a mixture of halophytic species and the formerly typical, relatively well-developed stands were substituted by secondary vegetation.

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