Secondary succession in overgrazed Pannonian sandy grasslands

Sekundární sukcese v nadměrně spásaných panonských travních společenstvech

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We assessed vegetation changes on acidic sandy soils in permanent plots to follow secondary succession after cessation of intensive goose breeding in E Hungary. We also aimed to estimate the time required for vegetation regeneration and indicate differences in secondary succession patterns at different altitudes in sand dunes. Two sites in the low and two in the high parts of the dunes were chosen and sampled for twelve years. The initial stages are characterized by ruderal communities dominated by nitrophilous annual weeds. Ruderal vegetation was soon replaced by nutrient-poor communities dominated by short-lived pioneer dicotyledonous plants and grasses. In the last few years of the study, coinciding with a rainy period, the low sites were dominated by the perennial grasses, *Poa angustifolia*, *P. pratensis* and *Cynodon dactylon*. In contrast, in the high sites a less dense cover of perennials developed. The influence of initial composition on vegetation development decreased with time and the influence of altitude increased during succession. The altitude of the site had a significant effect on regeneration. Species richness and Shannon diversity of the high sites increased during vegetation development and that of the low sites decreased. Most annuals persisted in the high sites but became extinct in the low sites. The mean species turnover rate, irrespective of altitude, decreased during the study.

Keywords: elevation, denudation, goose breeding, Hungary, inland dunes, rate of succession, species richness

Introduction

The development of vegetation in old fields and other human disturbed habitats has been a focus of interest for several decades (Horn 1974, Bradshaw 1983). Most of the studies used the chronosequence method (space for time substitution), although the usefulness of this approach is often criticized (Foster & Tilman 2000, Pickett et al. 2001). Using chronosequences enables the generation of broad scale hypotheses, which should be tested at small scales (Prach & Řehounková 2006). Only a limited number of studies discuss results from permanent plot experiments though the use of such plots with a documented vegetation history provide the most accurate way of examining long term change in vegetation (Bakker et al. 1996). The results of detailed and comparable case studies based on permanent plots are needed to predict the outcome of vegetation change by spontaneous regeneration (Prach et al. 2001a).

Spontaneous successional processes are an important aspect of ecological restoration, which often influence the effect of restoration efforts and determine the final outcome. Results of these processes and restoration measures are usually intermingled and influence each other (Luken 1990). Therefore, spontaneous succession should be considered in all restoration projects. Moreover, some restoration programs simply rely on natural succession (Jongepierová et al. 2004). Use of spontaneous vegetation development in an ecosystem restoration program requires understanding of the processes and how they are likely to affect the specific aims.

Pathways in the primary succession on calcareous Pannonian sands, based on the "space-for-time" approach, have been identified and analysed (Soó 1957, Précsényi 1981, Zólyomi et al. 1987). The successive stages have been identified as *Festucion vaginatae/Corynephorion* (open sandy grasslands on calcareous/acidic ground), *Festucion rupicolae (*steppe meadows), *Junipero-Populetum albae* and *Festuco-Quercetum roboris* (bush and climax forest sand communities belonging to *Aceri tatarici-Quercion*). Fekete (1992) summarized the major pathways in primary succession and concluded that on sand they can form a complicated network, with a grazing-induced bifurcation leading to the pasture *Cynodonti-Festucetum pseudovinae* or even *Bromion tectorum*.

The same approach for secondary processes has been adopted by Csecserits & Rédei (2001). There are fewer studies on acidic sands using the permanent plot approach (Matus & Tóthmérész 1995, Matus et al. 2005), and the effect of altitude on succession has also hardly been addressed (Matus et al. 2003).

The factors causing the multiple pathways in succession (i.e., development of different vegetation types following a similar disturbance regime) include type and/or intensity of disturbance (Christensen & Peet 1984), spatial heterogeneity in seed rain (Abrams et al. 1985) and differences in resource availability (Inouye & Tilman 1988). Differences in microtopographical position and associated environmental characteristics (e.g., different soil moisture relations) influence the regeneration process (Titus 1990). The effect of microtopography has been identified and studied in various communities (e.g., deserts – Mott & McComb 1974, grasslands – del Moral & Deardorff 1976, abandoned pastures – Thomas & Dale 1976), but only a few studies evaluate the role of microtopography on annual-perennial dynamics (e.g., Pemadasa et al. 1974).

Sandy grasslands, like many other types of grassland in the Pannonian region have undergone major compositional changes during the last few decades due to changing management. Extensive grazing by cattle or sheep has often been abandoned or replaced by uncontrolled mass grazing by domestic geese. The latter became a widespread conservational problem from 1980s to the mid 1990s and totally devastated above-ground vegetation of these grasslands. The Martinka Pasture, which was subjected to intensive goose farming, was among the most affected and severely damaged sites. This type of management resulted in large-scale degradation (Matus & Tóthmérész 1994).

To assess changes in this widespread vegetation type, we used a permanent plot approach to follow vegetation development after cessation of intensive goose farming. Our hypotheses were based on some widely held views about succession: (i) During succession the successive dominants have longer life spans (Inouye et al. 1987, Lepš 1987, Myster & Pickett 1994, Prach & Řehounková 2006). (ii) The vegetation development in the first few years is determined by the initial species composition (Egler 1954). This effect decreases during succession and the species composition of the community later on tends to depend on the altitude of the sites. (iii) The number of species and Shannon diversity index increase with time because of the continuous immigration and establishment of new species (Odum 1969, Bazzaz 1975, Inouye et al. 1987). (iv) The species turnover rate decreases during succession in parallel with the development of a dense cover of perennials.

Material and methods

Site description and history

Sampling was carried out at the Martinka Pasture nature reserve located ca 15 km east of Debrecen, E Hungary (47°34'00"– 35'20"N; 21°46'30"– 48'40"E (CEU: 8496.2). The site has a slight inclination from east to west and is dominated by 3–10 m high dunes. Dunes are separated by flat dune slacks and small channels. The 2.8 km^2 reserve is mostly covered by unfertilized dry sandy grassland, *Cynodonti-Festucetum pseudovinae*, the pioneer grasslands on steep slopes (*Bassio laniflorae-Brometum tectorum*, *Festucetum vaginatae*; Soó 1957, Borhidi 2003, Matus et al. 2003) and wet meadows in dune slacks (*Magnocaricion elatae*, *Calthion*, *Deschampsion caespitosae*, *Arrhenatherion Juncenion effusi*; Nagy et al. 1991, Borhidi 2003). Overgrazing of the study sites by domestic geese occurred in 1989–1990. Animals were fed with fodder, which resulted in extra nutrient input near stables. Initial secondary succession depended on the soil seed bank, seed rain and the sporadically surviving perennials scattered throughout the denuded area.

