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SUCCESSION, MANAGEMENT AND RESTORATION OF DRY GRASSLANDS

Litter and graminoid biomass accumulation suppresses weedy forbs in grassland restoration

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Abstract

Accumulated biomass of sown species and litter plays an important role in success of restoration projects. We studied the effects of litter and graminoid biomass on species richness and biomass of early colonising forbs in former alfalfa fields sown with seed mixtures containing seeds of native grass species (*Festuca pseudovina*, *Festuca rupicola*, *Poa angustifolia*, *Bromus inermis*, 2005). The amount of litter, forbs and graminoids was measured in the first 3 years after sowing (2006–2008). Ten aboveground biomass samples (20 cm × 20 cm) per field were collected in June every year. We found significantly lower forb biomass in the second and third year, than in the first year after sowing. Litter and biomass of graminoids increased significantly during the study, and correlated negatively with the biomass and species richness of forbs. Mean scores of litter and graminoid biomass were two to three times higher in sown fields than in native grasslands. Our results suggest that the accumulation of litter and graminoid biomass is beneficial in suppression of weedy forbs, but in the long run it might also hamper the immigration of target species.

Keywords: *Biomass, Hortobágy National Park, species richness, weed control, competition*

Introduction

In many parts of the world, the decreasing rate of crop production favours grassland restoration actions in former croplands (Csecserits & Rédei 2001; Cramer et al. 2008). The major goals in such projects are (i) to suppress early colonising assemblages by late successional ones, (ii) restore native grassland diversity and (iii) restore ecosystem functions (Szentes et al. 2007; Reid et al. 2009; Török et al. 2011a). To meet these goals, it is often necessary to control the biomass production in the recovered grasslands using different management techniques (Házi et al. 2011). Thus, the study of biomass production in native and restored grasslands has become an important research topic in restoration ecology (Bischoff et al. 2005; Guo 2007).

The relation of total aboveground biomass and species richness can be often described by a hump-shaped curve where a negative correlation can be observed if high biomass scores are measured (Grime 1979; Oomes 1992; Guo 2007). Old-fields and restored grasslands can be characterised typically by higher biomass production than natural grasslands (Carson & Barrett 1988) because of a high residual nutrient content that regularly occurs following the termination of crop production (Huston 1999; Csecserits et al. 2011). In turn, high biomass production often results in a high rate of litter accumulation (Odum 1960).

Litter and graminoid biomass play a crucial role in grassland vegetation dynamics (Martin & Wilsey 2006). Increased graminoid biomass and accumulated litter usually inhibits germination (Foster & Gross 1998) by reducing the irradiance of the soil surface (Foster & Gross 1997), forming a physical barrier (Wedin & Tilman 1993), or altering the competitive environment (Kotorova & Lepš 1999; Rotundo & Aguiar 2005). A dense litter layer decreases the average soil temperature and reduces

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the variability of temperature by mitigating extreme fluctuations (Eckstein & Donath 2005), which decreases the germination rate of most forb species (Jutila & Grace 2002; Donath et al. 2006). Furthermore, increased graminoid production and litter reduce the amount of available water for forbs (Haugland & Froud-Williams 1999), although it may also help in preserving soil moisture under arid conditions (Fowler 1988). Nutrients (Facelli & Pickett 1991) and allelopathic compounds can be dissolved from the litter, which negatively affects overall diversity (Bonanomi et al. 2005; Ruprecht et al. 2008). From a conservation standpoint, it is a positive effect that graminoid biomass and litter may suppress the early colonising weedy forbs that are abundant after abandonment.

Here, we study the effects of litter and biomass of sown grasses on species richness and biomass of early colonising weedy forbs in former alfalfa fields sown with low-diversity seed mixtures in NE Hungary. Sowing low-diversity seed mixtures of native, competitive grass species followed by regular mowing is an effective method in grassland restoration because weedy forbs are usually quickly replaced (Lepš et al. 2007, Török et al. 2011b). However, most studies analyse only changes in cover and species richness and changes in biomass are typically neglected. Here, we measured both species richness and biomass of litter, forbs and sown grasses in the first 3 years after sowing and asked the following questions: (i) What is the effect of the accumulating biomass of graminoids and litter on the biomass of early colonisers? (ii) Is the amount of graminoid biomass and litter higher, and the heterogeneity of these scores lower in sown fields than in natural grasslands? (iii) Is the amount of forbs lower in restored fields than in native grasslands?

