COMMUNITY ECOLOGY 2(1):101-108, 2001

Possible role of the seed bank in the restoration of open sand grassland in old fields

M. Halassy

Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, 2163 Hungary.
E-mail: hmelinda@botanika.hu

Keywords: Dispersal, Dry grasslands, Old field succession, Recruitment, Seed separation

Abstract: The species composition of the seed bank and aboveground vegetation of an old field was compared to a reference grassland stand. The relative importance of dispersal and recruitment as limiting factors was analysed, and measures for appropriate restoration are proposed. Grassland species were able to re-establish in the old field soon after abandonment of cultivation, with *Stipa borysthenica* as the dominant species. Five years after abandonment of cultivation, the seed bank was still dominated by weedy annuals while grassland species made a relatively high contribution to the seed bank in the reference site. The results do not support recruitment to be the limiting factor in recently abandoned fields, because grassland species that occurred in the seed bank were also present in the vegetation. A rapid regeneration of the matrix species is predicted due to their good dispersal capacity and the vicinity of the open sand grassland. However, the introduction of subordinate species and the control of invasive plants might require human intervention.

Nomenclature follows: Horváth et al. 1995.

Introduction

Restoration ecology has emerged within the last few decades as a science that tests potential practical applications of ecological principles in search for scientifically based schemes for environmental reconstruction (Urbanska et al. 1997). There is a strong tendency among restoration ecologists to try to find ways in which semi-natural habitats or even complete ecosystems can be restored relying on natural processes for conserving biodiversity, rather than creating man-made habitats (Dobson et al. 1997, Jordán et al. 1987). Under certain circumstances, e.g., when the disturbed sites are small, environmental conditions are fairly stable and there are appropriate propagule sources nearby, spontaneous succession becomes a viable alternative for the restoration of damaged ecosystems (Prach 1998).

Natural regeneration of arable fields is generally slow and ‘unreliable’, because long-term cultivation results in gross reduction of both aboveground and belowground diversity (see Bakker et al. 1996, Dobson et al. 1997, for reviews). However, the development of grasslands on old fields was found to be rather rapid in a Hungarian steppe landscape (Molnár and Botta-Dukát 1998). Perennial generalist species formed close, low diversity grasslands in the first ten years. On sandy soils, Csecserits (1999, see also Csecserits and Rédei, in press) found rapid changes in the first few years after abandonment of arable lands. Species characteristic of the open sand grassland community were able to colonize old fields in ten years. Despite the considerably fast re-establishment of the major species, plant diversity remained low in the colonised areas.

Re-establishment of semi-natural vegetation after disturbance can be divided into different phases, i.e., arrival, establishment, survival and propagation of particular species, and the development of vegetation structure and ecosystem functioning. Grime (1979) outlined five different types of revegetative strategy: (i) vegetative expansion; (ii) seasonal revegetation in vegetation gaps; (iii) a persistent seed bank; (iv) wind dispersed seeds and (v) a bank of persistent seedlings. When disturbance lasts long, only species with a long-term persistent seed bank will re-establish from the community pool, but those with short term persistency or transient seeds must be dispersed from the local species pool (Zobel et al. 1998). The3 seed bank, seedlings or vegetative remnants of previous natural vegetation can hardly survive in agricultural fields, except for seeds buried at greater depths as a result of ploughing (Fekete 1975). Successful re-colonisation or restoration of arable lands therefore has to rely on species transported to the site by some vector (Bakker et al. 1996).

Low colonisation rate of the desired species can be due either to dispersal or recruitment limitation (van der Valk and Pederson 1989). No re-appearance of species is possible when dispersal is limited. If species can arrive to the site, but their establishment is hindered by unsuitable site conditions (abiotic constraints or competition), they can enter the "fresh seed bank" (*sensu* Bakker et al. 1996). Finally, species with good dispersal capacities and little or no recruitment limitation can establish in the vegetation and can propagate further on.

The investigation of seed banks is an important step towards the understanding of limiting factors during the colonisation process, and helps decision-making when selecting restoration measures and also in predicting their success (Strykstra et al. 1998). If dispersal is limited, restoration methods such as seeding and planting have to be applied to re-create diversity. Restoration can focus on the establishment phase relying on old or fresh seed banks if dispersal is satisfactory in space and/or time. In other cases, when dispersal and recruitment is adequate, ecosystems can be allowed to re-generate by themselves.

Two restoration studies that began a few years ago in the Kiskunság National Park focussed on using different treatments to change soil properties, in order to hinder weed dominance and to enhance colonisation of sand grassland species. The effect of carbon amendment on nitrogen immobilization through increased microbial activity was tested on an abandoned field (Török et al. 2000). The results of the first year were encouraging; microbial activity was increased and nitrogen availability decreased, but more time is needed for vegetation response. Mowing decreased the abundance of undesirable annuals and slightly increased the colonisation of grassland species in clear-cut black locust (*Robinia pseudo-acacia*) plantations with neighbouring sand grasslands (Török and Halassy 1999). Treatments did not accelerate secondary succession in the absence of surrounding grasslands, showing the importance of propagule availability.

