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# Seed Bank and Vegetation Development of Sandy Grasslands After Goose Breeding

**P. Török · G. Matus · M. Papp · B. Tóthmérész**

**Abstract** Four hypotheses were tested using long-term observations of vegetation development (12 years) and present-day seed bank data in a sandy grassland area overgrazed by domestic geese: *i*) Gap regeneration is crucial in maintaining species richness; thus, closed vegetation of the lower sites prevents continuous establishment of short-lived species. *ii*) Short-lived, early successional species comprise most of the seed banks and late successional perennials have at most sparse seed banks. *iii*) Composition of seed banks is more similar to pioneer vegetation than to later successional stages. *iv*) The similarity is higher between vegetation and seed banks in the upper-positioned plots than in the closed, lower-positioned ones. Two sites, located in the upper part of dune slopes, and another two, positioned on the lower part, were studied. In each site five 2×2 m permanent plots were surveyed between 1991 and 2002. Percentage cover was estimated three times a year. In the last study year, soil seed banks were sampled. Two vertical segments (0–5, 5–10 cm) were separately analyzed. The seedling emergence method was applied on concentrated samples. We found that the vegetation developed from open, annual dominated weedy assemblages to grasslands dominated by perennial graminoids. In the lower-positioned sites perennial clonal grasses (*Cynodon dactylon*, *Poa angustifolia* and *P. pratensis*) formed more closed vegetation, which was accompanied by lower species richness compared to the upper-positioned sites. Seed density varied between 10,300 and 40,900 seeds/m$^2$. Significantly higher seed densities were found in upper sites than in the lower ones. Annuals and short-lived perennial dicots comprised most of the seed bank. The dominant perennial graminoids also built up dense seed banks.

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We found a low to medium similarity between vegetation and the seed bank; similarity was the highest with the vegetation of the 1994–1998 period. In the upper sites the similarity between seed bank and the vegetation of the last studied years was also high. The vertical position had a significant effect on regeneration after overgrazing. The large cover of grasses in lower sites decreased species richness and it also decreased the seed density preventing the seed bank formation of annuals and short-lived perennials. Here, further management practices are needed to increase the species richness.

**Keywords** *Cynodonti-Festucetum* · Disturbance · Grazing · Inland dune · Permanent plot · Seedling emergence

**Plant nomenclature**

| | | |
|---|---|---|
| Simon | (2000) | for taxa |
| Borhidi | (2003) | for syntaxa |

## Introduction

Soil seed banks represent a successional memory that transfers information on earlier vegetation dynamical events (Willems 1995; Bakker et al. 1996; Bekker et al. 1997). Buried viable seeds also have a significant influence on dynamics triggered by abiotic (e.g., severe drought) or human-induced disturbance (overgrazing, ploughing) (Bossuyt et al. 2001; Wagner et al. 2003). In the case of well-developed soil seed banks of late successional species, degraded sites can recover spontaneously without expensive restoration management (Blanckenhagen and Poschlod 2005). Contrary, high densities of persisting early successional weeds can hinder vegetation development after disturbance events (Tsuyuzaki and Fusayuki 1992). Therefore, analysis of composition and density of soil seed banks and specific longevities pays off when planning ecological restoration of degraded sites (McDonald et al. 1996; Bakker et al. 1996). Despite the predictive force of seed bank data there is a definite shortage of this type of information; less than half of the species are covered in North-Western Europe's seed bank type classification (Thompson et al. 1997). Records are available only for about one-fourth of the Hungarian flora (Csontos 1998). The lack of data is especially serious for predicting the dynamics of dry grasslands, where regeneration from soil seed banks is among the most important mechanisms (Levassor et al. 1990; Espigares and Peco 1993) and the same holds for the Pannonian psammophilous vegetation (Matus et al. 2003).

Subcontinental, perennial sandy grasslands and pastures, developed after forest clearing and maintained by grazing, are widespread in central parts of the Carpathian Basin (Soó 1957). Like many other types of grasslands in Hungary, sandy grasslands have undergone major changes in composition due to fluctuating agricultural use. In the last few decades their traditional management, i.e., extensive grazing by cattle or sheep, has often been replaced with uncontrolled intensive grazing by domestic geese. This type of management has brought on their large-scale degradation (Matus and Tóthmérész 1994). In many areas conservation authorities are seeking to restore these grasslands. It is therefore useful to study the natural regeneration capacity of these grasslands to assess the extent to which further human actions are required. Data on seed bank formation, especially on longevity of early successional species, offer valuable information for understanding dynamics and assessing restoration prospects of degraded stands.

Using permanent plots, we analyzed vegetation regeneration of sandy grasslands after denudation and intense fertilization from geese. We also collected data on seed bank formation with special emphasis on longevity of successional pioneers. We aimed at testing the following hypotheses: *i*) Gap regeneration is crucial in maintaining species richness; thus, closed vegetation of perennial graminoids in the lower sites prevent continuous establishment of short-lived species. *ii*) Short-lived, early successional species comprise most of the seed banks, whereas perennials, dominating late successional vegetation, have at most sparse seed banks. *iii*) Soil seed banks represent a kind of successional memory of vegetation development. Thus, seed bank composition has higher similarity to pioneer vegetation than to later successional stages, including the year the samples were collected. *iv*) We expect higher similarity between vegetation and seed banks in the more open, upper-positioned vegetation than in the more closed, lower-positioned one.