Sampling setup

Four sites, located on goose farms abandoned in 1990, were chosen for study. Two of them (H1, L1) were located in the eastern part of the reserve where the height of dune slacks is 132.5 m and the other two (H2, L2) in the western part of the reserve where the dune slack height is 129.2 m. Pairs of sites were at similar altitudes. Low sites (L1, L2) were ca 1.5 m above the level of the surrounding dune slack whereas the high sites (H1, H2) were ca 2.7–2.9 m above the dune slacks. Slope inclination was below 5° at all sites. All sites were subject only to spontaneous succession.

Five 2 × 2 m permanent plots per site were sampled between 1991–2002. Percentage cover of vascular species was estimated in June. Chemical characteristics of the soil samples, collected yearly in April 1998–2002, were analysed. Ten subsamples per site, each of about 100 cm^3, were collected from close (< 0.2 m) to the plots from the 0–10 cm layer of soil, and pooled. Soil samples were analysed at the Debrecen Laboratory of Plant and Soil Protection Service (NETVÁ) to an accuracy of 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 %, respectively.

Mean annual precipitation and mean annual temperature for the study period and multi-year averages were obtained from meteorological stations of the Hungarian Meteorological Service (OMSZ) and the Regional Hydrological Directorate (TIVIZIG).

Soil

Soil at the study sites is calcium-free, moderately to strongly acidic Pleistocene sand with a typical grain size of 0.1–0.3 mm and low to moderate humus content, low nitrate plus nitrite and low ammonium contents. Potassium and phosphorous contents varied greatly between sites. H1 was the poorest and L2 the richest in all nutrients; the latter had the highest humus content and pH value. Sites H2 and L1 had an intermediate nutrient content (Table 1).

Climate and weather conditions

The climate is moderately continental with a mean annual temperature of 10.0 ºC (January –2.5 ºC, July 21.2 ºC). The mean annual precipitation is 600 mm, of which 300–350 mm fall in April–September. Large fluctuations in mean temperatures and especially annual rainfall is typical. Mean yearly temperatures varied between 9.4–11.4 ºC, and that for April–September varied between 16.5–18.4 ºC. Extreme mean monthly temperatures ranged between –5.5 ºC (December 1998) and 24.9 ºC (August 1992). Annual precipitation varied between 430–960 mm and precipitation in April–September ranged between 280–640 mm. These fluctuations correspond to ca 80% of that recorded over the last 150 years for temperature and last 40 years for precipitation, respectively. Dry periods occurred during the study period. The most serious, long-lasting droughts were in 1992–1993 and 2000, and periods of high rain fall in 1998–1999 and 2002 .

Data processing

Raunkiaer's life-form categories and indicator values of Ellenberg for moisture (W) and nitrogen (N) adapted to Hungarian conditions (Borhidi 1995) were used to characterize the vegetation. We used weighted averages, where the percentage cover of the species is expressed in terms of weight. We calculated species turnover rates using the following formula: $TOR = (b+c) / (a+b+c)$, where TOR is the turnover rate, a is the number of species present in both years, b the number of species detected only in the first year, c the number of species detected only in the second year, and $(a+b+c)$ is the total number of species detected in both years.

Number of plant species per plot was compared using ANOVA or Kruskal-Wallis nonparametric test, depending on the result of testing for equality of variance (F-test) and normality (Kolmogorov-Smirnov test) (Zar 1999). In the case of significant differences Student-Newman-Keuls pairwise comparisons were used. By comparing two samples, depending on the results of the normality tests, a t-test or Mann-Whitney test was applied. To test the relationship between two variables, Spearman rank correlation was applied. DCA ordination was applied to the percentage cover data sets (ter Braak & Šmilauer 1998, Lepš & Šmilauer 2003).

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

Results

Composition and development of vegetation

Altogether 109 vascular species were recorded over the 12 years. Local species richness of the sites was similar (60–67 species). Vegetation in the first year was characterized by nitrophilous weedy annuals (*Amaranthus albus*, *Capsella bursa-pastoris*), but in the second year their cover decreased. The weedy annuals were replaced by short-lived ruderals and pioneering dicots *(Anthemis ruthenica*, *Cerastium semidecandrum*, *Conyza canadensis*, *Digitaria sanguinalis* and *Erysimum diffusum*). Later on, annual grasses *Apera spica-venti* and *Bromus tectorum* became temporarily dominant (See Electronic Appendix 1 for temporal changes in dominants), followed by perennial graminoids (*Poaceae*, *Cyperaceae*, especially *Poa angustifolia*, *Poa pratensis*, *Cynodon dactylon* and

