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Impact of management on vegetation dynamics and seed bank formation of inland dune grassland in Hungary

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Abstract

Seed bank formation and 7 years of vegetation dynamics were studied on permanent plots of a dry sandy pasture, Cynodonti-Festucetum pseudovinae. A stand overgrazed by domestic geese and a reference stand void of overgrazing were compared. Apart from this both stands were accidentally grazed by cattle. Vegetation of the overgrazed stand was significantly more species-rich, especially in summer annuals. The reference was dominated with perennials and winter annuals. Composition and dominance changed considerably at both stands but only composition became more alike. Declining species richness and increasing dominance of perennials was found in the overgrazed stand. The reference stand became dominated with the dwarf-shrub *Thymus degenianus*. Species richness of the overgrazed stand showed greater seasonal and year-to-year variation than that of the reference. No temporal change of nutrient availability was found and neither was a difference detected between the stands.

Greenhouse germination revealed more dense and more species-rich seed bank in the overgrazed stand. Its established vegetation and soil seed bank were also more alike. Higher species richness of the overgrazed stand can be associated with intensive propagule dispersal of geese, as indicated by dense seed banks of zoochorous hygrophytes delivered from neighbouring wetlands. Relatively high representation of persistent seed bank records suggests that, except for some sensitive perennials, the studied community is adapted to recurrent disturbances. Community regeneration seems to be limited by slow spread of perennial graminoids.

Keywords: Disturbance; Grazing; Permanent plots; Propagule dispersal; Secondary succession; Seedling emergence

Nomenclature
Simon (2000) for taxa, Borhidi (2003) for syntaxa.

Introduction

Subcontinental perennial sandy pastures, developing after forest clearing and maintained by grazing, form a widespread successional stage in central parts of the Carpathian Basin (Soó, 1957). These communities had significant agricultural importance and are of great conservational interest in Hungary (Précsényi, 1981; Margóczi, 1993). In the changing economic conditions in the last few decades, their traditional management,

Abbreviations: CANOCO, canonical correspondence analysis; MDS, Non-metric multidimensional scaling

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i.e. extensive grazing by cattle or sheep, has often been replaced with uncontrolled grazing by domestic geese. This type of management has lead to denudation, nutrient enrichment and finally degradation through invasion of weeds (Matus and Tóthmérész, 1994, 1995). Still little is known about dynamics and restoration prospects of degraded stands.

The knowledge of specific seed longevities is especially useful in the planning of restoration projects (McDonald et al., 1996; Bakker et al., 1996). Regeneration from soil seed banks is a crucial mechanism in dynamics of dry grasslands (Levassor et al., 1990; Espigares and Peco, 1993; Jentsch and Beyschlag, 2003).

In contrast to North-Western Europe where seed bank type classification already covered ca. 50% of species (Thompson et al., 1997), records for only ca. 20% of the rich Hungarian flora are available (Csontos, 1998). In spite of recent achievements (Halassy, 2001; Matus et al., 2003a) the same holds for the psammophilous vegetation. Large-scale geographic variation of specific seed longevities (Thompson et al., 1997) and floristic difference can limit application of foreign sources and underlines the necessity for collecting independent data.

In this study we analysed how overgrazing and abandonment were reflected in long-term vegetation dynamics of a widespread type of sandy pasture. We were also aiming to collect data on seed bank formation and possible mechanisms of seed dispersal. Our ultimate goal was to contribute to the knowledge of community dynamics and the planning of restoration projects for degraded Pannonian sandy vegetation.

Materials and methods

Site description and history

Sampling was carried out at 'Daru-hegyek' nature reserve, 25 km ESE of the city of Debrecen, East-Hungary (47°28′N; 21°57′E). The site is characterized by 5–10 m high dunes built from early Pleistocene calcium-free sand with a typical grain size of 0.1–0.3 mm (Borsy et al., 1981). The climate is moderately continental with mean annual temperature of 10.0 °C (January −2.5 °C, July 21.2 °C). Mean annual precipitation is 570–600 mm out of which 300–350 mm falls in the April–September period (Justyák and Tar, 1994). The dominant vegetation type of the site is the dry sandy pasture, Cynodonti-Festucetum pseudovinae Soó (Aszód, 1935) 1957. It is intermingled with small sandy steppes as well as open pioneer grasslands on steep dunes and wet grasslands in dune slacks (Précsényi et al., 1990; Nagy et al., 1991).

In 1981–82 a ca. 20 ha fenced area, including part of a 10 m high dune and its surroundings, was denuded by thousands of domestic geese (Nagy et al., 1991). Geese moved freely from dunetops to dune slacks and were also fed at a stable. Secondary succession started from a denuded surface in 1983. The 4.5 km^2 area of the reserve was traditionally grazed by about 250 diary cattle from May to October till the late 1980s but livestock gradually declined to only 30–40 cattle by 2000. Cattle grazing concentrated mainly on dune slack meadows, and the dunes became ungrazed. No fertilizers, mineral or organic, were applied.