## Material and Methods

### *Site Description and History*

The study sites were at the ‘Martinkai-legelő’ protected area located near Hajdúsámson, Hajdú-Bihar County, East-Hungary (CEU: 8496.2). The site has 3–10 m high parabolic dunes that are built up from wind-blown, calcium-free Pleistocene sand. Typical particle size of the parent material is 0.1–0.3 mm.The climate is moderately continental with a mean yearly temperature of 10.0°C and an annual precipitation of 600 mm.

Dry sandy grasslands, *Cynodonti*- and *Potentillo-Festucetum pseudovinae* dominate the site. On steep slopes pioneer grasslands (*Festucetum vaginatae*) (Soó 1957; Borhidi 2003; Matus et al. 2003), whereas in dune slacks wet meadows were present. Prior to the beginning of the study, in 1989–1990, thousands of geese that devastated aboveground vegetation severely overgrazed large parts of the reserve. Secondary succession started from sporadically surviving perennials and from the soil seed bank.

At former goose farming stables (abandoned in 1990), two upper (U1 and U2) and two lower (L1 and L2) positioned sites were selected for study. The upper-positioned sites were located ca. 2.7–2.9 m above the dune slacks near the top of the dunes. The other two, lower elevated sites were positioned ca. 1.5 m above the dune slacks. Slope inclination was below 5° at all sites. The U1 and L1 sites were located in the eastern part (132.5 m a.s.l.), whereas the U2 and L2 sites were located in the western part of the reserve (129.2 m a.s.l.). The vegetation of the sites regenerated spontaneously without any restoration management. For a detailed description of site, climatic conditions during the study period as well as vegetation development see Török et al. (2008).

The soil in all sites was calcium-free, moderately to strongly acidic sand ($pH_{KCl}$: 4.01–5.88). Low to moderate humus content (0.6%–1.9%), low nitrate plus nitrite (<2 ppm) as well as low ammonium (<12 ppm) contents were detected. Potassium and phosphorous contents were high and varied greatly between sites (sampled in the 1999–2002 period). At the upper elevated sites phosphorous contents varied from 149 ppm to 576 ppm; while at the lower elevated sites it varied from 241 ppm to 1121 ppm. At the upper sites potassium contents varied from 61 ppm to 117 ppm; while at the lower elevated sites it varied from 120 ppm to 236 ppm.

### *Sampling Setup*

Percentage cover of vascular plant species was recorded in three seasons (April, June and September, between 1991–2002) in permanently marked plots (five 2 × 2 m plots per site). Seed banks were sampled after natural winter stratification in late February 2002. Thirty soil cores per site (six cores/plot, each 4 cm in diameter and 10 cm in depth, altogether 3,770 $cm^3$/site) were drilled. Two vertical segments (0–5 cm, 5–10 cm) were separated. Identical segments drilled from the same plot were pooled on the spot. Pooled samples were treated with a bulk reduction procedure (ter Heerdt et al. 1996). Samples were washed over a coarse sieve (3.0 mm mesh) to retain vegetative organs, and seed-free fine soil components were removed on a 0.2 mm fine mesh. Sample volume was reduced by 65%–70%.

Concentrated samples were spread in a maximum 3–4 mm thick layer on trays, previously filled with 4 cm of normal and 4 cm of steam-sterilized potting soil. Trays were illuminated with natural light in a greenhouse of the Botanical Garden of Debrecen University. In the greenhouse, shaded with Rachel-nets from early May to August, temperature varied typically between 30°C/18°C at day/night. In early July, when no new seedlings emerged, watering was stopped, and dried sample layers were crumbled and turned. In early September watering was re-started and continued until late October. Germination altogether lasted for 37 weeks. Seedlings were regularly counted, identified (Csapody 1968) and then removed. Unidentified taxa were transplanted. Transplants of *Cyperaceae*, *Juncaceae* and *Poaceae* were mostly identified in the following spring when flowering. Seed rain was monitored in sample-free control trays filled with sterilized soil. Contaminant species, e.g., greenhouse weeds (*Oxalis corniculata*, *Cymbalaria muralis*) and the wind-dispersed tree, *Betula pendula*, were excluded from analyses.

### *Data Processing*

In field surveys it has not always been possible to distinguish *Veronica dillenii* and *V. verna*. High seedling mortality in summer also did not enable us to distinguish this pair in the greenhouse. These species have been pooled in analyses as *Veronica* spp. Rare seed bank species (<3 seeds), and the horsetails (*Equisetum* spp.) were excluded from seed bank classification (Thompson et al. 1997). Raunkiaer's life-form categories as well as indicator values of Ellenberg for moisture ($W$) and nutrients ($N$) adapted to Hungarian conditions (Borhidi 1995) were used in the analysis of vegetation and seed bank samples. Ellenberg $N$ and $W$ indicator values offer a useful method to compare the nutrient and moisture availability of sites without expensive measurements of site characteristics. These indicator values are used to estimate the value of an environmental factor by averaging the weighted indicator values of all detected species.

Differences between the mean species richness of vegetation and seed banks as well as the mean seed numbers of sites were tested using one way ANOVA or the Kruskal-Wallis nonparametric test, depending on the equality of variance (*F*-test) and/or normality (Kolmogorov-Smirnov-test) (Zar 1999). In the case of significant differences Student-Newman-Keuls pairwise comparisons were used. Temporal changes in cover and species richness were analyzed using Repeated Measures ANOVA; in the cases of statistically significant differences the Student-Newman-Keuls pairwise comparisons were used to indicate different groups. Depending on the normality, a *t*-test or Mann-Whitney-test was applied to compare the mean seed densities and means of weighted Ellenberg values. To compare the mean seed density of upper and lower soil layers a paired *t*-test was used. Jaccard similarity index was used to compare the species composition of established vegetation and seed bank samples. The seed bank's similarity was determined using the whole year vegetation; therefore, pooled species lists from the three seasons' vegetation were used in calculations. Similarity was also calculated without hygrophytes ($W \geq 7$) as these are irrelevant for vegetation development on dry dunes. To demonstrate the tendencies in the changes of percentage cover and number of species a LOWESS smoother was used. This smoothing is based on locally weighted polynomial regression (Cleveland 1979). During the calculation the R program package (R Development Core Team 2008) was applied.