The present paper is a contribution to the debate on dispersal versus recruitment limitation during old field succession. The species contribution to the seed bank and the aboveground vegetation of an old field community was examined on sandy soils, and compared to that of a reference open sand grassland stand. We hypothesize that species with appropriate dispersal capacities, but incapable of recruitment because of environmental constraints or competition, can remain as dormant seeds in the soil. The absence of a species from both the vegetation and the seed bank is the sign of dispersal limitation.

Methods

The study area is an abandoned farm at the edge of a strictly protected land of sand dunes near Fülöpháza (46^o52'88"N, 19^o24'55"E), Hungary. The whole Danube-Tisza Mid-Region, characterised by a warm temperate climate with an annual mean temperature between 10.2 and 10.8^{o}C and an annual mean precipitation of 513 mm, with two maxima (May and November), lies in the forest steppe biome. The height of the water table has decreased by 2-4 m during the last 20 years in this region, resulting in significant vegetational and floristic changes (Körmöczi 1991, Szalay and Lóczy 1994). The farm is surrounded by a mosaic of open sand grasslands (*Festucetum vaginatae*), juniper-poplar forests, black locust plantations and arable fields (Fig. 1). Relatively little is

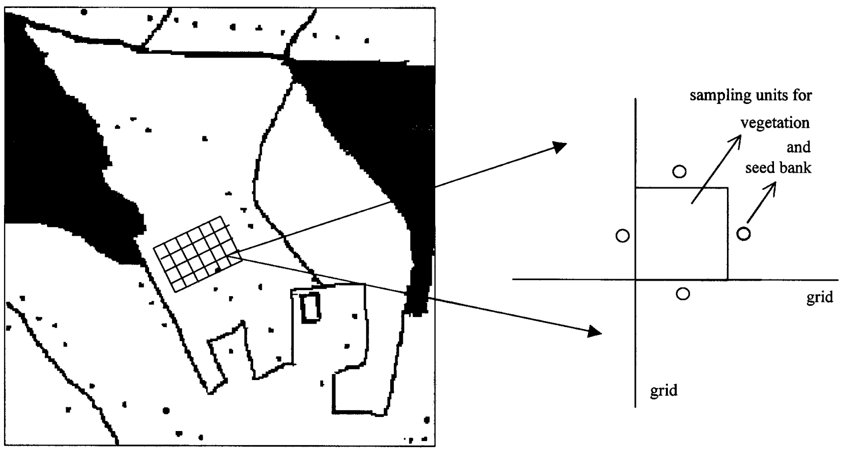

Figure 1. Schematic map of the study area in the Kiskunság National Park near Fülöpháza. Dark colours indicate forests, the rest of the surrounding area has secondary grassland vegetation with trees (dots) and paths (lines). Plots for vegetation sampling were located at grid points. The arrangement of sampling units for seed bank analysis around a 1 m^2 vegetation plot is shown.

known about the history of the area. The first available maps show vineyards in the investigated location in 1951. Aerial photographs from 1965 confirm vine cultivation, although the farm looks homogeneous as croplands from 1954. From 1975, vineyards no longer exist on the photos in the section of the farm treated in this study. Cultivation of the field stopped about five years before this study (1994), according to aerial photographs and local people. The last crop most probably was maize, but alfalfa was also cultivated for some period. Soil nitrogen content in the old field (0.03% total N and 5.17 mg/kg available N) was similar to that of sandy soils (0.03% total N) in 1997.

The aboveground vegetation of the old field was sampled in June, 1999, using a 30 m by 20 m grid of twenty-four 5 m by 5 m units, approximately 20 m distant from the edge of the field (Fig. 1). The transition zone was excluded from the study, because of the confounding effect of changing the field border during cultivation. Percentage cover of all vascular species, cryptogams and bare ground was estimated in 1 m^2 units placed at the grid intersections (n=35) in June. Two reference areas were chosen in the nearby open sand grassland. Cover was estimated by the author in one patch (1 m^2 random units). Data taken in the vicinity were also included, see Elek (2000) for details (*n*=33 altogether).