Sampling setup

Two typical stands, covered originally with Cynodonti-Festucetum (Borhidi, 2003), were chosen for study. One of the stands, located within the fenced area ca. 100 m away from the stable, is referred to as 'overgrazed stand' whereas the other stand, 150 m apart, out of the fence and void of goose grazing, is referred to as 'reference'. Vegetation of five 2 m × 2 m sized permanent plots was sampled at both stands between 1994 and 2000. Percentage cover of vascular species was estimated in April, June and September including all short-lived annuals. Seed banks were sampled in mid March 2000, after natural winter stratification. Thirty soil cores per stand (six cores/plot, 4 cm in diameter and 10 cm in depth, altogether 3,770 cm^3/stand), were drilled. Using this sampling setup the minimal detectable density with a 95% confidence level is ca. 80 seeds/m^2, provided Poisson distribution prevails (Thompson et al., 1997). Two vertical soil segments (0–5, 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). Vegetative organs were retained by washing over a coarse sieve (3.0 mm mesh) while seed-free fine soil components were removed on a 0.2 mm mesh. Sample volume was reduced by about 75%.

Concentrated samples were spread in a maximum 3–4 mm thick layer on trays, previously filled with 8 cm of potting soil, then covered with a thin layer of sterilized sand. Trays were illuminated with natural light in a greenhouse of the Debrecen Botanical Garden. The greenhouse was shaded with Rachel-nets from early May to August. Temperature varied typically between 30 °C/18 °C at day/night. In late May, when no new seedlings emerged, watering was stopped, dried sample layers were crumbled, turned and watered again. In late July samples were let to dry out again and then collected. The first author as holder of a scholarship spent the following period in Haren, The Netherlands. Samples were transported there too and re-spread on trays, previously filled with 4 cm of normal and 4 cm of steam-sterilized potting soil, then covered with a thin layer of sterilized sand. Samples were illuminated with fluorescent tubes in a climate chamber where temperature fluctuation was set to 18 °C/10 °C at day/night. Germination altogether lasted for 28 weeks and was finished in late October.

Seedlings were regularly counted, identified (Csapody, 1968; Muller, 1978) then removed. Unidentified taxa were transplanted. Transplants of *Cyperaceae*, *Juncaceae* and *Poaceae* were mostly identified the following spring when flowering. Seed rain was monitored in sample-free control trays. Contaminant species e.g. greenhouse weeds, *Oxalis corniculata*, *Cymbalaria muralis* (Debrecen) and *Spergularia rubra* (Haren), and the wind-dispersed *Betula pendula* (both gardens), were excluded from analyses.

Soil characteristics

Samples collected yearly in April between 1994 and 2000 were analyzed. Ten subsamples per stand, each of about 100 cm^3, were collected from the close vicinity (<0.2 m) of plots from the 0–10 cm layer then pooled on the spot. Digital measurement of pH_{KCl} (Radelkis OP-211), determination of humus content (Contiflo, Labor MIM), that of NO_3+NO_2-N and NH_4-N (FIAstar, TECATOR) as well as that of P_2O_5-P and K_2O-K (ICP Thermo Jarrel Ash Polyscan 61E) were carried out at the internationally accredited Debrecen Laboratory of Plant and Soil Protection Service (NETVÁ) according to Hungarian standards (MSZ-08-0205, 08-0452 and 20135).

Data processing

Vegetative individuals of *Carex stenophylla* and *C. praecox*, *Koeleria cristata* and *K. glauca* were not distinguished in the field. Neither were seedlings (greenhouse) or dried specimens (field) of *Veronica verna* and *V. triphyllos* distinguished. These species were pooled by pair in analyses. The fern *Equisetum ramosissimum* was excluded from analyses.

The number of taxa per plot in vegetation and seed bank samples as well as the number of seedlings per plot was compared between stands and years using one way ANOVA. Normality of the samples were tested by the Kolmogorov-Smirnov test. In the case of significant differences pairwise comparisons were also used. Depending on the equality of variances (*F*-test) *t*-test or Welch-test was applied (Zar, 1999).

Non-metric multidimensional scaling (MDS) was applied during the ordination of the vegetation relevés (Tóthmérész, 1993); percentage cover data was used to calculate the Bray-Curtis index of dissimilarity (Legendre and Legendre, 1998). Five relevés of the same stand at the same time (season) were pooled during the MDS ordination. Canonical correspondence analysis was performed by the CANOCO package (Ter Braak, 1995); it was based on the presence–absence data of the vegetation relevés and the seed-bank samples. Species detected only at a single site with low frequencies either in the vegetation or in the seed bank were eliminated before the analysis (Matus et al., 2003b).

Results

Vegetation

The total number of species and species richness/plot were higher in the overgrazed stand irrespective of the season (Table 1). Declining species density was detected in the overgrazed stand, whereas in reference year-to-year fluctuations were found. Significantly declining species richness from spring to autumn was also typical.