Materials and methods

Sampling setup

We studied changes in biomass and species richness of 10 former alfalfa fields sown with low diversity alkali (4 fields) and loess (6 fields) seed mixtures. Grassland restoration was a part of a LIFE-Nature project (http://life2004.hnp.hu/index.html) in the 'Egyek-Pusztakócsi mocsarak' marsh and grassland complex in Hortobágy National Park (NE Hungary, N 47° 34′ E 20° 55′). The elevation of the area is between 87 and 98 m a.s.l. The climate is moderately continental, characterised by a mean annual temperature of 9.5°C and a mean annual precipitation of 550 mm. The studied fields have moderately heavy topsoils with a neutral pH and high topsoil fertility. Seed mixtures were sown in a density of 25 kg/ha following soil preparation in October, 2005. Alkali seed mixture contained the seeds of *Festuca pseudovina* and *Poa angustifolia*; while loess seed mixture contained the seeds of *Festuca rupicola*, *Poa angustifolia* and *Bromus inermis*. The fields were mown once in June every year after sowing. For the study, one 5 × 5-m sized sampling plot per field was randomly marked. In each plot, 10 aboveground biomass samples (20 cm × 20 cm sized) were collected randomly in June before mowing, in every year between 2006 and 2008. The species list of forbs in every biomass sample was recorded. Samples were dried (65°C, 24 h), then sorted as litter, graminoid (*Poaceae* and *Cyperaceae*) and forb (non-graminoid monocots and dicots). The forb biomass collected in the sown fields was sorted by species and then grouped into weed and non-weed species groups according to Grime's CSR strategy types (Grime 1979) modified and adapted to Hungarian conditions by Borhidi (1995). The dry weights of the biomass samples were measured with 0.01 g accuracy. The biomass of three reference (restoration target) alkali (*Achilleo setaceae – Festucetum pseudovinae*) and three reference loess (*Salvio nemorosae–Festucetum rupicolae* with *B. inermis* dominance) grasslands was similarly sampled (10 biomass samples per plot, in 2008) as described above.

Data processing

Temporal dynamics of biomass (litter and graminoid biomass) in the sown fields was compared with repeated-measures ANOVA, and Tukey test, averaging the samples from the same field for each year (Zar 1999). The biomass differences in alkali seed mixtures sown fields and reference grasslands, and loess seed mixtures sown fields and reference grasslands, respectively, were analysed using linear mixed-effects model (LMEM) using state (i.e. restored or reference field) as fixed, and field ID as random factor (Zuur et al. 2009). Normality was tested using Kolmogorov–Smirnov test. We calculated the heterogeneity of graminoid biomass and litter using the Gini-coefficient (Zar 1999). Correlation between the litter, graminoid biomass, species richness and biomass of weedy forbs was calculated by Spearman's rank-correlation (for each field separately, Zar 1999). Statistics were calculated using R (R-Development Core Team 2010). Detrended correspondence analysis (DCA) ordination was plotted by CANOCO based on presence–absence datasets of biomass samples pooled for each field and year (ter Braak & Šmilauer 2002).

Results

Temporal change of biomass in sown fields

Total biomass decreased significantly in restored fields from Year 1 to Year 2 regardless of the seed mixture sown (from a mean range of 1459–1480 g/m^2 to 696–789 g/m^2, RM ANOVA, alkali seed mixture: $F_{3,11} = 6.27$, $p = 0.034$, and for the loess seed mixture: $N = 6$, $F_{5,17} = 33.44$, $p < 0.001$, respectively). A significant increase in total biomass was detected between Year 2 and Year 3, but these figures were lower than the scores detected in the first year in both mixtures sown fields.

The biomass of the sown graminoids increased continuously, and the detected scores were typically more than two times higher in Year 3 than in Year 1 (RM ANOVA, alkali seed mixture $F_{3,11} = 10.00$, $p = 0.012$, and loess seed mixture: $F_{5,17} = 7.68$, $p = 0.01$, Figure 1). Total graminoid biomass was highest in Year 3, coinciding with the increase of sown grasses in both types of mixtures (RM ANOVA, alkali: $F_{3,11} = 27.83$, $p < 0.001$; loess: $F_{5,17} = 12.09$, $p = 0.002$, Figure 1).