Samples for soil seed bank determination were collected in April 1999, after the autumn and early spring germination periods. One sample was taken outside of and adjacent to each of the four sides of each vegetation sampling unit, using a 5 cm diameter core with a 5 cm depth (Fig. 1). Samples belonging to the same vegetation plot were mixed and 100 cm^3 of each bulk sample (a total of 35 samples) was analysed by the seed separation method. Additional samples (33) were taken randomly in the two reference open sand grassland patches. All samples were sieved using two different mesh sizes (0.3 and 1 mm) to facilitate seed separation (Virágh and Gelencsér 1988). Seeds were identified under a microscope using Schermann's atlas (1966) and the comparative materials of the Botanical Garden in Vácrátót and the Natural History Museum. A simple method proposed by Zelenchuk (1961, see also Robert 1981) was chosen to estimate the viability of seeds. The term seed bank in this paper refers to all apparently intact seeds or fruits that resisted a gentle pressure. Note that this method overestimates the number of viable seeds in the soil.

Species with frequency greater than 5% in the vegetation or in the seed bank were used for statistical analysis. Seed bank data were merged into clusters of five samples per group to achieve greater sample sizes. Groups were formed according to distance zones in the old field and randomly in the reference area (the two patches were treated separately). Their dissimilarity was expressed by the complement of the Jaccard index for presence-absence data and by the Marczewski - Steinhaus coefficient (= 1 - RuOička index) for abundance data standardized by the total within each group. Average linkage clustering (UPGMA) was used to classify the seed bank and the aboveground vegetation sample units at different distances from the field border (SYN-TAX 2000 program package, Podani 2001).

Results

A total of 80 species were found in our investigation, but only 65 species reached at least 5% frequency. The old field had higher species richness than the reference grassland area, considering both the total number of species (68 and 52, respectively) and the average number of species per plot (see Table 1).

Average vegetation cover per plot was similar in the old field and the reference area. Dominant species of old field vegetation include *Medicago minima* (73%) and *Agropyron repens* (63%) followed by *Stipa borysthenica, Bromus tectorum* and *Secale sylvestre* in that order. The rest of the species made minor contribution to the vegetation cover, but some of them had a high frequency, e.g. *Silene conica* was found in every plot, and *Ambrosia artemisiifolia* had a frequency of 96%.

Most characteristic species of the open sand grassland reappeared five years after abandonment of cultivation or earlier, the exceptions being *Alkanna tinctoria, Bothriochloa ischaemum* and *Dianthus serotinus*. *Stipa borysthenica* became dominant close to the edge of the old field, and reached abundance values comparable to that in the grassland. *Festuca vaginata, Fumana procumbens* and other grassland species remained underrepresented in the aboveground vegetation of the old field. Other species lacking from the old field were common weeds (e.g., *Anthriscus caucalis, Capsella bursa-pastoris, Stellaria media*) found only in the soil of the grassland patches in the vicinity of *Robinia* plantations.

Despite the re-establishment of several grassland species and the great abundance of *Stipa borysthenica*, the similarity between the aboveground vegetation of the old field and the grassland was very low considering both species composition and abundance (Fig. 2). Reference grasslands were dominated by their matrix species, *Festuca vaginata* (69%), *Stipa borysthenica* (55%) and *Fumana procumbens* (22%). The relatively high abundance of *Secale sylvestre, Crepis rhoeadifolia* and *Medicago*

Table 1. Summary of data for aboveground vegetation (mean % cover) and seed bank (mean no. of species) of an old field and a reference grassland in the sandy region of Kiskunság. OV- Old field vegetation, OS - Old field seed bank, RV - Reference vegetation, RS - Reference seed bank.