## Results

### *Vegetation Development*

Short-lived assemblages were typical in the first years of the vegetation regeneration. The nitrophilous weedy assemblages were rapidly replaced in all sites by short-lived ruderal and/or pioneering dicots and monocots. In the first year after the cessation of goose breeding (1991) *Amaranthus albus* dominated most sites. In 1992–1993 *Conyza canadensis*, *Anthemis ruthenica*, *Cerastium semidecandrum*, and *Bromus tectorum* were typical. In 1994–1998 clonal graminoid-dominated (*Poa angustifolia*, *P. pratensis*, and *Cynodon dactylon*) perennial communities subsequently replaced the short-lived assemblages. Development of perennial-dominated vegetation varied according to the sites' vertical position; in lower sites clonal grasses became dominant within three years but it took seven to eight years in the upper ones (see Török et al. 2008).

Based on the pooled vegetation records of the three seasons, altogether 142 vascular species were detected during the study. In the lower-positioned sites perennial clonal grasses dominated the vegetation, which was accompanied by significantly lower species richness from 2000 (ANOVA, $P<0.001$) compared to the upper-positioned sites (Table 1). Species richness changed the most remarkably in early successional stages, usually in the first 8 years. In general, species richness in the lower sites decreased significantly during succession (RM ANOVA, $P<0.001$). The species richness of the upper sites increased during the 12 years of succession, but the increase was not significant. In 2002 the relative cover values were significantly higher in the lower sites (Fig. 1, ANOVA, $P<0.001$). The cover

Table 1 The species richness of aboveground vegetation and seed bank densities (both in 2002)

| | U1 | U2 | L1 | L2 |
|---|---|---|---|---|
| Vegetation | | | | |
| Total number of species | 41 | 39 | 26 | 21 |
| Species richness (4 $m^2$) | $24.6 \pm 2.02^a$ | $26.2 \pm 1.66^a$ | $12.6 \pm 2.23^b$ | $10.00 \pm 1.14^b$ |
| Total number of xerophytes ($W \leq 4$) | 32 | 30 | 20 | 15 |
| Total number of hygrophytes ($W \geq 7$) | 1 | 0 | 0 | 1 |
| Seedbank | | | | |
| Total number of species | 40 | 41 | 35 | 45 |
| Species richness (4 $m^2$) | $21.4 \pm 1.12^{a*}$ | $23.0 \pm 0.78^{a*}$ | $16.8 \pm 1.50^{b*}$ | $23.0 \pm 1.18^{a*}$ |
| Total number of xerophytes ($W \leq 4$) | 24 | 25 | 19 | 25 |
| Total number of hygrophytes ($W \geq 7$) | 9 | 7 | 9 | 12 |
| Upper seed density (0–5 cm, $m^2$/5 cm) | $39307^a$ | $22922^b$ | $8490^c$ | $17493^b$ |
| Lower seed density (5–10 cm, $m^2$/5 cm) | $1593^a$ | $4478^a$ | $1810^a$ | $1407^a$ |

Upper sites - U1 and U2, Lower sites - L1 and L2, *W* - Ellenberg values for moisture. Significant differences between the groups were tested with ANOVA or $^*$ Kruskal-Wallis test, and are indicated with different superscripted letters)

increased significantly in the lower sites during succession (RM ANOVA, $P<0.001$), whereas no clear trends were found in the upper sites.

The highest cover weighted *N* (nutrients) values were found in the first years of secondary vegetation development. The cover weighted *W* (moisture) and *N* (nutrients) values showed high fluctuations in the early years, and these values were stabilized in the last five years with significantly higher scores at the end of the study in the lower sites than that of the upper ones (2002, Mann-Whitney, both $P<0.001$, $N=20$).

### *Aboveground Vegetation and Seed Banks*

Of the 96 species detected in the aboveground vegetation in 2002, 24 species were missing from seed banks. 37 species were present in the vegetation and seed banks, while a further 35 species were found only in the soil seed banks (Appendix). A limited number of species comprised most of the seed banks. The most frequent ones were annuals (*Anthemis ruthenica*, *Arenaria serpyllifolia*, *Capsella bursa-pastoris*, *Cerastium semidecandrum*, *Conyza canadensis*, *Erysimum diffusum* and *Trifolium arvense*) or short-lived perennial dicots (*Potentilla argentea*, *Rumex acetosella*). Of the perennial graminoids the following species built up dense seed banks: *Carex stenophylla*, *Cynodon dactylon* and *Poa angustifolia*. Most species were sparse or sporadic (Appendix).

All species with considerable vegetation cover also had detectably dense seed banks, except for *Chondrilla juncea* and *Eryngium campestre*. The number of germinated species did not differ greatly among sites. In the upper sites more xerophytes, while in the lower sites more hygrophytes were detected. The dominance weighted *W* values of the lower sites for seed banks were significantly higher than that of the upper ones (mean±s.e., upper sites: 2.30±0.03 and 2.59±0.07, lower sites: 3.68±0.30 and 3.31±0.14 respectively, ANOVA, $P<0.001$).