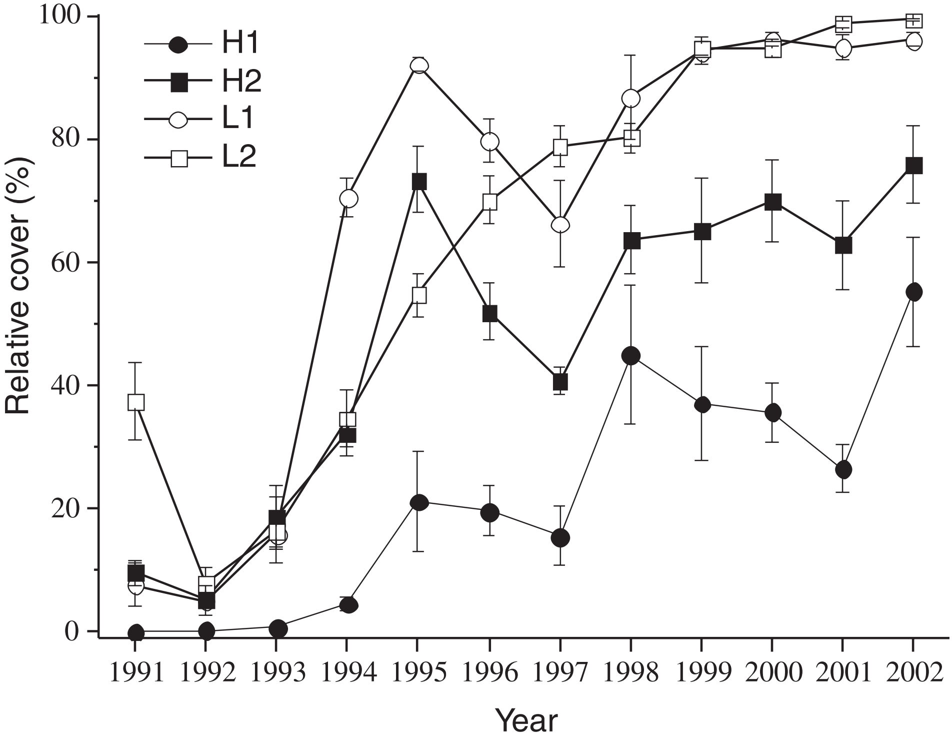


Fig. 1. – Relative cover (mean per $4m^2$ plot ± SE) of perennial graminoids (*Poaceae* and *Cyperaceae*) over the 12 years of succession (H1: high site 1, L1: low site 1, H2: high site 2, L2: low site 2).

Carex stenophylla). The highest indicator values for nitrogen were recorded in the pioneer phase. Marked fluctuations in indicator values for nitrogen occurred until 1999 and in those for moisture until 1997, but in the last few years of the study both remained approximately constant. In the last year of the study (2002) significantly lower values for nitrogen and soil moisture were recorded at the high than at the low sites (Table 2).

In spite of large fluctuations across sites and over years, vegetation cover increased significantly during the study period (Spearman rank correlation; $r = 0.33$, $P < 0.001$, $n = 240$). Cover of perennial graminoids increased (Spearman rank correlation $r = 0.72$, $P < 0.001$, $n = 240$), whereas that of annuals decreased (Spearman rank correlation $r = –0.71$, $P < 0.001$, $n = 240$). Development of perennial vegetation varied depending on the altitude of the sites. In low sites clonal grasses became dominant within three years, reaching a total cover of 90–95%. It took seven to eight years in high sites and their cover only reached 55–70% (Fig. 1). The cover of annuals decreased strongly as that of perennial graminoids increased (Spearman rank correlation, $r = –0.72$, $P < 0.001$, $n = 240$).

In the early phase of succession the plot composition at high sites was more similar to that of the close by low sites (H1 vs. L1 and H2 vs. L2) than to each other. After 12 years the sites of similar altitude were more similar (Fig. 2).

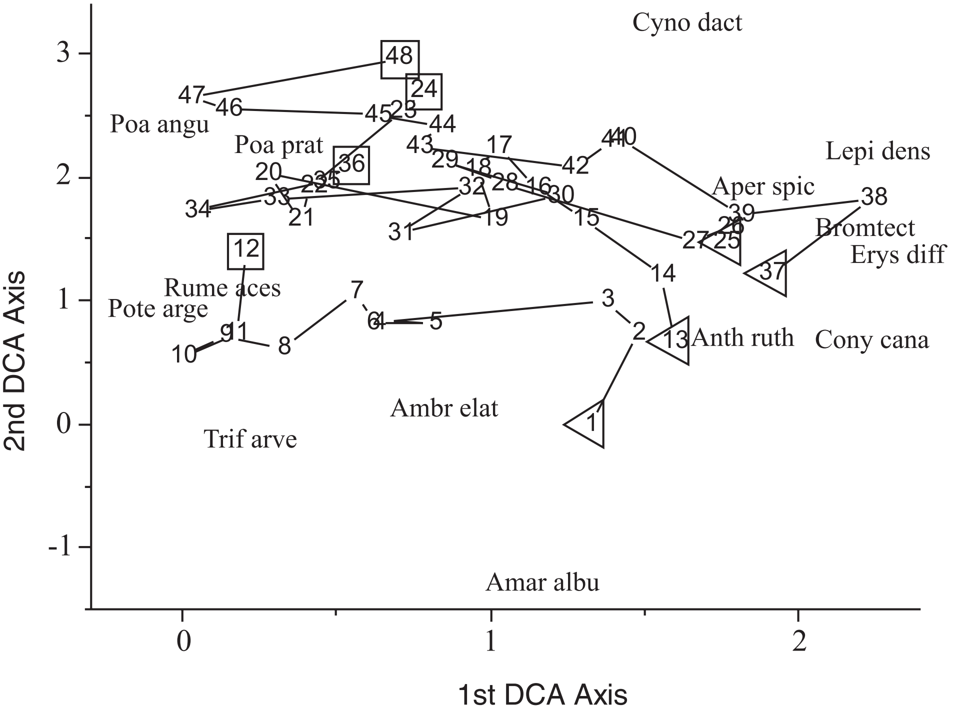


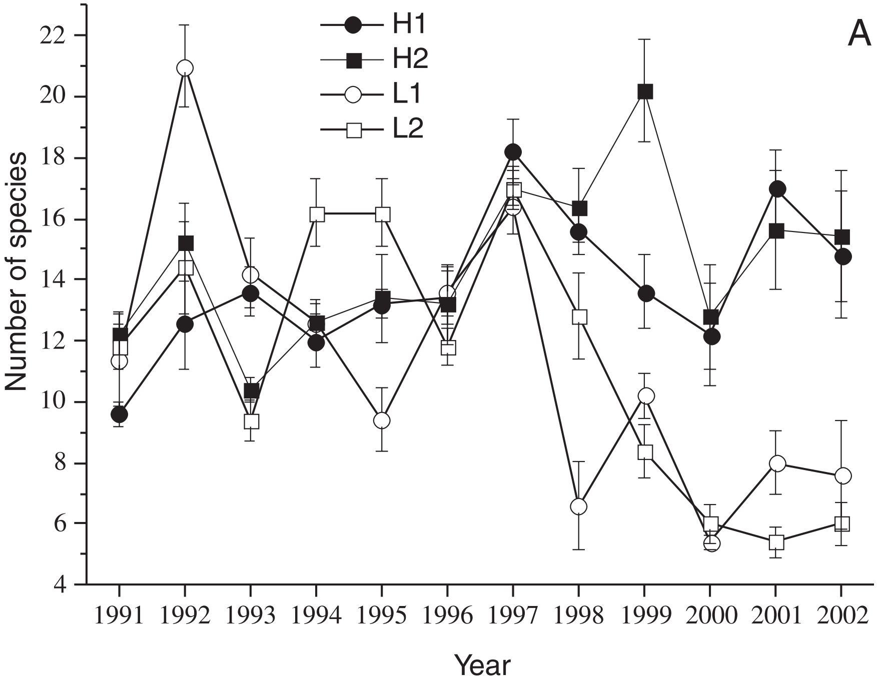
Fig. 2. – Ordination biplot (DCA) of the vegetation relevés and dominant species based on species cover. Triangles denote the 1st year of succession, squares denote the end of study (H1: 1–12, L1: 13–24, H2: 25–36, L2: 37–48).