Vegetation									
	OV	**OS**	**RV**	**RS**		**OV**	**OS**	**RV**	**RS**
Alkanna tinctoria	0	0	0.8	0	Medicago sativa	0.9	0	0	0
Alyssum montanum	0	0	0.1	0	Melandrium album	0.4	0	0	0
Anthemis ruthenica	0.4	0	0.4	0	Muscari comosum	0	0	1.2	0
Artemisia campestris	0	0	8.5	0	Myosotis stricta	0	0	0	0
Botriochloa ischemum	0	0	21.0	0	Plantago arenaria	2.3	0	0	0
Bromus mollis	0	0	0	0	Poa angustifolia	2.3	0	0	0
Bromus squarrosus	1.0	0	1.0	0	Robinia pseudo-acacia	0.9	0	0	0
Cynoglossum officinale	0.4	0	0	0	Salsola kali	0	0	0.1	0
Echium vulgare	0.1	0	0	0	Silene conica	2.6	0	2.8	0
Equisetum ramosissimum	0	0	0	0	Silene otites	5.0	0	0.5	0
Eryngium campestre	0	0	0	0	Stipa capillata	0.7	0	0	0
Gypsophila paniculata	1.0	0	0.5	0	Syrenia cana	0.3	0	0	0
Kochia laniflora	0.2	0	0.5	0	Tragopogon dubius	0.3	0	0	0
Lactuca saligna	1.7	0	0	0	Vicia cracca	1.6	0	0	0
Linaria genistifolia	0	0	0.2	0	Vicia lathyroides	0.3	0	0	0
Vegetation & seed bank									
	OV	**OS**	**RV**	**RS**		**OV**	**OS**	**RV**	**RS**
Agropyron repens	62.5	86	0	0	Euphorbia segueriana	2.6	86	1.9	150
Ambrosia elatior	2.1	2000	0	0	Festuca vaginata	0.9	214	69.2	817
Arenaria serpyllifolia	0.1	1000	2.7	83	Fumana procumbens	0	0	22.1	233
Asclepias syriaca	9.0	14	0	33	Holosteum umbellatum	0	4614	0.1	233
Bilderdykia convolvulus	0	1143	0	0	Lithospermum arvense	0	214	0	0
Bromus tectorum	24.4	600	0.3	0	Medicago minima	73.1	57	12.6	0
Cenchrus incertus	0.1	1086	0.2	0	Minuartia glomerata	3.0	14	0	233
Centaurea arenaria	2.4	514	0.1	0	Minuartia verna	0.1	971	0.2	200
Cerastium semidecandrum	0	400	0	100	Polygonum arenarium	0.2	1029	0.4	450
Corispermum nitidum	0	786	0.1	383	Scabiosa ochroleuca	0	14	0.1	33
Crepis rhoeadifolia	2.0	14	10.2	0	Secale sylvestre	24.4	2271	20.4	583
Erigeron canadensis	0.4	5329	0.1	17	Stipa borysthenica	39.0	0	55.4	17
Seed bank									
	OV	**OS**	**RV**	**RS**		**OV**	**OS**	**RV**	**RS**
Amaranthus albus	0	71	0	0	Fumaria schleicheri	0	0	0	183
Amaranthus retroflexus	0	1657	0	17	Lamium amplexicaule	0	0	0	133
Anthriscus caucalis	0	0	0	317	Lolium perenne	0	171	0	0
Bromus sterilis	0	114	0	0	Poa bulbosa	0	114	0	17
Capsella bursa-pastoris	0	0	0	50	Polygonum aviculare	0	371	0	683
Carex liparicarpos	0	57	0	0	Portulaca oleracea	0	1400	0	0
Chenopodium album	0	4914	0	67	Schoenoplectus lacustris	0	57	0	0
Cirsium arvense	0	14	0	0	Setaria viridis	0	443	0	33
Crataegus monogyna	0	43	0	17	Silene vulgaris	0	0	0	383
Crepis biennis	0	14	0	0	Stellaria media	0	0	0	17
Dianthus serotinus	0	0	0	17	Tribulus terrestris	0	200	0	0
Erysimum odoratum	0	0	0	17	Veronica arvensis	0	0	0	33
Euphorbia cyparissias	0	14	0	1100	Viola arvensis	0	86	0	117

	OV	**OS**	**RV**	**RS**
# of species	23.3	26	17.7	12
% cover	47.0	0	46.7	0
# of seeds/m^2	0	32200	0	6767

minima indicates previous disturbance in the grassland (Table 1).

Differences in the soil seed bank of the two habitat types were even greater. Average seed density was almost five times higher in the soil in the old field than in the grassland (32 200 and 6 767 seeds/m^2, respectively). The seed bank of the old field accumulated annual weeds (*Erigeron canadensis, Chenopodium album, Secale sylvestre* and *Ambrosia artemisiifolia*) as expected. The early spring ephemeral *Holosteum umbellatum* was also abundant in the soil seed bank, although it had already disappeared from the vegetation by June.

Annuals and perennials had a balanced ratio in the soil of the reference grassland patches. The species composition of annual species differed greatly from that of the old field. Only *Secale sylvestre* was relatively abundant in the soil, the other dominant species of the old field being replaced by *Euphorbia cyparissias* and *Polygonum* species. The high density of *Festuca vaginata* seeds (817 seeds/m^2) contradicted our expectations that perennial grasses would be underrepresented in the soil, even under grassland vegetation.

The species composition of the aboveground vegetation and the soil seed bank differed greatly in both habitat types. Seed bank data formed a cluster distinct from that of aboveground vegetation in the UPGMA dendrogram (Fig. 2) for both species composition (at a dissimilarity of 0.82) and standardized species abundance (dissimilarity was 0.95 this time). The difference is due to species with a persistent seed bank that had low occurrence in or were absent from the vegetation. Twenty-six species were present only in the seed bank in this study. On the other hand, species dominant in the vegetation were usually underrepresented in the seed bank or lacking, except for *Festuca vaginata*, which was dominant both aboveground and in the seed bank at the grassland. The old field and the reference area were separated both for the vegetation, at dissimilarity value of 0.68 and 0.91 for species composition and percentage cover, respectively, and for the seed bank (0.78 for species composition and 0.91 for number of seeds).