Seedling density varied between 10,300 (L1) and 40,900 seeds/$m^2$ (U1). Significantly higher densities were found in the upper sites than in the lower ones

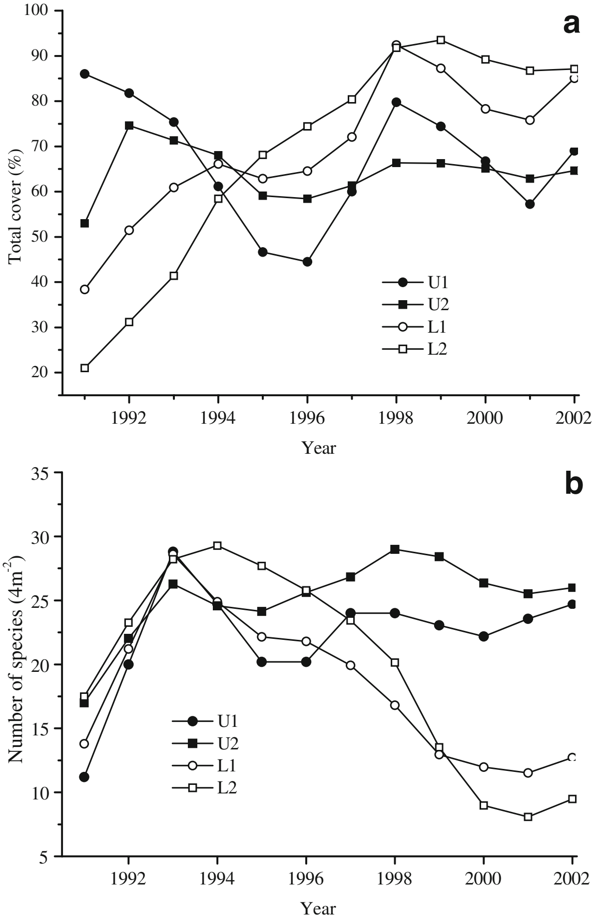


**Fig. 1** The changes of mean cover (**a**) and species numbers (**b**) during 12 years of vegetation development. The means of cover were calculated from the vegetation cover data of the summer records, whereas the mean species numbers were calculated using the pooled species lists of the vegetation records of the three seasons. Curves were smoothed using a LOWESS smoother. For abbreviations of site names see Table 1

(Mann-Whitney, $P<0.001$, $N=20$). Irrespective of the site, more species and many more seedlings were detected in upper soil layers (0–5 cm) than in deeper ones (5–10 cm) (paired *t*-test, $P<0.001$). More than 90% of species and 80%–96% of all germinated seeds were found in the upper soil layer. Most weeds (e.g., *Chenopodium album*, *Amaranthus retroflexus*, *Digitaria sanguinalis*) and short-lived species (e.g., *Erysimum diffusum*, *Arenaria serpyllifolia*, *Cerastium fontanum*) had dense seed banks also in the lower layers (10%–30% of their total seed banks were located there). The seed banks of dominant graminoids (e.g., *Cynodon dactylon*, *Poa angustifolia* and *Carex stenophylla*) were located mainly in the upper soil layer; more than 90% of their seeds were found in the upper layer.

### *Seed Banks and Vegetation History*

Several species formerly present in aboveground vegetation were still detected in seed banks. The lower layer contained more of them. These species typically occurred in the vegetation 3–6 years prior to seed bank sampling. The highest seed longevities were found in *Pholiurus pannonicus* (10 yrs) and *Solanum nigrum* (11 yrs). A significant part of seed bank species (17%–27%, depending on site) were hygrophytes (e.g., *Carex acutiformis, C. oederi, Juncus* spp., *Typha angustifolia*); all of them were absent from the vegetation.

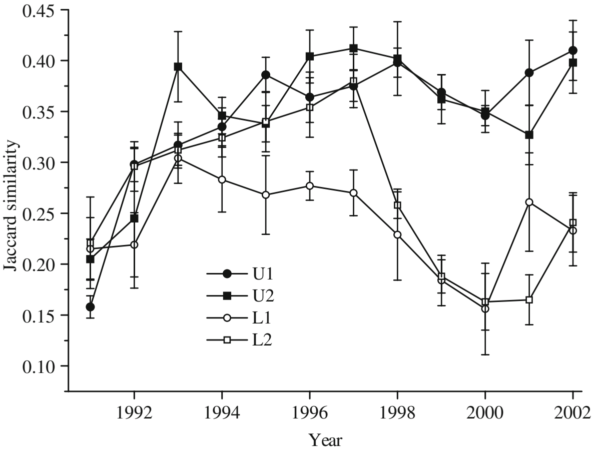
We found a low to medium similarity between the aboveground vegetation and seed banks. In the last year of the study the means of Jaccard index (J) were significantly higher for the upper sites than for the lower ones (mean±s.e.: $J_{U1}=0.41\pm0.03$, $J_{U2}=0.40\pm0.04$, $J_{L1}=0.23\pm0.03$, $J_{L2}=0.24\pm0.03$; $t$-test, $N=10$, $P<0.001$). It did not differ among sites of similar vertical position. The seed banks showed high similarity to the vegetation of the 1994–1998 period. In the upper sites the similarity between seed banks and vegetation of the last studied year were also high (Fig. 2).