Table 1. – Characteristics of spring collected soil samples (mean±SE, April, 1998–2002). Different letters indicate that differences between sites exceeded the double of upper accuracy level of the given analysis. The accuracy was as follows: 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% (U1: upper site 1, L1: lower site 1, U2: upper site 2, L2: lower site 2).

	H1	H2	L1	L2
pH (KCl)	4.17±0.04^{c}	5.29±0.14^{b}	4.19±0.08^{c}	5.74±0.06^{a}
Humus (%)	0.83±0.05^{b}	0.95±0.08^{b}	0.75±0.05^{b}	1.78±0.04^{a}
NH_4-N	5.28±1.47^{b}	4.08±0.72^{b}	5.24±0.92^{b}	8.58±1.48^{a}
P_2O_5-P	181.00±21.69^{d}	475.40±36.19^{b}	276.40±29.34^{c}	860.60±73.34^{a}
K_2O-K	84.80±4.16^{d}	109.20±4.81^{c}	137.40±5.78^{b}	218.40±9.06^{a}

Table 2. – Some important characteristics of vegetation samples collected in 2002 (mean ± SE). All data are based on plots of 4 m^2. Significant differences between the groups were tested with ANOVA or a Kruskal-Wallis test, as indicated by different superscripted letters. For site abbreviations see Table 1.

	H1	H2	L1	L2
Species richness	14.8±2.08^{a}	15.4±2.16^{a}	7.6±1.81^{b}	6.0±0.71^{b}
Shannon diversity	1.58±0.12^{a}	1.57±0.20^{a}	0.97±0.08^{b}	0.96±0.11^{b}
Cover (%)	67±2.00^{a}	65±3.54^{a}	83±2.55^{b}	87±1.23^{b}
WB score	2.56±0.07^{a}	2.72±0.07^{a}	2.92±0.03^{b}	3.28±0.24^{b}
NB score	2.43±0.17^{a}	3.63±0.13^{bc}	3.98±0.07^{b}	4.21±0.16^{c}



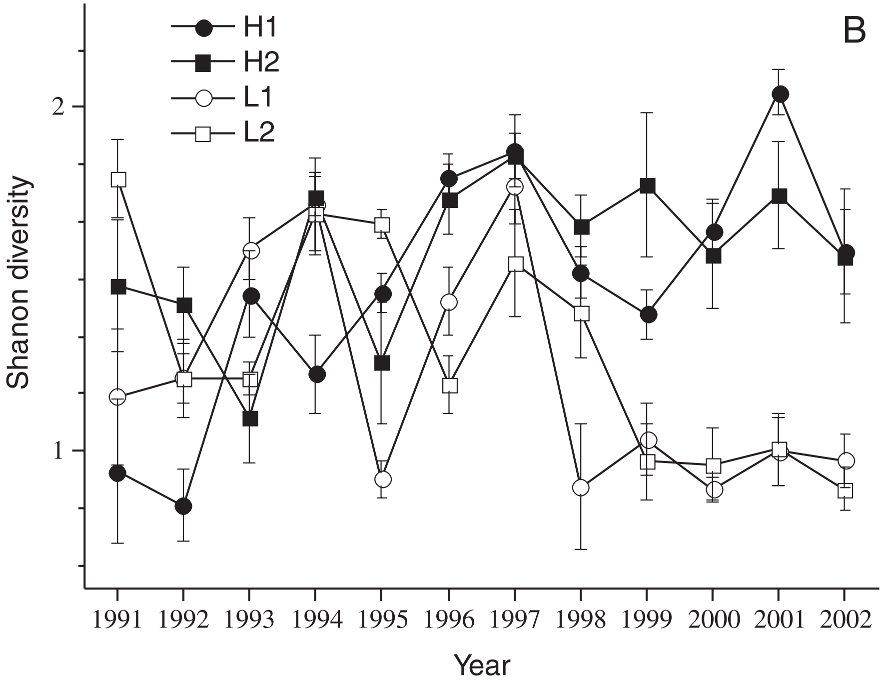


Fig. 3. – (A) Species richness (mean per 4 m^2 plot ± SE) over the 12 years of the succession. (B) Shannon diversity (mean per 4 m^2 plot ± SE) over the 12 years of succession (H1: high site 1, L1: low site 1, H2: high site 2, L2: low site 2).

Species richness and turnover rate

Species richness changed strikingly in the early successional phases but remained relatively stable from the 8th year onwards. The mean number of species and the mean Shannon diversity index of the vegetation at the high sites increased (Spearman rank correlation, $r = 0.36$, $P < 0.001$, $n = 120$ and $r = 0.42$, $P < 0.001$, $n = 120$, respectively), while at the low sites it decreased (Spearman rank correlation, $r = –0.59$ $P < 0.001$, $n = 120$ and $r = –0.50$, $P < 0.001$, $n = 120$, respectively). Species richness was also weakly negatively correlated with the cover of perennial graminoids (Spearman rank correlation, $r = –0.31$, $P < 0.001$, $n = 240$). Species richness and the Shannon diversity index of the high sites was significantly greater than those of the low sites in 2000 (ANOVA, $P < 0.001$, Fig. 3, Table 1). The mean species turnover rate, independent of the sites, decreased during vegetation development (Spearman rank correlation, high sites: $r = –0.59$, $P < 0.001$, $n = 22$ and low sites: $r = –0.73$, $P < 0.001$, $n = 22$, respectively, Fig. 4).