Five years after abandonment of cultivation, the proportion of perennial species in the old field vegetation reached 50%, while more than 90% of species in the soil seed bank were annuals (Fig. 3). Only a few grassland

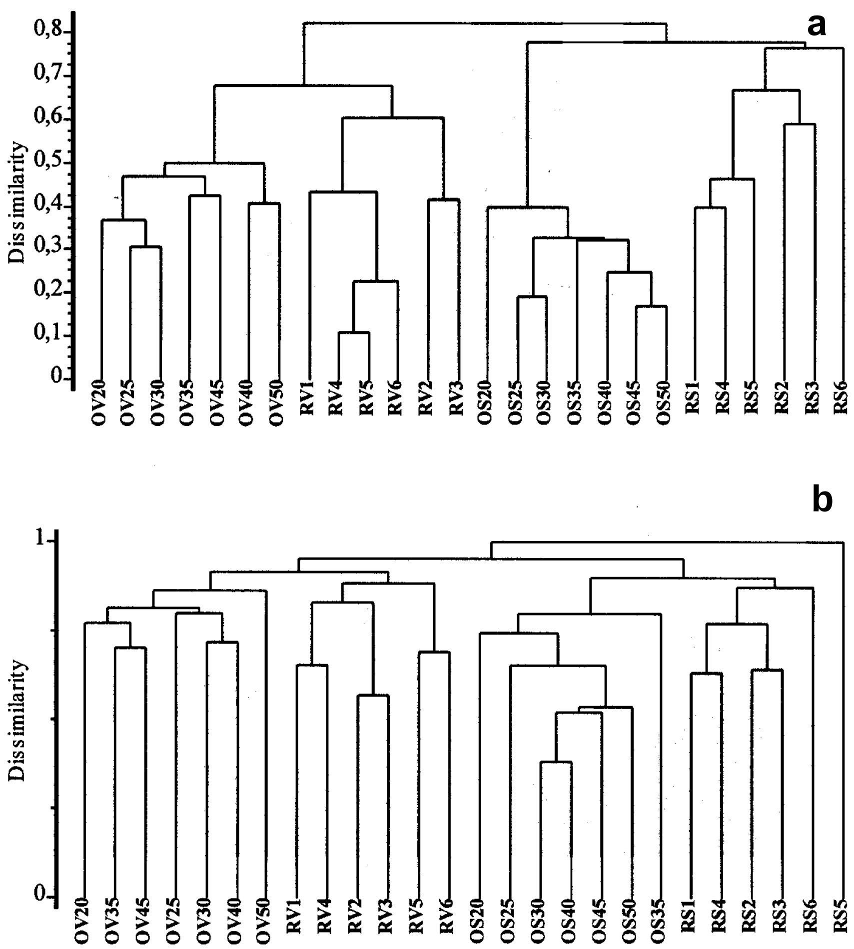

Figure 2. Dendrograms representing the results of average linkage clustering of aboveground vegetation and seed banks in the old field at different distances from the field border and in the reference open sand grassland in the sandy region of Kiskunság. Dissimilarity was the complement of the Jaccard-index for presence-absence data (**a**) and the Marczewski - Steinhaus coefficeint for abundance data (**b**). OV –old field vegetation, RV- reference vegetation, OS – old field seed bank, RS – reference seed bank, numbers represent distance (m) from border in the old field and random groups in the reference area.

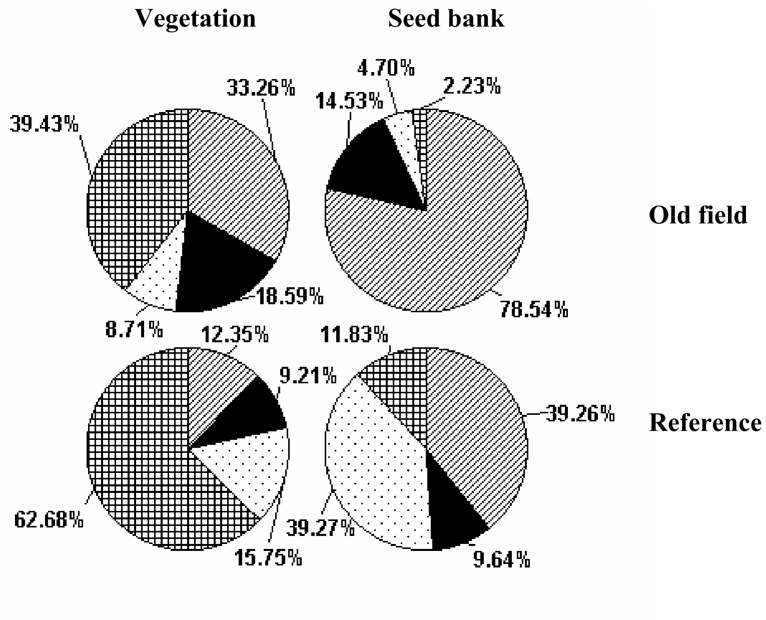

Figure 3. Contribution of particular life form categories to the aboveground vegetation and the seed bank of the old field and the reference grassland in the sandy region of Kiskunság. Annual and biennial forbs - striped, annual grasses - black, perennial forbs and shrubs - dotted, perennial grasses and sedges - checked.

species could be found in the soil, although most of them were already present in the vegetation. Reference samples were separated from that of the old field in the cluster analysis. In the grassland, 80% of the species were perennials and the share of perennials in the seed bank was seven times higher than at the old field.