Season as well as year had significant ($p<0.001$) effect on the variation of total species richness (Table 2). These factors interacted in the variation of annuals at both stands, but in variation of perennials at neither stand. Effect of season and year were similarly important in variation of annuals at the overgrazed stand. Variation in number of annuals ($p<0.001$; both factors, both stands) exceeded that of perennials. Variation of perennials was affected significantly by both factors in the overgrazed stand but only by year in reference ($p<0.01$).

Seed bank

Total species richness of seed bank as well as frequency of species was higher in the overgrazed stand than in the reference. Number of species, species frequencies and density of viable seeds were decreasing with soil depth at both stands. In the upper layer seedling density of the overgrazed stand was significantly higher. In the lower segment seedling density of stands was not different significantly (Table 1).

Composition and dominance

Out of the 65 species in vegetation 34 were exclusively detected in the overgrazed stand, 21 were common with reference stand while 10 were unique to this stand (Table 3). Annuals comprised 51% of local species set at overgrazed stand whereas only 40% in reference. Similarly, representation of annuals also differed in plots as these formed 40% of all species records in the overgrazed but only 25% in reference. Frequency of perennials per plot and per stand, however, exceeded that of annuals (both stands; $p<0.001$).

Out of the totally recorded 86 species, 28 were found only in vegetation, 22 only in seed banks whereas 36 (42%) were detected both above and below-ground. In

Table 1. Species richness of vegetation (1994–2000), that of seed bank samples and estimated seed densities (2000) (Each seedling found corresponds with a seed density of 26.53 m^{-2})

		Overgrazed	Reference	p
Vegetation				
Total species number		55	31	
Species number/4 m^2 year	($n = 15$)			
1994		21.40 ± 3.14^{ab}	11.40 ± 2.06^{ab}	***
1995		21.93 ± 4.68^{ab}	11.40 ± 1.85^{ab}	***
1996		23.67 ± 3.60^{a}	11.13 ± 1.13^{a}	***
1997		20.87 ± 4.19^{b}	12.07 ± 2.22^{a}	***
1998		20.47 ± 2.29^{b}	10.93 ± 0.88^{b}	***
1999		15.67 ± 3.13^{c}	10.07 ± 0.96^{c}	***
2000		15.87 ± 4.56^{c}	11.27 ± 2.25^{ab}	**
Season	($n = 35$)			
Spring		22.94 ± 4.19^{a}	12.31 ± 1.91^{a}	***
Summer		19.40 ± 3.97^{b}	11.11 ± 1.37^{b}	***
Autumn		17.60 ± 4.07^{c}	10.14 ± 1.24^{c}	***
All surveys	($n = 105$)	20.68 ± 3.52	11.18 ± 1.35	***
Seed bank				
Total species number (cm)				
0–5		45	30	
5–10		27	14	
0–10		51	32	
Species/plot (cm)				
0–5		21.67 ± 3.93^{a}	12.33 ± 2.88^{a}	***
5–10		9.17 ± 3.19^{b}	3.83 ± 2.23^{b}	**
0–10		24.33 ± 2.80^{a}	13.83 ± 3.97^{a}	***
Seed/plot				
(Seed/m^2)				
0–5 cm		130.0 ± 22.69^{a}	78.5 ± 35.13^{a}	*
		(20,700)	(12,300)	
5–10 cm		25.0 ± 24.04^{b}	10.17 ± 3.76^{b}	ns
		(3,900)	(1,600)	
0–10 cm		155.0 ± 25.57^{a}	88.67 ± 33.92^{a}	**
		(24,600)	(13,900)	

In case of significant differences indicated by ANOVA, separate *t*-test or Welch-test was applied. Within stands different letters indicate significant ($p < 0.1$) differences of species richness and seedling density, among years and layers respectively. In comparison of stands level of significant differences is indicated as *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns not significant.

Table 2. Results from two-way ANOVAs for changes in species density (*F* values)

Effect	Overgrazed			Reference		
	Total	Annuals	Perennials	Total	Annuals	Perennials
Year	17.17***	51.64***	2.67*	4.89***	23.88***	3.57**
Season	31.74***	54.24***	4.94**	36.39***	49.06***	2.01
Year × Season	1.76	4.22***	1.51	8.08***	3.64***	0.01

ANOVAs tested for effect of year (1994–2000), season (April, June, September) and their interaction. Level of significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

the overgrazed stand vegetation and seed bank shared 41% of the local species set whereas this figure was 32% in the reference. Without hydrophytes the Jaccard similarity index between seed bank and vegetation measured 48% for the overgrazed stand and 39% for the reference (Table 3).