Discussion

Some specific abiotic and biotic factors (e.g., high nutrient levels, local diaspore bank) are known to determine vegetation structure and composition in early succession (Keever 1979, Myster & Pickett 1988, Csecserits & Rédei 2001). High nutrient content favours nitrophilous species, which when nutrients are leached out of the soil become rare or disappear. The initial stages of secondary succession were characterized by ruderal communities which soon turned into nutrient-poor communities (dominated by pioneering dicots and short-lived grasses). This accords with the results of other studies on similar grasslands (Matus & Tóthmérész 1995, Walker et al. 2003, Matus et al. 2005). The vegetation change, following the fast leaching of nutrients from the topsoil, is typical in the initial phase of succession after overgrazing sandy grasslands (Matus & Tóthmérész 1994). After 12 years of secondary vegetation development, nitrogen content of the soil is lower, but even still higher than that recorded in other acidic sandy grasslands (Jentsch & Beyschlag 2003). Based on the earlier results of Matus et al. (2005) a further significant but slow leaching of potassium and phosphorus is expected.

The initial species composition is determined by the community species pool (Egler 1954). This accords well with our findings. The initial vegetation on adjacent sites, despite the differences in altitude, was more similar, than that recorded for sites of similar altitude. In the last few years of the study, coinciding with a rainy period in 1998–1999, the low sites became dominated by the perennial grasses, *Poa angustifolia*, *P. pratensis* and *Cynodon dactylon*, and the high sites by a sparse cover of perennials. The formation of a dense perennial cover possibly resulted in a higher moisture and humus content of the soil. Soil moisture, zonation and nutrient content have been identified as the major factors differentiating sandy vegetation (van der Maarel et al. 1985). Evidence gained from the experimental manipulation of water availability (van der Maarel 1981) suggests that weather fluctuations or minor differences in altitude may have a decisive effect on vegetation succession in this system.

Large fluctuations in species richness and diversity were detected between 1991–1997. Species richness and diversity at the high sites increased but showed marked fluctuations during the development of the vegetation. These figures for the low sites declined sharply

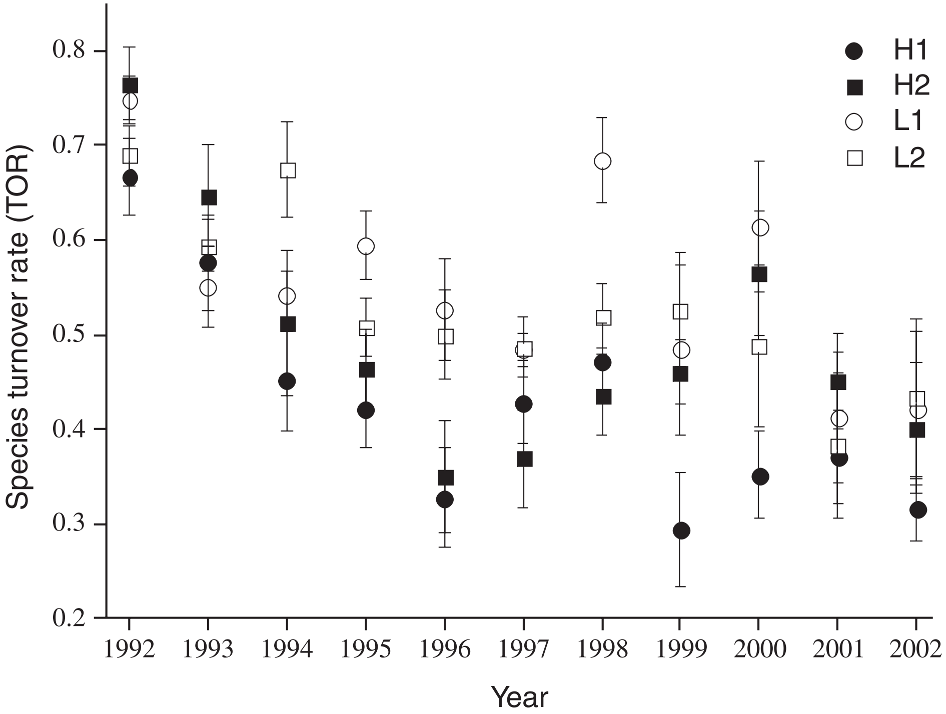


Fig. 4. – Species turnover rate (TOR) over the 12 years of succession.

from 1997 onwards and remained lower than those recorded at the high sites. A possible mechanism resulting in the decrease in species richness and diversity at low sites, is the germination requirements. Short-lived gap-colonizers tend to germinate in full light (Bazzaz 1979). Moreover their seedlings are very sensitive to competition from neighbouring plants (Fenner 1978). Tall-growing graminoids prevent the germination of pioneers and/or outcompete their seedlings (Odum 1969). Therefore competition for light may be an important factor determining the decrease in species richness.

Most annuals persisted at the high sites, whereas the majority of them disappeared from the low sites although there was an abundance of seed in the soil seed banks (Matus et al. 2003). This is due to the absence of patches of bare soil necessary for the regeneration and establishment of annuals, which are important for maintaining species richness (Geißelbrecht-Taferner et al. 1997, Rebollo et al. 2001). Studying sandy communities Pemadasa et al. (1974) found that the abundance of annuals is negatively correlated with that of the dominant perennial grass *Festuca rubra* and positively with altitude. Similar results are presented by Sharitz & McCormick (1973) and for a short-lived perennial *Medicago lupulina* by Pavone & Reader (1985). Analysis of species richness in a similar but lightly grazed dune revealed an opposite pattern: somewhat more species at the low site (Matus et al. 2003). Our results contradict former findings for an established

Potentillo-Festucetum where there were more species at low sites. The novelty of our results is that the development of the post-disturbance vegetation with the encroachment of stoloniferous grasses, mostly *Cynodon dactylon* and *Poa angustifolia,* can greatly reduce species richness in low sites.