## Discussion

### *Vegetation Development*

In the beginning of succession pioneer dicots replaced nitrophilous weeds. Then short-lived grasses replaced the pioneer dicots. Coinciding with the rainy period in 1998–1999, perennial grasses (*Poa angustifolia*, *P. pratensis* and *Cynodon dactylon*) dominated the lower-positioned sites. Ruderal assemblages characterized the initial stages as in the findings of Matus and Tóthmérész (1994). The ruderal nitrophilous vegetation soon turned into nutrient-poor vegetation dominated by annuals as reported in nearby study areas (Matus and Tóthmérész 1995; Matus et al. 2005). This vegetation change follows the leaching of a large nutrient surplus, typical in the topsoil in the initial successional phase after overgrazing (Matus and Tóthmérész 1994). After 12 years of vegetation development, low nitrogen contents were already typical, but even these figures were higher than in the soil of other acidic sandy grasslands (Jentsch and Beyschlag 2003; Jentsch 2004). A slow further decrease of potassium and phosphorous contents can be foreseen (Matus et al. 2005).

**Fig. 2** Changes in the Jaccard similarities between the seed bank (sampled in 2002) and vegetation data. We used the species lists for the whole vegetation period for the calculation. For abbreviations of site names see Table 1



The increased cover of vegetation in the lower sites can inhibit the germination of species, which can then contribute to the poor species richness in the lower-positioned sites. Short-lived gap colonizers tend to germinate in intense light (Bazzaz 1979). Moreover, their seedlings are sensitive to competition from neighbouring plants (Fenner 1978) and in this way tall-growing graminoids can prevent the germination of pioneers and/or outcompete the germinated pioneers (Odum 1969). Therefore, competition for light can be a mechanism for the detected decrease in species richness. Most pioneer annuals persisted in the vegetation of the upper sites. Most pioneer annuals disappeared from the lower sites in spite of having abundant soil seed banks. This discrepancy underlines the necessity of gaps in regeneration and shows their importance in maintaining species richness (Geißelbrecht-Taferner et al. 1997; Rebollo et al. 2001).

### *Vegetation and Seed Banks*

We found medium similarity between vegetation and seed banks when hygrophytes, as species irrelevant in vegetation development of xerophilous grasslands, were excluded. Comparing the species lists of plots to the seed banks, the detected medium similarities were somewhat higher than most findings from grasslands (Thompson 1986; D'Angela et al. 1988; Peco et al. 1998; Jentsch 2004; Handlová and Münzbergová 2006).

There are various specific and technical sources that reduce similarity between vegetation and seed banks: *i*) Several psammophilous pioneer annuals are reported to follow wind-dispersal. These species do not build up dense seed banks but rather re-colonize gaps by transient, wind-dispersed seeds (Jentsch and Beyschlag 2003). *ii*) Generative reproduction seems to be subordinated compared to the vegetative spreading for many dominant perennials (Champness and Morris 1948) and/or their seeds are short-lived (Bakker et al. 1996, 1997). *iii*) The difficulty of recording rare and/or aggregated species in the soil also contributes technically to the dissimilarity between the vegetation and seed bank samples (Thompson et al. 1997). Irregular or insufficient sampling of vegetation (missing years, neglected seasonal dynamics) can lead to non-detection of ephemeral species. *iv*) A further source is the dispersal of hygrophytes from neighbouring wetlands. These species never contribute to the dynamics of a xeric site (Matus et al. 2003) even though they are present in the seed banks. Wetland species were detected in all sampled sandy grassland stands of the region (2000–2004: 18 stands), irrespectively of goose breeding. Usually more species and more dense seed banks of hygrophytes were detected in goose-grazed ones. Some species dispersed by anemochory (*Typha angustifolia*); but most hygrophytes found in the soil of dry grasslands lack any specific adaptation to wind dispersal. This indicates that there is a constant, low chance for the species being dispersed among (and within) communities; but this is only obvious in hygrophytes. Animals (cattle, sheep, hare) are the most likely dispersal agents, and goose breeding may increase the intensity of dispersal.

The number of species in the vegetation (Fig. **1a**) and the Jaccard similarity between the seed bank and vegetation data (Fig. **2**) changed in a similar way during the studied period. The species richness and Jaccard similarity were relatively high in all sites in the 1994–1998 period. Similarity of the vegetation and the seed bank decreased considerably from 1999 in the lower sites. The high cover of graminoid species prevented continuous establishment of short-lived species, resulting in a lower species richness and similarity. The species richness of vegetation and the similarity of vegetation and seed bank remained high in the upper sites even after 1999. Here, the lower graminoid cover did not prevent gap regeneration of short-lived species.

### *Seed Density*

The detected seed densities in our study (10,300–40,900 seeds/m$^2$) are well in accordance with several previous records in sandy grasslands. In early successional stages of dry acidic sandy grasslands relatively low densities were recorded both in Poland (*Spergulo-Corynephoretum*, 1,900 to 3,500 seeds/m$^2$; Symonides 1978) and in southern Germany (7,600 to 21,100 seeds/m$^2$; Jentsch 2001). In our former studies in East-Hungarian sandy pastures (*Potentillo-Festucetum)* densities were between 11,200 and 16,000 seeds/m$^2$ (Matus et al. 2003) and in steppe meadows (*Pulsatillo-Festucetum*) between 12,300 and 24,600 seeds/m$^2$ (Matus et al. 2005). Somewhat higher records were published from established sandy grasslands, *Festuco-Koelerietum glaucae* (38,000 to 48,000 seeds/m$^2$; Symonides 1979). These figures are remarkably higher than those found in calcareous sands (400–1,200 seeds/m$^2$; Schwabe et al. 2000), other calcareous grasslands in Germany (6,000 to 7,000 seeds/m$^2$; Poschlod and Jackel 1993) or in a secondary English chalk grassland (6,800 seeds/m$^2$; Graham and Hutchings 1988). Somewhat higher records were published from calcareous alvar grasslands of southern Sweden (5,600–13,000 seeds/m$^2$; Bakker et al. 1997).