Table 3. Detailed vegetation (1994–2000) and seed bank records (2000)B

AH	Life form	Species	Overgrazed				Reference				SBT min
			Vegetation fr.	Seed bank		Last yr	Vegetation fr.	Seed bank		Last yr	
				0–5	5–10			0–5	5–10		
	Vegetation										
	WA	*Bromus tectorum*	V			<1					**T**<
	P	*Euphorbia cyparissias*	V			<1					T<
	SA	*Kochia laniflora*	III			<1					T<
	P	*Rumex acetosa*	II			<1					T<
	WA	*Erodium cicutarium*	II			>3					T<
	P	*Cynoglossum hungaricum*	I			>1					**T**<
	P	*Silene otites*	I			>1					T<
	WA	*Capsella bursa-pastoris*	I			>4					T<
	P	*Melandrium album*	I			>2					T<
	P	*Centaurea arenaria*	I			<1					**T**
	P	*Cynodon dactylon*	V			<1	V			<1	**T**
*	P	*Eryngium campestre*	V			<1	V			<1	**T**
	P	*Gagea pratensis*	IV			<1	III			<1	**T**
*	P	*Chondrilla juncea*	III			<1	III			<1	T
	P	*Taraxacum officinale*	II			>2	II			<1	T<
	P	*Carex supina*					V			<1	**T**<
	WA-B	*Jasione montana*					I			>5	T
	Vegetation and seed bank										
	Overgrazed stand										
	P	*Plantago lanceolata*	V	39	3	<1					SP<
	SA	*Plantago arenaria*	V	9	1	<1					**SP**
	SA	*Ambrosia artemisiifolia*	V	6		<1					T
	WA	*Apera spica-venti*	V	2		<1					T
	P	*Potentilla argentea*	IV	15	1	<1					SP<
	P	*Berteroa incana*	III	2		<1					T<
	P	*Anchusa officinalis*	II	1		<1					T<
	WA	*Bromus mollis*	II	1		<1					T<
	SA	*Gypsophila muralis*	II	32	7	>2					LP
	WA	*Erophila verna*	I	1	1	>2					LP
	Both stands										
	P	*Festuca vaginata*	V	1		<1	III			<1	**T**
	P	*Poa bulbosa*	V	1		<1	II			< 1	T
	WA	*Scleranthus annuus*	IV	54	4	<1	I		1	< 1	SP<
	P	*Poa angustifolia*	V	4		<1		1		>5	**LP**
	B	*Verbascum phlomoides*	IV	95	4	<1		1		>5	LP
	WA	*Myosotis stricta*	IV	10	3	<1		4	2	>5	LP
	WA	*Vicia lathyroides*	IV	2	2	<1		2		>5	**LP**
	WA	*Arenaria leptoclados*	III	13	7	<1		1	2	>5	LP
	WA	*Veronica arvensis*	III	4		<1		1		>5	LP
	SA	*Chenopodium album*	I	5		>5				>5	LP
	P	*Rumex acetosella*	V	292	34	<1	V	220	37	<1	LP
	WA	*Anthemis ruthenica*	V	35	5	<1	IV	9		<1	**SP**
*	WA	*Conyza canadensis*	V	30		<1	IV	32		>1	T<
	P	*Potentilla arenaria*	V	6	1	<1	II	2	1	<1	**SP/LP**
	WA	*Cerastium semidecandrum*	V	3	4	<1	III	5		<1	SP/LP
	P	*Achillea setacea*	V	5	1	<1	I	1		<1	SP<
	P	*Koeleria cristata* and *K. glauca*	V	5		<1	V	5	1	<1<1	SP
	P	*Festuca pseudovina*	V	1	2	<1	V	1		<1	**SP**
	WA	*Veronica verna* and *V. triphyllos*	IV	8		<1	IV	39	2	<1	**SP**
	WA	*Erysimum diffusum*	IV	4		>1	II	1		>1	SP
	P	*Carex praecox* and *C. stenophylla*	V			<1	IV	1		<1	**T**<
*	WA	*Crepis tectorum*	IV			>1	III	1		<1	**T**<
*	SA	*Filago arvensis*	I			>5	II	16		<1	**T**<

Table 3. (*continued*)

AH	Life form	Species	Overgrazed				Reference				SBT min
			Vegetation fr.	Seed bank		Last yr	Vegetation fr.	Seed bank		Last yr	
				0–5	5–10			0–5	5–10		
	Reference stand										
	DS	*Thymus degenianus*					V	8		<1	**T**
	P	*Hypericum perforatum*					III	98	2	<1	SP<
Seed bank											
x	P	*Juncus conglomeratus*		4	4	>5					LP
x	SA	*Cyperus fuscus*		6		>5			4	>5	LP
	SA	*Juncus bufonius*		38		>5		5		>5	LP
x	P	*Juncus effusus*		20		>5		1		>5	LP
x	P	*Juncus inflexus*		12		>5		1	1	>5	LP
	P	*Carex hirta*		4		>5		11	5	>5	LP
x	P	*Juncus articulatus*		2		>5		1	1	>5	LP

Frequency of species in vegetation (max.: 5 plots × 6 yr = 30): I—present in 1–6 plot × yr, …, V—present in 25–30 plot × yr. Number of seedlings in seed bank samples. Each seedling found corresponds with 26.53 germinable seeds/m^2). *—wind dispersed species (A); x—wetland species (H); life form: SA—summer annuals, WA—winter annuals, B—biennial, P—perennial, DS—dwarf shrub, W—woody species (shrub saplings) (Simon, 2000). <1: grown less than 1 yr before seed bank sampling (1999), >1: grown more than 1 yr ago (1998); SBT—seed bank type determined in this study: T—transient, S—short-term persistent, L—long-term persistent (Thompson et al., 1997). Bold letters stand for new classifications whereas '<' indicates that there are already more persistent records published about the given or a closely related species.