A significant litter accumulation was observed from Year 1 to Year 2 in every restored field. Litter scores increased by one order of magnitude (RM ANOVA, alkali seed mixture: $F_{3,11} = 8.24$, $p = 0.019$, loess seed mixture: $F_{5,17} = 5.06$, $p = 0.03$; Figure 2). No significant changes were found in litter scores between Year 2 and Year 3, regardless of the seed mixture sown. Forb biomass in Year 1 was dominated by short-lived weeds in every field, regardless of the seed mixture type (mean proportions were 99 % for the alkali and 95 % for the loess seed mixture).

The vegetation in Year 1 was characterised by high biomass and frequency of weedy forbs (Figure 3, Table I). Biomass of forbs (incl. weeds) decreased significantly in every restored field from Year 1 to the Year 2, typically by two orders of magnitude, regardless of seed mixture (RM ANOVA, alkali seed mixture: $F_{3,11} = 9.59$, $p = 0.014$; loess seed mixture $F_{5,17} = 52.93$, $p < 0.001$). Biomass scores of forbs remained low (less than 18 g/m^2 in every sown field) from Year 2 onwards. Coinciding with the decrease of forb biomass, the species numbers of forbs also decreased both in alkali and loess restorations from Year 1 to Year 2, and remained stable and low from Year 2 onwards (RM ANOVA, alkali seed mixture: $F_{3,11} = 151.68$, $p < 0.001$; loess seed mixture: $F_{5,17} = 38.50$, $p < 0.001$). In most fields, graminoid biomass and litter were negatively correlated with forb species richness and biomass. Forb biomass and species richness showed a medium strong negative correlation with graminoid biomass and a strong negative correlation with litter (Table II). The heterogeneity of litter and graminoid biomass was the highest in Year 1, and much lower scores were typical in both type of restorations in the later years (Figures 1 and 2). No significant differences were found between the heterogeneity of litter and graminoid biomass in Year 3 in restorations and in native grasslands.

Sown fields and native grasslands

In Year 3, we observed significantly higher graminoid biomass in alkali restorations compared to

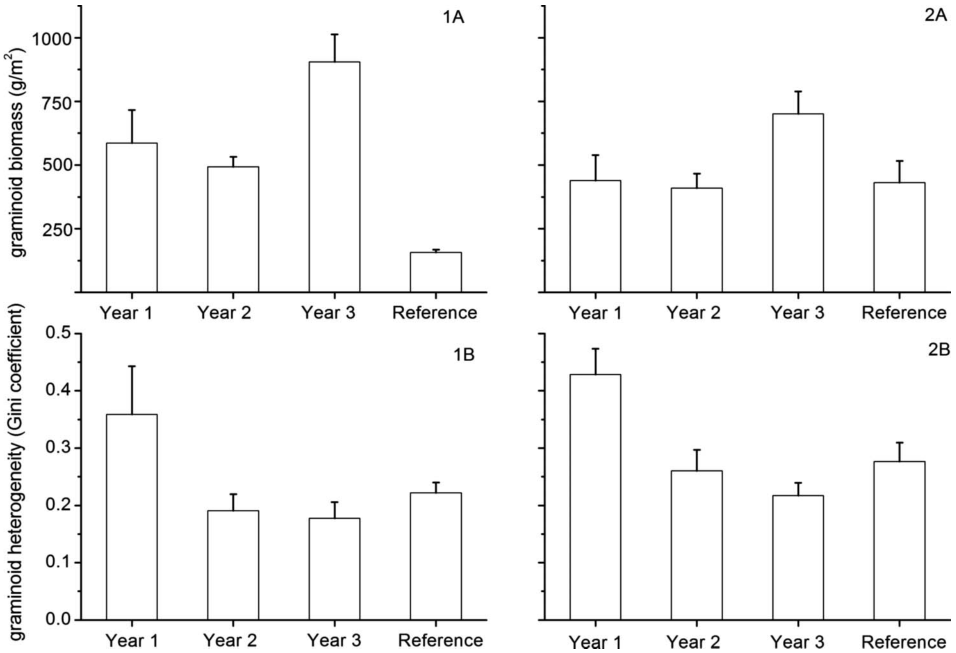

Figure 1. Biomass (A) and biomass heterogeneity (B) scores of graminoids in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean ± SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores for loess native grasslands are shown).