Discussion

The size of the seed bank in arable fields varies considerably, depending on the type and intensity of weed control. Cavers and Benoit (1989) report 2 080 and 130 300 seeds/m^2 from various soil depths (15, 25, 45 cm) in maize fields estimated from direct counts. In our study an average density of 32 200 seeds/m^2 was found in the upper 5 cm of the soil five years after abandonment of maize crop. The vast majority of seeds entering the seed bank in arable land come from annual weeds growing on that land (Roberts 1981). In the studied site, such species, mainly non-indigenous weeds or pioneer species, still dominated the seed bank five years after abandonment of cultivation. However, the seeds of some grassland species were also found in a limited number. These seeds have probably arrived from the surrounding vegetation after cultivation stopped.

The target community of some restoration efforts (Török and Halassy 1999, Török et al. 2000) in the Kiskunság is the open sand grassland (*Festucetum vaginatae danubiale*), the most widespread natural community of this region. Average seed density in the soil of the reference grassland patch was 6 767 seeds/m^2, and the individual samples showed considerable differences, a clear sign of non-random distribution of seeds in the soil (Thompson 1986, Csontos 1997). Perennial species contributed to 51% of the seed bank, and most of them were *Festuca vaginata* and *Stipa borysthenica*, the two most important grass species of the open sand grassland community. These results are inconsistent with other grassland studies (e.g., Major and Pyott 1966, Hayashi and Numata 1971, Ungar and Woodell 1996), where perennial grasses with a large contribution to the aboveground vegetation made only a small or no contribution to the seed bank. The dominant perennial grasses of late successional stages make a minor contribution to the formation of seed banks, as they generally have a low seed production and their seeds have a short-term persistence in the soil (Thompson and Grime 1979, Bakker 1989; Rice 1989). Csontos et al. (1995) began a long-term seed viability test for different habitat types and taxonomic groups in Hungary. According to their tests, *Stipa borysthenica* seeds show short term persistency in the soil (Csontos 1999). We have to mention that the inconsistency could be due to the methods applied, as the seed extraction method used during this survey overestimates the seed bank, compared to germination studies (Csontos 2000).

A low correspondence has been found between the seed bank and the aboveground vegetation in many grassland studies (e.g., Thompson and Grime 1979, Thompson 1986, Bigwood and Inouye 1988). Frequent disturbance may increase the similarity between seed bank and vegetation composition, because disturbance limits vegetation composition to pioneer species that rely on more persistent seed banks (Moore 1980). Henderson et al. (1988) observed a high degree of correspondence between the seed bank and the vegetation in a desert short grass community in New Mexico. This ecosystem is characterised by a frequent and unpredictable disturbance regime and, as a result, by the predominance of annual species.

The *Festucetum vaginatae danubiale* is a pioneer community on sand dunes. The climate and the soil properties of the sand dunes resulted in a vegetation structure that resembles semi-desert vegetation types (Zólyomi 1958). On the basis of seed bank investigations in deserts, we expected a greater compositional similarity between the aboveground vegetation and the seed bank. Despite the relatively high contribution of perennial grasses, especially that of *Festuca vaginata*, to the seed bank of the reference grassland, similarity between the species composition of the aboveground vegetation and the seed bank remained low. Our studies confirm the general observation that similarity of seed bank and vegetation is low in grasslands. This can be explained by the fact that not all species form a seed bank, persistent species reflect past vegetation (Livingston and Alessio 1968, Bakker 1989, Leck et al. 1989), and intercommunity colonisation occurs through active dispersal (Beatty 1991).

A nice example of how species of previous vegetation types can survive in the soil was *Schoenoplectus lacustris* in our study. This species is accomodated to wet habitats, and wet patches indicated by darker tints on the aerial photographs could be identified where its seeds were found, although the species has disappeared from the vegetation. Comparing aboveground vegetation and seed bank helps to determine seed longevity in the soil (Thompson et al. 1997). Plants with a persistent seed bank were mostly annual weeds of cultivated soils (see species present only in the seed bank, Table 1). Seeds of grassland species found in the soil do not confirm persistency, since all these species were present in the vegetation at the same time (species present in the vegetation and the seed bank in Table 1).