Rare species excluded from multivariate analyses and not classified into a seed bank type; sporadic and temporal in vegetation (fr. I, <3 plot x year) or accidental in seed bank samples (1 plot/stand or altogether <3 seeds). **Vegetation O 1995:** W *Crataegus monogyna*; **1996:** SA *Polygonum arenarium*, SA *Portulaca oleracea*; **1999:** * P *Leontodon hispidus*; **2000:** * B *Carduus* cf. *nutans*, * B *Tragopogon dubius,* WA *Viola arvensis*. **R 1994:** * SA *Crepis rhoeadifolia*, WA *Minuartia viscosa*; **1995:** WA *Spergula pentandra*, WA *Trifolium arvense*; **1998-99:** * P *Hypochoeris radicata*. **Seed bank O**: SA *Amaranthus albus*, x SA *Eleocharis* cf. *palustris*, SA *Eragrostis pilosa*, SA *Geranium molle*, SA *Matricaria discoidea*, WA *Minuartia viscosa*, x P *Poa pratensis*, SA *Polycnemum arvense*, SA *Polygonum aviculare*, x P *Potentilla anserina*, x *Ranunculus sceleratus*. **O and R:** x P *Juncus compressus*, * x P *Typha angustifolia*; **R:** * x P *Epilobium tetragonum*, x P *Trifolium repens*, x P *Verbena officinalis*.

Rumex acetosella dominated seed bank samples whereas *Conyza canadensis* was frequent (among the most abundant 20% of species) at both stands. In the overgrazed stand *Anthemis ruthenic*, *Arenaria leptoclados*, *Gypsophila muralis*, some *Juncus* spp., *Plantago lanceolata*, *Scleranthus annuus* and *Verbascum phlomoides* were frequent, in the reference *Carex hirta, Filago arvensis*, *Hypericum perforatum,* and *Veronica verna* together with *V. triphyllos*. The rest of the species was rare. Soils of both stands contained hygrophytes missing in the aboveground vegetation. In the overgrazed stand a many times higher seed density and a higher species number of these plant species were remarkable, especially obvious that of *Juncus* spp. (Table 3).

Vegetation of the overgrazed and reference stands were separated along the first axis of the MDS ordination (Fig. 1). There was a similar trend of the vegetation change in each season. Changes were more pronounced for the overgrazed stand. Vegetation of the spring samples were relatively different from the summer and autumn vegetation in the reference stand, while summer and autumn vegetation were similar to each other for each year.

Samples of the vegetation and the seed bank of the overgrazed and the reference stands were separated along the first axis of the Canonical Correspondence Analysis (Fig. 2). Summer and autumn samples were similar, but spring samples were separated. Species composition of the seed bank was more similar to the spring samples than to the summer or autumn samples for both the overgrazed and reference stands (Fig. 2). The biplot diagram reveals that *Achillea setacea*, *Bromus tectorum, Festuca vaginata*, *Plantago lanceolata*, *Poa angustifolia, Potentilla* spp., *Scleranthus annuus* and *Verbascum phlomoides* were the most characteristic for the overgrazed stand, while *Carex supina*, *Eryngium campestre, Thymus degenianus* and *Hypericum perforatum* for the reference. Typical species common to spring vegetation and the seed banks at both stands involved *Anthemis ruthenica, Carex stenophylla* and *C. praecox, Scleranthus annuus* and *Veronica verna* and *V. triphyllos. Juncus* spp. were characteristic to the seed banks whereas the dominant grasses, *Cynodon dactylon*, *Festuca pseudovina* and *Koeleria* spp. for vegetation at both stands.

Soil characteristics

Most pedological characteristics proved highly similar between stands and no obvious trends were detected. All