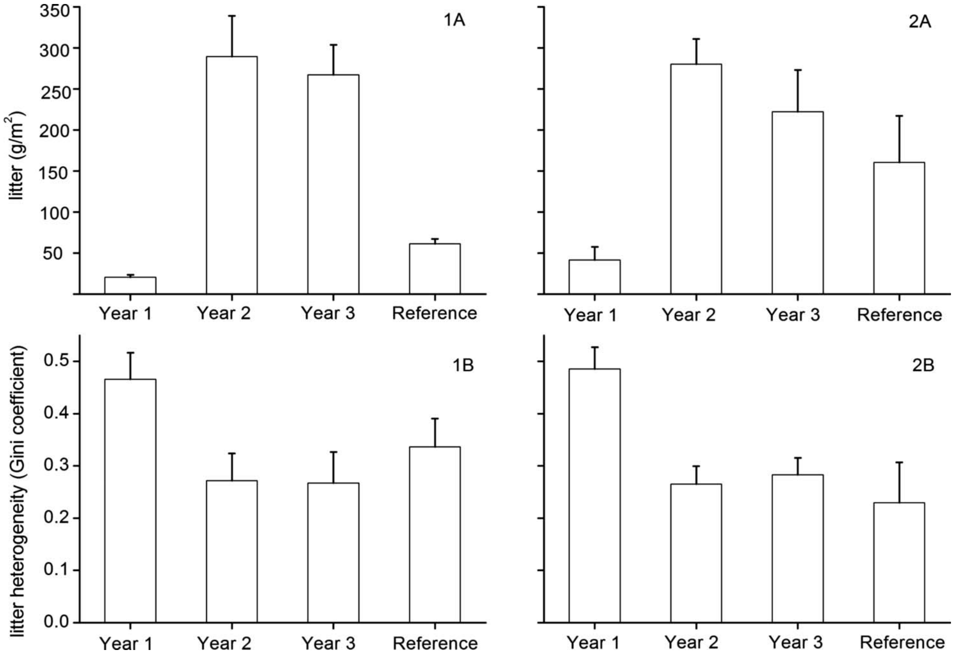

Figure 2. Litter (A) and litter heterogeneity (B) scores for graminoid biomass in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean ± SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores for loess native grasslands are shown).

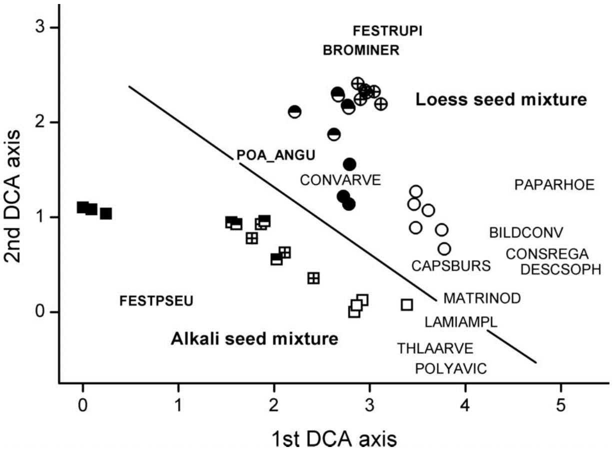

Figure 3. The species composition of biomass in alkali and loess mixtures sown fields and reference grasslands showed using a DCA ordination and presence–absence datasets. Notations: Circle = loess mixtures sown fields and loess reference grasslands, rectangles = alkali mixtures sown fields and alkali reference grasslands. Empty symbols = Year 1, crossed symbols = Year 2, half-empty symbols = Year 3, filled symbols = reference grasslands. Species abbreviations: species names were added using four letters of genus and four letters of species names of **sown grasses** and the most frequent 10 weedy forbs shown also in Table I.

native alkali grasslands (LMEM, $t = 10.32$, $p < 0.001$). The mean scores of graminoid biomass detected in the alkali restorations ranged from 616 to 1112 g/m^2, whereas these scores were much lower in native grasslands (range 140–178 g/m^2). In loess restorations, graminoid biomass scores were also significantly higher than that of the native loess grasslands (range 468–987 g/m^2 and 262–520 g/m^2, respectively; LMEM, $t = 3.58$, $p < 0.001$).

In Year 3, significantly higher litter scores were found in alkali restorations than in native alkali and loess grasslands (LMEM, $p < 0.001$, $t = 7.29$). The detected mean scores of litter were three to five times higher in alkali restorations than in native alkali grasslands (ranges 175–353 in restorations and 51–72 g/m^2 in native grasslands). Also, significant differences were found in the litter scores between loess restorations and native loess grasslands (range 130–466 g/m^2 in restorations and 95–273 g/m^2 in native grasslands, LMEM, $p < 0.002$, $t = 3.16$).