The seed density and the number of species, as in general in undisturbed soil profiles, decline sharply with increasing depth (Fenner 1985). Number of viable seeds in the topsoil proved significantly higher in contrasting vegetation types (Maas and Schopp-Guth 1995; Chang et al. 2001; Smith et al. 2002). In our study we found that the seed density in the 5–10 cm layer, depending on the sites, was ca. 5%–20% of that of the upper layer (0–5 cm).

Our findings do not support the widespread view that grasses would be unable to build up dense seed banks (Bakker 1989; Thompson 1992; Peco et al. 1998). Density of viable seeds in the dominant graminoids, *Carex stenophylla*, *Cynodon dactylon*, and *Poa angustifolia* reached up to 1,200 to 1,400 seeds/m$^2$ in our early successional sites. This corresponds with evidence for a decreasing reproductive allocation in psammophilous perennials through successional stages (Fekete et al. 1988). We would like to stress the importance of this kind of flexibility of perennials, when predicting grassland dynamics.

### *Implication for Restoration*

Our results indicate that the spontaneous regeneration after geese denudation is relatively fast, which could be important for restoration in the future. After 12 years of vegetation development, graminoid perennials dominate the spontaneously regenerated grasslands. At the lower elevated sites graminoid cover became so dense that only a few annual and perennial forbs remained in the present-day vegetation.

All parts of the studied area (Martinka) were at least partly grazed or overgrazed by geese; selecting a traditionally managed reference was possible around the neighbouring village (Bagamér, 20 km to SE from Martinka). Present-day vegetation and seed bank data from sites with different vertical positioning (upper- and lower-positioned sites) and vegetation history (overgrazed by geese and non-disturbed) are available, and can provide a comparison. Endangered psammophytes (e.g., *Iris humilis* subsp. *arenaria*, *Onosma arenaria*, *Pulsatilla pratensis* subsp. *hungarica*) were missing from the grazed stands similar to our study sites. These species were present only in few scattered spots on the non-overgrazed part of that area. Analysis of two sites with different vertical positions at one of the few well-preserved fragments revealed the following patterns: We found an identically low share of annuals in vegetation in the lower and upper positions. Somewhat higher species density of vegetation and more dense seed banks in the lower-positioned samples were found (Matus et al. 2003). Comparing partly regenerated stands (overgrazed 17 years ago) and its traditionally managed counterpart we detected higher species richness in vegetation, as well as more dense and more species-rich seed banks in the overgrazed stand (Matus et al. 2005).

Establishment of threatened species was not detected, although most typical species became established and a closed perennial-dominated grassland developed during the studied 12-year period. In spite of the proper abiotic site conditions (e.g., low nitrogen content), these species, present at the site in sparse populations, did not colonize, possibly because of limits of propagule dispersal. Missing also from soil seed banks, these species apparently rely on diaspore transfer with hay, topsoil transfer (Stroh et al. 2002; Donath et al. 2003; Hölzel and Otte 2003) or grazing animals (Fischer et al. 1996; Poschlod et al. 1998). Soil disturbance should, however, be avoided to prevent germination of weedy pioneers that have built up dense, persistent soil seed banks.

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## Appendix

Detailed vegetation and seed bank records (both in 2002). Species detected both in vegetation and seed bank (I) and found only in vegetation or seed bank (II). Lf: Raunkiaer's life-form groups (A - "annual" group: annuals and biennials, P - "perennial" group: hemicryptophytes, geophytes and chamaephytes). Vnp - Number of plots, where the species occurred in the vegetation (1–5 plots). Snp - Number of plots, where the species occurred in the seed bank (1–5 plots). VMC - Vegetation mean cover (%). No. sl: Number of seedlings in seed bank samples. Each seedling found corresponds with 26.53 germinable seeds/m$^2$). SBT - Seed bank type categories = 1: transient, 2: short-term persistent, 3: long-term persistent (Thompson et al. 1997). Species with low frequency (<3) and vegetation cover (altogether <0.5%) or rare in seed banks (<3 seedlings) were not classified into a seed bank type