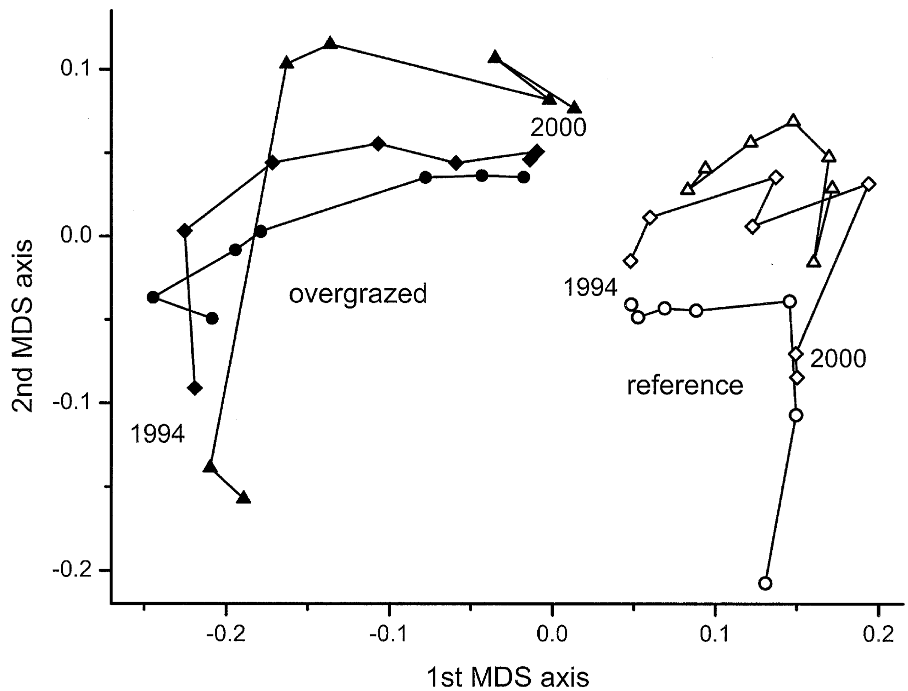

Fig. 1. MDS ordination of the seasonal vegetation of the overgrazed and reference stands (stress = 0.115). Percentage cover data were compared by the Bray-Curtis dissimilarity. Notations: open symbols – reference stand; full symbols – overgrazed stand; triangles – spring; circle – summer; rhomboid – autumn samples.

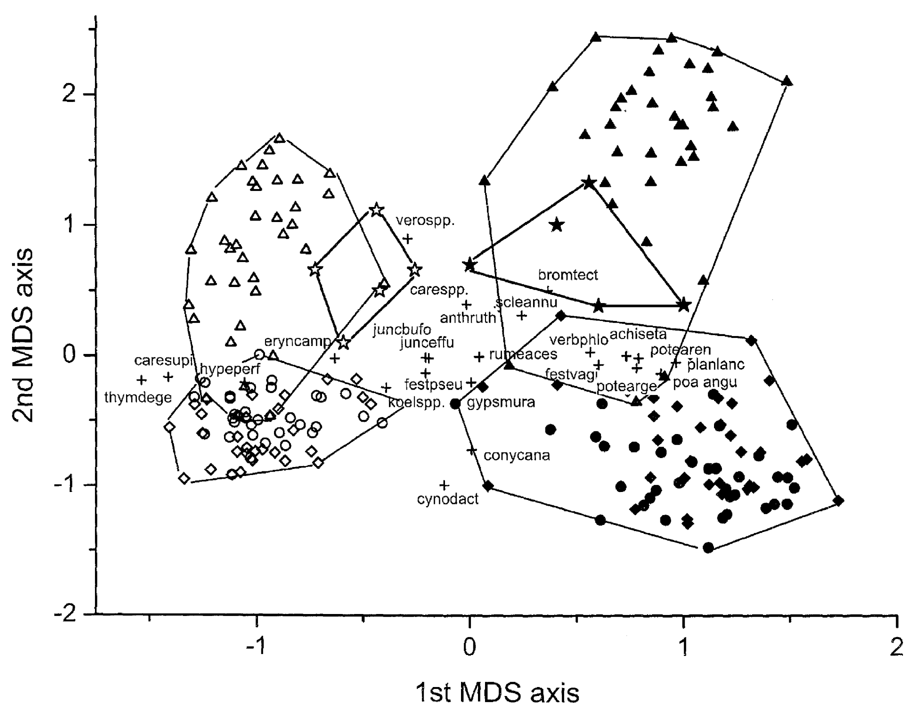

Fig. 2. CANOCO biplot of vegetation relevés and seed-bank samples based on the species composition. Notation not mentioned in Fig. 1: asterics – seed bank samples. Position of the 24 most frequent taxa (in vegetation and/or seed bank samples) is shown; they are abbreviated as achiseta = *Achillea setacea*, anthruth = *Anthemis ruthenica*, bromtect = *Bromus tectorum*, carespp. = *Carex praecox* and *C. stenophylla*, caresupi = *C. supina*, conycana = *Conyza canadensis*, cynodact = *Cynodon dactylon*, eryncamp = *Eryngium campestre*, festpseu = *Festuca pseudovina*, festvagi = *F. vaginata*, gypsmura = *Gypsophila muralis*, hypeperf = *Hypericum perforatum*, juncbufo = *Juncus bufonius*, junceffu = *J. effusus*, koelspp. = *Koeleria cristata* and *K. glauca*, planlanc = *Plantago lanceolata*, poa angu = *Poa angustifolia*, potearen = *Potentilla arenaria*, potearge = *P. argentea*, rumeaces = *Rumex acetosella*, scleannu = *Scleranthus annuus*, thymdege = *Thymus degenianus*, verbphlo = *Verbascum phlomoides*, verospp. = *Veronica verna* and *V. triphyllos*.