Depending on the site significant changes in species richness occurred in the 7–10th year of the succession. From the 11th year the cover remained more or less constant. These results are in accordance with the findings for various fallows in the Pannonian region (Csecserits & Rédei 2001, Ruprecht 2005). Species turnover rate decreased, whereas composition and diversity, especially in the low sites, remained approximately stable from the 10th year until the end of the study (2002). At the low sites only minor changes were observed in the 10–12th years of the succession. Ellenberg indicator values for moisture and nitrogen stabilized in the 7th and 9th year, respectively. Our results support the hypothesis that succession slows down after the stabilization of the dominance relations between the different species groups (Bornkamm 1981, Inouye et al. 1987, Myster & Pickett 1994, Foster & Tilman 2000). Several factors can cause a decline in the rate of succession, including a decline in availability of microsites for establishment (Harper 1977), intensification of interspecific interactions (i.e., allelopathy), interspecific competition (Bazzaz 1979, Foster & Tilman 2000) and an increase in the lifespan of the constituent species resulting in an increasing resistance of the community to colonization (Lepš 1987).

Our results indicate that the establishment of closed perennial dominated vegetation on sand, after denudation by geese, is relatively fast. This could be important for restoration in the future (Prach et al. 2001b, Matus et al. 2003). Within a decade graminoid perennials dominate the spontaneously regenerated fields. The altitude of the site also has a significant effect on the rate of regeneration. At the low sites the cover of graminoids became so dense that only a few annual and perennial forbs survived. At the high sites the less perennial-dominated vegetation enables more species to persist. Unfortunately, the weedy *Ambrosia artemisiifolia*, producing allergenic pollen, is frequently recorded among these annuals.

We found that the early development of vegetation was rapid; the fluctuations in species richness and diversity were high. Vegetation changes started to slow down after a few years. Our results suggest that after the pioneer phase the spontaneous regeneration of damaged sites is very slow and resulted at the end of this study in only a partial regeneration. The results of a previous study of similar goose-grazed grasslands in the same region, which was sampled in the 12th–20th year (Matus et al. 2005), also support the idea of slow vegetation regeneration after the first decade.

These results indicate that spontaneous regeneration of species-rich sandy grasslands could be accelerated by propagule transfer. Diaspores of target species could be introduced via the application of hay or topsoil (Stroh et al. 2002, Donath et al. 2003, Hölzel & Otte 2003), or by grazing animals (Fischer et al. 1996, Poschlod et al. 1998). A good time for this type of manipulation is when the abiotic conditions stabilize, in particular the leaching out of nitrogen in 3rd–5th year. The best time for this could be at least the 20th year of succession at high sites (Matus et al. 2003). In contrast, at low sites this window closes in the 8–10th year after which the increased dominance of clonal graminoids will hamper the colonization of target species for an unknown period.

See http://www.preslia.cz for Electronic Appendix 1.

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Souhrn

Na kyselých písčitých půdách ve východním Maďarsku byla sledována sekundární sukcese poté, co ustal vliv intenzivního spásání husami. Cílem práce bylo dále zjistit dobu potřebnou k regeneraci vegetačního krytu a popsat rozdíly v průběhu sukcese na místech v různé části výškového gradientu. Dvě plochy na výše a dvě na níže položených lokalitách byly sledovány po dobu 12 let. V iniciálních stádiích sukcese dominovala nitrofilní ruderální společenstva s převahou jednoletých druhů, která byla později nahrazena společenstvy živinami chudých půd s převahou krátce vytrvávajících pionýrských dvouděložných druhů a trav. V posledních několika letech sukcese, která byla nadprůměrně deštivá, dominovaly na níže položených plochách vytrvalé trávy *Poa angustifolia*, *P. pratensis* a *Cynodon dactylon*, zatímco na výše položených plochách se vytvořila méně zapojená vegetace s vytrvalými druhy. Vliv počátečního druhového složení na průběh sukcese byl postupně méně patrný; vliv nadmořské výšky se postupně zvyšoval a měl průkazný vliv na regeneraci vegetačního krytu. Počet druhů a druhová diverzita, vyjádřená Shannonovým indexem, se během sukcese zvyšovaly na výše položených plochách, zatímco v nižší nadmořské výšce klesaly. Většina jednoletých druhů přetrvala na výše položených plochách, ale vymizela z níže položených. Rychlost směny druhů v průběhu studia klesala bez ohledu na nadmořskou výšku.

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Electronic Appendix 1. – Temporal change of successional dominants (percentage cover values ± SE) during the study period. Species with a cumulated average cover over 2.5% at least at one site are listed. H – high sites, L – low sites.