| | | U1 | | | | U2 | | | | L1 | | | | L2 | | | | SBT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Lf | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | |
| **I** | | | | | | | | | | | | | | | | | | |
| In vegetation and seedbank | | | | | | | | | | | | | | | | | | |
| *Ambrosia artemisifolia* | A | 4 | 5 | 1.7 | 37 | 2 | 3 | 0.2 | 6 | | 2 | | 3 | | | | | 1/2 |
| *Anthemis ruthenica* | A | 4 | 5 | 1.5 | 40 | 5 | 5 | 1.7 | 38 | 4 | 5 | 0.2 | 18 | | 3 | | 6 | 1/2 |
| *Apera spica-venti* | A | 1 | 4 | < 0.1 | 20 | | 3 | | 6 | 2 | 4 | 0.1 | 16 | | 4 | | 14 | 1/2 |
| *Arenaria serpyllifolia* | A | 2 | 3 | < 0.1 | 4 | 5 | 5 | 0.3 | 185 | | 1 | | 1 | 1 | 5 | 0.1 | 78 | 1/2 |
| *Bromus mollis* | A | 2 | 1 | < 0.1 | 1 | 3 | 1 | 0.1 | 1 | 1 | | 0.1 | | | | | | 1/2 |
| *Cerastium fontanum* | A | | 1 | | 1 | 1 | 5 | 0.1 | 17 | | 2 | | 2 | | 4 | | 17 | 1/2 |
| *Cerastium semidecandrum* | A | 5 | 3 | 0.1 | 7 | 5 | 5 | 0.5 | 55 | | 3 | | 5 | 2 | 5 | < 0.1 | 82 | 1/2 |
| *Chenopodium album* | A | 2 | 4 | 0.2 | 13 | | 1 | | 1 | 4 | 2 | 0.2 | 9 | | 2 | | 3 | 1/2 |
| *Conyza canadensis* | A | 4 | 5 | 6 | 29 | 4 | 5 | 2.8 | 29 | 5 | 5 | 0.2 | 74 | 3 | 5 | 0.1 | 20 | 2 |
| *Crepis tectorum* | A | 1 | | < 0.1 | | 5 | 1 | 0.2 | 2 | | | | | | | | | 1/2 |
| *Erophila verna* | A | | | | | 2 | 4 | < 0.1 | 5 | | 1 | | 1 | | 1 | | 2 | 1/2 |
| *Erysimum diffusum* | A | 5 | 5 | 0.9 | 53 | 2 | 5 | 0.1 | 29 | 2 | 2 | 0.1 | 2 | | 3 | | 11 | 1/2 |
| *Geranium molle* | A | | | | | | | | | | | | | 1 | 2 | < 0.1 | 2 | |
| *Lepidium densiflorum* | A | | 2 | | 2 | | 2 | | 3 | 1 | | 0.1 | | | 3 | | 5 | 1/2 |
| *Myosotis stricta* | A | 3 | 4 | 0.2 | 15 | 5 | 3 | 0.4 | 8 | 1 | | 0.1 | | 1 | 1 | < 0.1 | 1 | 2 |
| *Melandrium album* | A | 2 | 1 | 0.1 | 1 | | | | | | | | | | | | | |
| *Petrorhagia prolifera* | A | | | | | | | | | 2 | 1 | < 0.1 | 2 | | 3 | | 7 | 1/2 |
| *Poa bulbosa* | A | 3 | | 1 | | 5 | 1 | 11.3 | 4 | | | | | | | | | 1/2 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Trifolium arvense* | A | 5 | 5 | 0.4 | 447 | 1 | | < 0.1 | | | 1 | | 1 | 1 | 1 | < 0.1 | 1 | 2/3 |
| *Trifolium campestre* | A | | | | | 1 | 1 | 0.1 | 11 | | | | | | | | | 2 |
| *Verbascum phlomoides* | A | | 1 | | 1 | | 4 | | 8 | 1 | 5 | 0.3 | 44 | 1 | 5 | < 0.1 | 55 | 2/3 |
| *Veronica arvensis* | A | 2 | 1 | 0.1 | 1 | 3 | 3 | 0.2 | 14 | 1 | | < 0.1 | | 5 | 5 | 0.5 | 34 | 1/2 |
| *Veronica triphyllos/verna* | A | 4 | 5 | 0.4 | 23 | 5 | 5 | 0.3 | 14 | 2 | 4 | 0.2 | 5 | 1 | 1 | < 0.1 | 1 | 2 |
| *Vicia lathyroides* | A | 5 | 4 | 0.2 | 22 | 5 | 4 | 2.6 | 30 | 1 | | < 0.1 | | 1 | | < 0.1 | | 1/2 |
| *Agrostis stolonifera* | P | 2 | | 1 | | | | | | | 1 | | 1 | 2 | | 0.6 | | 1 |
| *Artemisia campestris* | P | 3 | 2 | 6.6 | 9 | | | | | | | | | | | | | 1 |
| *Carex stenophylla* | P | 2 | 1 | 1 | 1 | 5 | 4 | 5.6 | 50 | | | | | 5 | 5 | 1.3 | 11 | 1/2 |
| *Cynodon dactylon* | P | 3 | | 2.8 | | 5 | 5 | 42.6 | 19 | 5 | 4 | 64.6 | 22 | 5 | 5 | 70 | 52 | 2 |
| *Festuca pseudovina* | P | 5 | 3 | 6.3 | 4 | 4 | | 1.5 | | 5 | | 4.9 | | | | | | 1 |
| *Hypericum perforatum* | P | 1 | 1 | 0.1 | 1 | | | | | | | | | | 1 | | 1 | |
| *Plantago lanceolata* | P | | | | | 3 | 2 | 0.3 | 2 | | | | | | | | | 1 |
| *Poa angustifolia* | P | 5 | 5 | 33.4 | 44 | 5 | 5 | 39 | 13 | 5 | 5 | 61 | 43 | 5 | 5 | 33.2 | 44 | 1/2 |
| *Poa pratensis* | P | 3 | 1 | 0.1 | 1 | | 2 | | 2 | 3 | 1 | 0.3 | 1 | 4 | 2 | 10.9 | 9 | 1 |
| *Potentilla arenaria* | P | | 1 | | 1 | 3 | 2 | 1.3 | 2 | | | | | | 1 | | 1 | 1 |
| *Potentilla argentea* | P | 5 | 5 | 11.3 | 255 | 5 | 5 | 1.4 | 40 | | 1 | | 1 | 2 | 5 | < 0.1 | 149 | 1/2 |
| *Rumex acetosella* | P | 5 | 5 | 4.7 | 467 | 5 | 5 | 7.9 | 418 | 3 | 5 | 0.4 | 70 | | 2 | | 4 | 3 |
| *Silene otites* | P | 1 | 2 | < 0.1 | 2 | 2 | 1 | 0.7 | 1 | | | | | | | | | 3 |
| **II** | | | | | | | | | | | | | | | | | | |
| Only in vegetation | | | | | | | | | | | | | | | | | | |
| *Bromus tectorum* | A | 4 | | 0.2 | | 5 | | 0.4 | | 2 | | 0.1 | | | | | | 1 |
| *Crepis rhoeadifolia* | A | 1 | | 0.1 | | 2 | | 0.2 | | | | | | | | | | 1 |
| *Polygonum aviculare* | A | | | | | 1 | | 0.1 | | | | | | 1 | | < 0.1 | | |
| *Achillea millefolium* | P | 4 | | 0.5 | | 4 | | 0.1 | | | | | | | | | | 1 |
| *Chondrilla juncea* | P | 2 | | 0.2 | | 5 | | 2.9 | | 1 | | 0.3 | | 4 | | 0.7 | | 1 |
| *Convolvulus arvensis* | P | | | | | 1 | | 0.1 | | 1 | | 0.1 | | | | | | |
| *Equisetum ramosissimum* | P | 5 | | 1.8 | | | | | | 3 | | 0.1 | | | | | | – |
| *Eryngium campestre* | P | 5 | | 7.0 | | 2 | | 0.6 | | 1 | | 0.1 | | | | | | 1 |
| *Euphorbia cyparissias* | P | 4 | | 0.3 | | 1 | | < 0.1 | | | | | | | | | | 1 |
| *Festuca rubra* | P | | | | | 1 | | < 0.1 | | 1 | | 0.1 | | | | | | |
| *Taraxacum officinale* | P | | | | | 1 | | < 0.1 | | | | | | 1 | | 0.1 | | |