Table 4. Selected soil characteristics of the stands

	Overgrazed	Reference
pH_{KCl}	4.15 ± 0.17^a	4.06 ± 0.06^a
humus (%)	1.17 ± 0.17^a	1.26 ± 0.19^a
$NO_3 + NO_2$-N (mg kg^{-1})	0.95 ± 0.29^a	0.84 ± 0.27^a
NH_4-N (mg kg^{-1})	5.61 ± 1.44^a	6.57 ± 1.72^a
K_2O-K (mg kg^{-1})	81.14 ± 18.85^a	71.86 ± 18.06^a
P_2O_5-P (mg kg^{-1})	103.43 ± 17.66^b	48.71 ± 14.45^a

Average and standard error of yearly spring samples (1994–2000). Different letters indicate that differences between stands exceeded the double of upper accuracy level of the given analysis. The accuracy was pH_{KCl}: 0.05, humus: 2.5–7.5%, $NO_3 + NO_2$-N, NH_4-N: 5–10%, P_2O_5-P, K_2O-K: 2.5–5.0%.

samples were calcium-free, moderately to strongly acidic with low humus and nitrogen contents. Only the content of potassium was moderately and that of phosphorus was noticeably higher in the overgrazed stand than in reference (Table 4).

Discussion

Vegetation change

As found in this study, secondary successions are generally characterized by increasing cover of annuals after disturbance followed by their gradual decline (Hayashi, 1977; Foster and Tilman, 2000). Also in agreement with other studies in the region (Matus and Tóthmérész, 1995; Halassy, 2001) early phases of succession are dominated by summer annuals. In this study summer annuals formed 24% of the local species set in the overgrazed stand but only 6% in the reference. Having similar phenology, summer annuals compete with perennials and are restricted to the pioneer phase with low vegetation cover (Hayashi, 1977; Matus and Tóthmérész, 1994, 1995). In contrast, winter annuals tend to persist in late successional phases. Life-cycle of these species enables their coexistence and makes them successful colonizers of seasonal gaps in dry grasslands (Geißelbrecht-Taferner et al., 1997; Rebollo et al., 2001). In agreement with this, winter annuals maintain 33% in the local species set in reference stand but only 24% in overgrazed stand.

The pioneer phase of a ruderal sandy succession after goose breeding, as found in similar sites, is characterized with extremely high nutrient levels and is dominated by ruderal associations (Tribulo-Eragrostion, Sisymbrion) (Matus and Tóthmérész, 1994). After fast leaching of nitrogen, on well-drained soils poor in humus, vegetation soon turned into nutrient-poor associations dominated by annuals (Bassio laniflorae-Bromion tectorum) (Matus and Tóthmérész, 1995). In this study, started in the 11th successional year, already low nitrogen contents were detected and the transition from an annual dominated to a perennial dominated community was not apparently driven by changing nutrient contents.

The reference stand had a high floristic similarity with the *Cynodon* facies of *Potentillo-Festucetum* sampled at the site (Précsényi et al., 1990). Higher frequency and cover of short-lived species indicate somewhat higher grazing pressure in the late 1980s. Vegetation change in the reference is mostly associated with increasing dominance of the dwarf shrub *Thymus degenianus* (Figs. 1 and 2). In accordance with other studies in dry grasslands this can be a consequence of gradually decreased stocking density. Heavy grazing reportedly eliminated dwarf shrubs (Wang et al., 2002) whereas removal of grazing can result in their increased cover (Hulme et al., 1999). The above pattern of vegetation development was found in a study based on a pseudo-replication. However, the studied locality was selected through detailed, long-term knowledge of the region.

Seed dispersal

Propagule dispersal plays a decisive role in maintaining community diversity (Bakker et al., 1996). In this study, increased dispersal can be an important factor in higher species richness of the overgrazed stand. Hygrophytes, unable to establish on dry dunes, should have been dispersed to the stands; therefore, these can be considered as markers for the dispersal. Being anemochorous hygrophytes accidental, different densities of wetland species in the soil of stands can indicate different intensities of zoochory. This assumption is in line with recent findings on the importance of animals in seed dispersal (Poschlod, 1996; Fisher et al., 1996). Dissimilarities in the way of grazing of geese and cattle can explain different intensity of seed dispersal. Unlike cattle, geese feed also on below-ground plant organs and on earth-dwelling animals and therefore consume seeds in soil (Poschlod pers. comm.). *Juncus* species with dense seed banks in wetlands (several sources cited in Thompson et al., 1997), are likely to be dispersed by endozoochory. Seeds of rushes, known to become sticky when wet, can also be dispersed by ektozoochory (Grime et al., 1988). Non-anemochorous xerophytes could have been dispersed in similar ways either from surrounding vegetation or from fodder for geese. Importance of gaps for seedling establishment is widely accepted (Ortega et al., 1997; Touzard et al., 2002; Amiaud and Touzard, 2004) therefore in our study the establishment of weedy xerophytes could have been supported by large open surfaces after abandonment of goose grazing. In contrast, typical threatened perennials of the community (e.g. *Iris humulis* subsp. *arenaria*, *Onosma arenaria* subsp. *tuberculata*; Borhidi, 2003), which were and are present in the vicinity (Nagy et al., 1991; Matus and Papp, 2001), were neither detected in seed banks nor did they became established. Different species richness and composition of stands reflects the former management and dispersal events rather than the small differences in actual nutrient availability.