Site/year	H1																							
Species	1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
Amaranthus albus	61.6	±10.7	0.0	±0.0	0.3	±0.1	0.0	±0.0	1.0	±1.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Ambrosia artemisiifolia	1.6	±1.1	1.1	±0.7	4.1	±2.7	5.8	±2.6	23.6	±5.5	10.6	±2.2	2.4	±0.5	11.8	±2.5	3.2	±0.5	0.1	±0.0	7.8	±1.0	0.1	±0.0
Anthemis ruthenica	0.3	±0.2	47.2	±13.2	18.4	±8.2	8.0	±4.2	0.1	±0.1	3.0	±0.3	13.0	±5.6	2.5	±0.7	1.0	±0.3	0.8	±0.6	2.8	±1.0	1.5	±0.6
Apera spica-venti	0.0	±0.0	0.3	±0.2	15.4	±6.5	56.0	±5.8	1.2	±0.3	0.3	±0.1	0.3	±0.1	0.8	±0.3	0.7	±0.6	0.1	±0.1	0.1	±0.1	0.0	±0.0
Bromus tectorum	0.0	±0.0	0.5	±0.3	0.0	±0.0	0.0	±0.0	0.2	±0.1	0.0	±0.0	7.2	±2.4	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Carex stenophylla	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.3	±0.3
Chondrilla juncea	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Conyza canadensis	3.1	±1.1	32.2	±16.8	19.0	±4.4	0.2	±0.1	0.5	±0.3	0.2	±0.0	0.5	±0.1	0.8	±0.3	0.5	±0.3	0.6	±0.4	0.1	±0.1	0.8	±0.3
Cynodon dactylon	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.9	±0.8	1.5	±1.4
Equisetum ramosissimum	0.7	±0.1	0.6	±0.1	1.6	±0.2	1.0	±0.2	1.5	±0.4	1.6	±0.5	0.3	±0.1	2.4	±1.9	0.4	±0.1	4.1	±1.3	1.5	±0.4	1.8	±0.6
Eryngium campestre	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.6	±0.3	1.9	±0.9	1.6	±0.7	2.7	±1.2	3.4	±1.0	3.9	±1.0	7.0	±3.0
Erysimum diffusum	0.0	±0.0	0.0	±0.0	1.6	±0.5	2.7	±1.3	3.5	±2.1	5.4	±1.7	4.1	±0.9	0.2	±0.1	0.0	±0.0	0.0	±0.0	1.9	±0.9	0.9	±0.5
Lepidium densiflorum	0.0	±0.0	0.0	±0.0	0.4	±0.4	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Poa angustifolia	0.0	±0.0	0.2	±0.1	0.2	±0.1	2.2	±0.9	6.4	±2.1	5.2	±1.6	9.8	±2.7	35.0	±8.8	38.0	±9.0	9.0	±1.1	16.6	±2.2	33.4	±4.7
Poa pratensis	0.0	±0.0	0.0	±0.0	0.1	±0.1	1.1	±0.6	0.3	±0.3	0.5	±0.4	0.7	±0.6	1.2	±1.0	0.8	±0.3	0.3	±0.2	0.7	±0.6	0.0	±0.0
Potentilla argentea	0.0	±0.0	0.0	±0.0	0.2	±0.1	0.5	±0.4	0.4	±0.2	0.6	±0.3	1.1	±0.3	3.0	±1.4	3.9	±1.4	9.3	±3.9	9.6	±2.5	11.3	±4.6
Rumex acetosella	2.6	±1.1	7.6	±4.2	0.9	±0.5	1.4	±0.5	0.8	±0.6	0.2	±0.1	6.0	±2.9	19.2	±8.5	11.0	±4.4	0.2	±0.1	2.2	±1.2	4.7	±1.2
Trifolium arvense	0.0	±0.0	0.2	±0.1	0.2	±0.1	7.3	±3.1	4.1	±1.9	0.3	±0.1	20.6	±6.1	0.1	±0.1	43.0	±14.7	0.0	±0.0	19.8	±1.6	0.1	±0.0

Site/year	H2																							
Species	1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
Amaranthus albus	2.7	±0.9	0.1	±0.0	0.1	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Ambrosia artemisiifolia	1.2	±0.7	0.0	±0.0	0.1	±0.1	0.2	±0.1	0.5	±0.4	0.3	±0.2	0.4	±0.3	4.2	±2.4	3.4	±1.9	0.2	±0.1	2.7	±1.2	0.1	±0.1
Anthemis ruthenica	0.1	±0.1	8.4	±1.5	2.3	±0.3	7.2	±2.3	1.8	±1.1	6.8	±1.4	20.6	±2.2	14.4	±2.6	5.3	±1.4	0.0	±0.0	2.4	±1.0	1.7	±0.7
Apera spica-venti	0.0	±0.0	6.2	±1.1	0.0	±0.0	16.8	±3.3	0.4	±0.2	3.6	±0.2	0.1	±0.1	0.2	±0.1	0.4	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Bromus tectorum	0.0	±0.0	47.1	±6.6	0.0	±0.0	0.5	±0.3	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Carex stenophylla	0.7	±0.4	0.3	±0.2	0.6	±0.2	1.6	±0.8	2.5	±1.0	1.8	±0.6	4.8	±1.5	6.8	±1.5	9.4	±5.4	0.8	±0.5	0.2	±0.1	1.7	±1.1
Chondrilla juncea	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.2	±0.1	1.4	±0.3	3.4	±0.7	4.1	±1.0	2.9	±1.1
Conyza canadensis	3.2	±1.0	2.0	±1.1	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.1	±0.0	0.3	±0.1	0.8	±0.2	1.2	±0.3	0.3	±0.2	0.4	±0.2	1.1	±0.4
Cynodon dactylon	4.2	±0.4	0.9	±0.8	5.0	±0.9	21.2	±2.7	36.8	±5.1	21.4	±3.2	23.0	±3.3	29.6	±3.7	28.0	±10.1	28.0	±4.1	25.6	±3.3	31.6	±3.4
Equisetum ramosissimum	0.3	±0.2	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.2	±0.1	0.0	±0.0	0.0	±0.0
Eryngium campestre	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1	1.5	±1.4	0.1	±0.1	0.4	±0.3	0.5	±0.3	0.6	±0.4	0.6	±0.4
Erysimum diffusum	1.4	±0.7	5.1	±1.6	22.6	±4.5	13.0	±2.6	0.5	±0.2	8.8	±0.9	5.8	±0.9	1.4	±0.5	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.1	±0.1
Lepidium densiflorum	0.3	±0.2	2.8	±0.7	1.3	±0.3	0.0	±0.0	0.1	±0.1	0.1	±0.1	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Poa angustifolia	0.7	±0.6	3.0	±1.5	0.0	±0.0	0.6	±0.4	4.4	±1.8	5.0	±1.6	3.8	±0.8	7.4	±2.2	14.2	±4.6	22.0	±4.8	19.6	±3.7	22.2	±3.9
Poa pratensis	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	1.0	±1.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Potentilla argentea	0.0	±0.0	0.1	±0.1	0.1	±0.1	0.7	±0.6	0.1	±0.1	0.0	±0.0	0.8	±0.6	0.7	±0.6	0.5	±0.1	2.3	±0.4	3.2	±1.0	1.4	±0.5
Rumex acetosella	0.0	±0.0	0.0	±0.0	0.2	±0.1	8.8	±1.7	10.4	±2.2	5.8	±1.6	11.4	±1.6	0.4	±0.3	3.4	±1.1	10.4	±3.2	11.6	±1.6	7.9	±2.4
Trifolium arvense	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0