(continued)

| | | U1 | | | | U2 | | | | L1 | | | | L2 | | | | SBT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Lf | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | Vnp | Snp | VMC | No.sl | |
| Only in seedbank | | | | | | | | | | | | | | | | | | |
| *Amaranthus retroflexus* | A | | 1 | | 1 | | 1 | | 1 | | 4 | | 23 | | 1 | | 1 | 3 |
| *Capsella bursa-pastoris* | A | | | | | | 1 | | 1 | | 4 | | 18 | | 5 | | 57 | 2/3 |
| *Digitaria sanguinalis* | A | | 4 | | 12 | | 3 | | 4 | | 3 | | 4 | | 4 | | 9 | 3 |
| *Pholiurus pannonicus* | A | | | | | | | | | | 2 | | 2 | | | | | 3 |
| *Stellaria media* | A | | 2 | | 2 | | | | | | 1 | | 1 | | 3 | | 8 | 2/3 |
| *Carex acutiformis* | P | | | | | | 3 | | 3 | | 2 | | 2 | | | | | 1/2 |
| *Carex oederi* | P | | 3 | | 3 | | | | | | | | | | 1 | | 1 | 1/2 |
| *Holoschoenus romanus* | P | | 1 | | 1 | | | | | | 2 | | 5 | | 1 | | 1 | 1/2 |
| *Juncus articulatus* | P | | 3 | | 5 | | | | | | 2 | | 2 | | 4 | | 8 | 1/2 |
| *Juncus compressus* | P | | 2 | | 8 | | 3 | | 3 | | | | | | 1 | | 1 | 1/2 |
| *Juncus effusus* | P | | | | | | | | | | 1 | | 2 | | 2 | | 2 | 1 |
| *Mentha aquatica* | P | | | | | | 1 | | 1 | | | | | | 1 | | 1 | |
| *Potentilla reptans* | P | | | | | | | | | | 1 | | 1 | | 1 | | 1 | |
| *Stachys palustris* | P | | 2 | | 2 | | | | | | | | | | 1 | | 1 | 1 |
| *Typha angustifolia* | P | | | | | | 1 | | 1 | | 1 | | 1 | | 2 | | 2 | 1 |

Rare species recorded in a single site with low frequency (Vnp or Snp: 1–2), and cover in vegetation (VMC<3%) or sporadic in the seed bank (No.sl<3 seeds). (v - vegetation, s - seedbank, VMC/Vnp or No.sl/Snp) U1: *Allium vineale* v(0.4/I), *Equisetum arvense* v(<0.1/2), *Kochia laniflora* v(<0.1/1), *Muscari comosum* v(0.1/1), *Spergula pentandra* v(<0.1/1), *Tragopogon dubius* v(<0.1/1), *Carex hirta* s(1/1), *Oenanthe aquatica* s(1/1), *Padus serotina* s(1/1), *Portulaca oleracea* s(1/1), U2: *Festuca vaginata* v(<0.1/1), *Hieracium pilosella* v(0.1/1), *Hypochoeris radicata* v(0.2/2), *Bilderdykia convolvulus* s(1/1), *Epilobium parviflorum* s(2/2), *Poa annua* s(1/1), *Scleranthus annuus* s(2/1), *Urtica dioica* s(1/1), L1: *Calamagrostis epigeios* v(2.2/3), *Viola arvensis* v(<0.1/1), *Centaurea micranthos* s(1/1), *Epilobium tetragonum* s(1/1), *Filago arvensis* s(2/2), *Gratiola officinalis* s(1/1), L2: *Cynoglossum hungaricum* v(0.1/1), *Galium mollugo* v(<0.1/1), *Carduus nutans* s(2/2), *Cirsium arvense* s(1/1), *Cyperus fuscus* s(1/1), *Lycopus europaeus* s(1/1), *Lythrum salicaria* s(1/1), *Poa compressa* s(1/1), *Solanum nigrum* s(2/1).

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