Seed bank formation

Specific records of seed bank type gained in this study are mostly in accordance with Thompson et al. (1997) and Csontos (1998). We newly classified seed longevity of several species not covered in former reviews (Table 3). A transient type was typical in some wind-dispersed dicots (e.g. *Chondrilla juncea*, *Eryngium campestre*), grasses (e.g. *Bromus tectorum*, *Cynodon dactylon*) and a bulbous geophyte (*Gagea pratensis*). At least short-term persistence was supposed in annuals which grew in the vegetation a few years before getting detected in seed bank samples (e.g. *Erophila verna*, *Erysimum diffusum*). Those annuals present in vegetation as well as in the soil of the overgrazed stand but only in soil of the reference are considered long-term persistent (e.g. *Arenaria leptoclados*, *Myosotis stricta*, *Vicia lathyroides*, *Verbascum phlomoides*). Those xero- (e.g. *Carex hirta*) and hygrophytes (e.g. *Juncus* spp.) detected only in seed banks are long-term persistent too. Apparent transient records in some *Caryophyllaceae* (*Silene otites*), *Chenopodiaceae* (*Kochia laniflora*) and *Cyperaceae* (*Carex* spp.), families dominated by persistent records (Thompson et al., 1997), could have resulted from undetectably sparse or aggregated seed banks.

We found that overgrazing, similarly to other ways of intensified land use (e.g. ploughing), resulted in an increased seed density and higher similarity of established vegetation and seed banks (Bakker et al., 1997; Bekker et al., 1997; Halassy, 2001; Touzard et al., 2002). The portion of species present both in vegetation and seed bank compared to the number of species only in vegetation was higher in the overgrazed stand (55%) than in the reference plot (48%). Our results also confirm a decreasing density of viable seeds with increasing successional age as found in several studies in disturbed grasslands (Donelan and Thompson, 1980; Symonides, 1986). We, however, did not confirm an increased representation of persistent species in the disturbed stand of the studied community. A reason for this can be that persistent species were already present in soil resulting from former disturbances and that the longevity spectrum of seeds from newly established species did not differ from that of resident ones.

The relatively high representation of persistent records (min. 51% of all classified species and min. 45% for xerophytes) was remarkable (Table 3). The seed bank spectrum of Cynodonti-Festucetum is therefore more similar to Mediterranean grasslands (Levassor et al., 1990; Russi et al., 1992; Peco et al., 1998) and subcontinental steppes (Virágh and Gerencsér, 1998; Matus et al., 2003a) rather than to mesophilous grasslands (Poschlod and Jackel, 1993; Bekker et al., 1998), alluvial wetlands (Touzard et al., 2002; Amiaud and Touzard, 2004) or fen-meadows (Pfadenhauer and Maas, 1987; Maas and Shopp-Guth, 1995; Matus et al., 2003b). Formation of persistent seed banks is apparently a generally favoured strategy in open habitats with many annuals (Thompson, 1992; Lavorel et al., 1993). In contrast, short distance dispersal with transient seeds dominates the regeneration of most pioneers in dry acidic grasslands (Sautter, 1994; Jentsch and Beyschlag, 2003). It is likely that these differences are linked to differences in gap availability (Peco et al., 1998).

In this study a large portion of species with persistent seeds in a dense seed bank can indicate adaptation to recurrent site disturbance (e.g. overgrazing or drought). Regarding the matrix species, this also implies a fast community regeneration. In contrast, overgrazing of extended areas greatly reduces the re-colonization chances of grazing-intolerant perennials with no persistent seed banks and effective seed dispersal.

Implication for restoration

In previous studies we showed that fast leaching of nutrients makes topsoil removal unnecessary (Matus and Tóthmérész, 1994, 1995). As seed banks are concentrated in the topsoil, this management will remove seeds of target species, which is undesirable. Restoration should avoid soil disturbance because it favours weedy summer annuals still present in the seed bank.

In the case of the studied site, about 15–20 years were necessary until a partial spontaneous regeneration occurred, i.e. till most typical species became established and a closed, perennial-dominated sward developed. In spite of the proper abiotic site conditions, establishment of threatened species in the community was not detected. Most of these species, present in sparse populations, are likely to be limited by propagule dispersal. Also lacking a detectable representation in seed banks, these plants apparently rely on diaspore inoculation via transfer of hay and/or topsoil inoculation or transfer (Stroh et al., 2002).

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