All grassland species that occurred in the seed bank of the old field were also present in the vegetation. Thus, the initial hypothesis has to be rejected, recruitment was not limiting in the early phases of secondary succession on the studied abandoned field of the Kiskunság region. The question of dispersal versus recruitment limitation cannot be answered entirely for grassland species with transient seeds, because there was only a single sampling date for the soil seed bank. Seed bank can facilitate secondary succession if there are enough propagules of target species in the soil, but can hinder re-establishment of the natural vegetation if it consists mainly of annual weeds as it was in our case. Five years after abandonment seeds of grassland species were found only in a limited number in the soil, although grassland species had high contribution to the aboveground vegetation. The species composition of aboveground vegetation and seed bank differed greatly even at the reference grassland. This suggests that restoration efforts cannot rely on soil seed bank when restoring sand grasslands.

The vicinity of the target vegetation type has greater influence and can increase the success of restoration efforts if dispersal is possible. One of the matrix species of sandy grasslands, *Stipa borysthenica* is wind dispersed, and can easily colonise abandoned fields from the borderlands. At the site being studied dispersal was not limiting for the majority of species. Thus, the characteristic species of open sand grassland are expected to extend their abundance rapidly (see also Csecserits 1999 and Csecserits and Rédei, in press). However, more time is needed for the re-establishment of rare species. Seeding or planting is necessary only if the whole series of sand grassland species is to be established in a short time frame. *Asclepias syriaca*, an invasive species in Hungary, was also found to expand in the vicinity of the investigated area. The aggressive expansion of this species can hinder the complete regeneration of disturbed sites and call for restoration intervention.

Acknowledgements: Special thanks are due to J. Bajzáth for her help in seed identification. I thank K. Török, P. Csontos and three anonymous reviewers for their comments on previous versions of the manuscript. This study was supported by the Hungarian National Science Fund (OTKA F025781)

References

Bakker, J.P. 1989. *Nature Management by Grazing and Cutting*. Kluwer, Dordrecht.

Bakker, J.P., P. Poschlod, R.J. Strykstra, R.M. Bekker and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.* 45(5):461-490.

Beatty, S.W. 1991. Colonization dynamics in a mosaic landscape: the buried seed pool. *J. Biogeogr* 18:553-563.

Bigwood, D.W. and D.W. Inouye. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. *J. Ecol.* 69:497-507.

Cavers, P.B. and D.L. Benoit. 1989. Seed banks in arable land. In: Leck, M.A., V.T. Parker and R.L. Simpson (eds), *Ecology of Soil Seed Banks*. Academic Press, San Diego, California, pp. 309-329.

Csecserits, A. 1999. *Felhagyott szőlők és szántók tájtörténete és másodlagos szukcessziójuk vizsgálata* (Landscape History and Secondary Succession of Abandoned Vineyards and Ploughlands). M.Sc. thesis in Hungarian, L. Eötvös University, Budapest, Hungary.

Csecserits, A. and T. Rédei. (in press) Secondary succession on 54 sandy old-fields in Hungary. *Appl. Veg. Sci.*

Csontos, P. 1997. A magbank ökológia alapjai: Definiciók és mintavételi kérdések. (Seed bank ecology: definition of seed bank and questions of its sampling). *Természetvédelmi közlemények* 5-6:17-26.

Csontos, P. 1999. Six years' results of a seed burial experiment involving 30 species native to Hungary. *Abstracts of the VIII Euro-*

pean Ecological Congress "The European Dimension in Ecology", 18-23 September , 1999, Chalkidiki, Greece, p. 251.

Csontos, P. 2000. A magbank ökológia alapjai II. A talajminták feldolgozásának módszerei és alkalmazhatóságuk elemzése (Seed bank ecology II. Estimation of seed bank in soil samples and comparison of methods). *Acta Agr. Óváriensis* 42(1):133-150.

Csontos, P., Á. Palásti and T. Kalapos. 1995. The experimental design and the first year results of a 30-year-long seed viability test. *Proceedings of the 7th European Ecological Congress "Ecological Processes: Current Status and Perspectives"*, 20-25 August, 1995, Budapest.

Dobson, A.P., A.D. Bradshaw and A.J.M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277:515-522.

Elek, J. 2000. *A kaszálás hatékonyságának vizsgálata homokpusztagyep regenerációjában* (The effectiveness of mowing in the regeneration of sand grasslands). M.Sc. thesis in Hungarian, L. Eötvös University, Budapest.

Fekete, R. 1975. Comparative weed-investigations in traditionally-cultivated and chemically-treated wheat and maize crops. IV. Study at the weed-seed contents of the soils of maize crops. *Acta Biol. Szeged.* 21:9-20.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.* John Wiley, New York.

Hayashi, I. and M. Numata 1971. Viable buried-seed population in the *Miscanthus*- and *Zoysia* type grasslands in Japan - Ecological studies on the buried-seed population in the soil related to plant succession VI. *Jap. J. Ecol.* 20 (6):243-252.