Site/year	L1																							
Species	1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
Amaranthus albus	25.2	±8.6	0.1	±0.1	1.0	±0.5	0.0	±0.0	0.2	±0.2	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Ambrosia artemisiifolia	0.1	±0.1	0.1	±0.1	0.0	±0.0	0.3	±0.2	0.2	±0.2	0.5	±0.3	0.3	±0.1	0.2	±0.1	0.3	±0.1	0.0	±0.0	0.2	±0.1	0.0	±0.0
Anthemis ruthenica	0.1	±0.1	7.6	±0.6	7.2	±0.6	1.5	±0.5	0.1	±0.1	1.9	±0.3	7.8	±1.7	0.2	±0.2	0.4	±0.1	0.0	±0.0	0.8	±0.6	0.2	±0.1
Apera spica-venti	0.0	±0.0	3.1	±0.7	28.8	±1.7	8.6	±1.6	0.1	±0.1	0.8	±0.4	1.0	±0.7	3.1	±3.0	0.8	±0.6	0.0	±0.0	0.2	±0.1	0.1	±0.1
Bromus tectorum	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.3	±0.1	0.0	±0.0	5.6	±1.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Carex stenophylla	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Chondrilla juncea	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.3	±0.2	0.2	±0.1	0.2	±0.2	0.3	±0.2	1.0	±0.6	0.9	±0.8	0.3	±0.3
Conyza canadensis	0.1	±0.1	49.8	±2.8	3.8	±0.7	1.3	±0.9	0.2	±0.1	0.2	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.2	±0.1
Cynodon dactylon	2.4	±0.8	1.5	±0.7	4.3	±1.6	14.9	±6.3	29.8	±10.4	14.2	±3.8	32.0	±5.4	25.0	±2.5	61.0	±4.9	35.0	±1.8	42.6	±2.2	42.2	±2.8
Equisetum ramosissimum	0.2	±0.1	0.1	±0.0	0.6	±0.3	0.0	±0.0	0.0	±0.0	0.2	±0.1	0.1	±0.1	0.0	±0.0	0.1	±0.1	0.7	±0.3	0.1	±0.1	0.1	±0.1
Eryngium campestre	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Erysimum diffusum	0.0	±0.0	0.2	±0.1	0.0	±0.0	3.6	±1.3	0.2	±0.2	0.7	±0.4	3.3	±1.6	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1	0.1	±0.1
Lepidium densiflorum	0.0	±0.0	0.1	±0.1	0.8	±0.3	0.0	±0.0	0.0	±0.0	0.4	±0.2	0.4	±0.4	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1
Poa angustifolia	0.0	±0.0	0.0	±0.0	3.3	±1.0	31.0	±6.8	35.0	±10.9	9.6	±2.8	21.0	±4.2	48.4	±15.8	29.0	±2.3	23.0	±1.9	33.8	±3.9	31.2	±2.1
Poa pratensis	0.0	±0.0	0.7	±0.2	0.2	±0.2	4.4	±2.3	0.0	±0.0	0.2	±0.1	0.8	±0.8	0.2	±0.2	0.6	±0.6	0.0	±0.0	0.0	±0.0	0.0	±0.0
Potentilla argentea	0.0	±0.0	0.4	±0.4	0.3	±0.3	1.5	±1.4	0.2	±0.2	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.2	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0
Rumex acetosella	0.0	±0.0	1.2	±0.7	0.0	±0.0	1.5	±0.6	0.0	±0.0	0.1	±0.1	4.3	±2.2	4.1	±2.5	2.7	±1.7	0.0	±0.0	0.0	±0.0	0.4	±0.3
Trifolium arvense	0.0	±0.0	0.1	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0

Site/year	L2																							
Species	1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
Amaranthus albus	0.5	±0.2	0.1	±0.0	0.1	±0.0	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Ambrosia artemisiifolia	0.2	±0.2	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Anthemis ruthenica	0.0	±0.0	0.4	±0.4	0.5	±0.4	0.3	±0.2	2.1	±0.9	1.0	±0.4	4.0	±1.2	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0
Apera spica-venti	0.0	±0.0	0.2	±0.1	0.1	±0.1	6.6	±2.7	15.4	±2.1	3.4	±0.8	2.5	±0.6	5.8	±1.2	2.9	±0.7	0.0	±0.0	0.0	±0.0	0.0	±0.0
Bromus tectorum	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.6	±0.2	2.9	±1.0	0.0	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Carex stenophylla	2.2	±1.0	0.7	±0.3	0.1	±0.1	1.9	±0.9	1.3	±0.6	0.6	±0.3	2.9	±0.8	6.6	±3.4	4.2	±3.2	0.2	±0.2	0.4	±0.3	0.2	±0.2
Chondrilla juncea	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.4	±0.4	0.0	±0.0	0.6	±0.4	0.7	±0.4	3.6	±1.2	0.8	±0.4	3.7	±1.1	0.5	±0.3	0.2	±0.1
Conyza canadensis	6.0	±1.3	0.4	±0.3	0.8	±0.2	0.1	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.1	±0.1
Cynodon dactylon	6.6	±2.6	4.3	±1.7	9.2	±4.3	21.4	±4.1	37.2	±2.5	38.0	±4.1	39.0	±6.9	54.0	±8.6	61.0	±10.3	54.0	±7.5	45.0	±3.3	48.4	±3.2
Equisetum ramosissimum	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Eryngium campestre	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Erysimum diffusum	1.0	±0.8	37.8	±4.9	19.6	±3.1	26.0	±4.2	2.1	±0.6	9.6	±1.9	0.1	±0.1	0.6	±0.4	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Lepidium densiflorum	0.1	±0.1	11.6	±4.0	16.0	±4.9	3.3	±1.0	1.8	±0.4	0.8	±0.4	0.2	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Poa angustifolia	0.4	±0.3	0.1	±0.1	0.0	±0.0	0.3	±0.2	2.1	±1.1	1.1	±0.6	9.6	±6.4	7.2	±3.2	17.6	±11.0	14.4	±4.8	28.2	±6.8	27.8	±6.6
Poa pratensis	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.4	±0.4	1.4	±0.9	10.8	±5.3	15.0	±6.9	11.0	±6.1	14.4	±6.6	13.0	±5.9	10.9	±6.5
Potentilla argentea	0.2	±0.1	0.3	±0.3	0.8	±0.4	0.9	±0.6	1.4	±0.6	0.7	±0.3	3.9	±1.6	9.0	±3.6	0.7	±0.4	0.8	±0.6	0.4	±0.3	0.0	±0.0
Rumex acetosella	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0
Trifolium arvense	0.1	±0.1	0.0	±0.0	0.1	±0.1	0.5	±0.1	0.2	±0.1	0.1	±0.0	0.1	±0.1	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0	0.0	±0.0