Henderson, C.B., K.E. Petersen, and R.A. Redak. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *J. Ecol.* 76:717-728.

Horváth, F., Z.K. Dobolyi, T. Morschhauser, L. Lőkös, L. Karas and T. Szerdahelyi. 1995. *Flóra adatbázis 1.2 Taxon-lista és attribútum állomány* (Flora Database 1.2. List of Taxa and Attributes*).* Vácrátót, Hungary.

Körmöczi, L. 1991. Drought-induced changes in a sandy grassland complex in the Great Hungarian Plain. *Acta Biol. Szeged* 37:63-74.

Leck, M.A., V.T. Parker and R.L. Simpson (eds.) 1989. *Ecology of Soil Seed Banks.* Academic Press, San Diego, California.

Livingston, R.B. and M.L. Alessio. 1968. Buried viable seed in successional field and forest stands, Harvard forest, Massachusetts. *Bull. Torrey Bot. Club* 95:58-69.

Major, J. and W.T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of the flora. *Vegetatio* 13:253-282.

Molnár, Zs. and Z. Botta-Dukát. 1998. Improved space-for-time substitution for hypothesis generation: secondary grasslands with documented site history in SE-Hungary. *Phytocoenologia* 28:1-29.

Moore, P.D. 1980. Soil seed bank. *Nature* 284:123-124.

Podani, J. 2001. *SYN-TAX 2000. User's Guide*. Scientia Publishing, Budapest.

Prach, K. 1998. Spontaneous succession as a way of ecosystem restoration - general remarks and case studies from central Europe. *Proceedings of the 2nd International Conference on Restoration Ecology*. 25-30 August 1998, Groningen, The Netherlands. pp. 36-37.

Rice, J. 1989. Impacts of seed banks on grassland community structure and population dynamics. In: Leck, M.A., V.T. Parker and R.L. Simpson (eds), *Ecology of Soil Seed Banks*. Academic Press, San Diego, California, pp. 211-230.

Roberts, H.A. 1981. Seed banks in soils. *Adv. Appl. Biol.* 6:1-55.

Schermann, Sz. 1966. *Magismeret I-II.* (Atlas of Seeds I-II). Akadémiai Kiadó, Budapest.

Strykstra, R.J., R.M. Bekker and J.P. Bakker 1998. Assessment of dispersule availability: its practical use in restoration management. *Acta Bot. Neerl.* 47:57-70.

Szalay, J. and D. Lóczy. 1994. Some trends in groundwater level change on the Danube-Tisza Interfluvial region, Hungary. *Mediterranean Desertification and Land Use Conference*. 1994. May 18-24.

Thompson, K. 1986. Small-scale heterogeneity in the seed bank of an acidic grassland. *J. Ecol.* 74:733-738.

Thompson , K. and J.P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67:893-921.

Thompson, K., J.P. Bakker and R.M. Bekker 1997. *Soil Seed Banks of North-West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge.

Török, K. and M. Halassy. 1999. Fighting invasive species: a case study of open sand grasslands in Hungary. *Proceedings of the VIth International Rangeland Congress*, Townsville, Australia, 19-23 July, 1999. pp. 610-612.

Török, K., T. Szili-Kovács, M. Halassy, T. Tóth, Zs. Hayek, M.W. Paschke and L.J. Wardell. 2000. Immobilization of soil nitrogen as a possible method for restoring sand grasslands. *Appl. Veg. Sci.* 3:7-14.

Ungar, I.A. and S.R.J. Woodell. 1996. Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. *Int. J. Plant Sci.* 157:746-749.

Urbanska, K.M., N.R. Webb and P.J. Edwards. 1997. *Restoration Ecology and Sustainable Development.* Cambridge University Press, Cambridge.

van der Valk, A.G. and R.L. Pederson. 1989. Seed banks and the management and restoration of natural vegetation. In: Leck, M.A., V.T. Parker and R.L. Simpson (eds), *Ecology of Soil Seed Banks*. Academic Press, San Diego, California, pp. 329-346.

Virágh, K. and L. Gelencsér. 1988. Seed bank in the soil and its role during secondary successions induced by some herbicides in a perennial grassland community. *Acta Bot. Hung.* 34:77-121.

Zelenchuk, T.K. 1961. The content of viable seed in meadow peaty soils of the L'vov region. *Byull. Mosk. Obshch. Ispyt. Prir., Otdel. Biol.* 66:77-92.

Zobel, M., E. van der Maarel and C. Dupré. 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci.*1:55-66.

Zólyomi, B. 1958. Budapest és környékének természetes növénytakarója. (Natural vegetation of Budapest and its surroundings). In: Pécsi, M. (ed.), *Budapest természeti képe* (Natural History of Budapest). Akadémiai Kiadó, Budapest. pp. 511-642.