Discussion

Changes in biomass and litter

This study provided three key results. First, we found significantly lower forb biomass in the second and third year, than in the first year after sowing. Second, litter and biomass of graminoids increased significantly during the study, and correlated negatively with the biomass and species richness of forbs. Finally, mean scores of litter and graminoid biomass were two to three times higher in sown fields than in native grasslands.

In our study, the highest total biomass scores were detected in the first year, conversely to Lepš et al. (2007), where an increase of biomass was detected

Table I. The biomass changes of the 10 most frequent weedy forbs in alkali (A1–A4) and loess seed mixtures (L1–L6) sown fields from Years 1–3 (mean, g/m^2).

		A1			A2			A3			A4			L1			L2			L3			L4			L5			L6		
	LF	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3
Matricaria inodora	S	501			1267			286			408			925			1332			516			379				3		1174	5	3
Capsella bursa-pastoris	S	180	7	3	7	4		8			9	3		11			48			61			35			497	3		15		
Polygonum aviculare	S	265	3		170			42	3		29			3			26			21			94			4			71		
Thlaspi arvense	S	180									3								3							46					
Descurainia sophia	S	52																								117					
Chenopodium album	S	3						3	3		3						3			16			4			18	3		46		
Convolvulus arvensis	P			3			2		3	3		3									3	7	6			2	3	5	3	4	40
Papaver rhoeas	S																						2						49		
Consolida regalis	S	3																		9			21								
Lamium amplexicaule	S	5			3						2						5			3			3			2			7		3

LF = life form type, S = short-lived, P = perennial.

Table II. Correlation coefficients (*r*) between species richness and biomass of herbaceous group and the amount of litter and sown grass biomass by Spearman non-parametric rank correlation.

	Field codes	SGB	Litter
Forb biomass	AM1	−0.62***	−0.75***
	AM2	−0.51**	−0.65**
	AM3	−0.43*	−0.64***
	AM4	−0.17	−0.63***
	LM1	0.17	−0.45*
	LM2	−0.66***	−0.84***
	LM3	−0.18	−0.64***
	LM4	−0.32	−0.56**
	LM5	−0.37*	−0.66***
	LM6	−0.41*	−0.59***
Forb species richness	AM1	−0.71***	−0.80***
	AM2	−0.47**	−0.67***
	AM3	−0.37*	−0.71***
	AM4	−0.17	−0.67***
	LM1	0.31	−0.37
	LM2	−0.67***	−0.85***
	LM3	−0.12	−0.65***
	LM4	−0.35	−0.55**
	LM5	−0.38*	−0.57**
	LM6	−0.53**	−0.57**

Notations: SGB = sown graminoid biomass; significance codes: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, no mark – not significant, $N = 12$; four plots per field and 3 years. Field abbreviations: AM1-4, Alkali seed mixture restored fields; LM1-6, Loess seed mixtures restored fields.

after sowing from the first year to the second. In a study by Lepš et al. (2007), the mean total biomass scores were at 300 g/m^2 in the first year; these scores increased in the second year to 430–720 g/m^2 depending on the used mixture and/or management. In our study, the first year's scores were at least four times higher than in the mentioned study (up to 1480 g/m^2). This difference was caused by the rapid development of weedy forb-dominance in the first year detected in our study. In the second year, similar scores were also typical in our study, which suggested that the rate of suppression was poorly correlated with the first year biomass.

Similarly to our study, a rapid increase in cover and richness of sown late-successional species was detected in former studies of grassland restoration using seed sowing (Pywell et al. 2002; Foster et al. 2007; Lepš et al. 2007). Our results confirmed that this increase of sown species holds also for the increase of their biomass. We detected a rapid accumulation of graminoid biomass and litter in the first 3 years of grassland restoration. Such a rapid increase of late-successional species was not detected in studies concerning spontaneous succession in old fields (Prach & Pyšek 2001; Bartha et al. 2003; Ruprecht 2006; Csecserits et al. 2007). The detected rapid biomass increase also supports the theory that the speed and success of grassland recovery is likely limited by diaspore availability of grassland species. Seed sowing is suggested to overcome the diaspore limitation (Pywell et al. 2002; Donath et al. 2003) and is recommended for directing vegetation changes if necessary (Lepš et al. 2007). Despite of the regular yearly mowing, we detected a litter accumulation between the first and second year. The litter scores increased from 21–42 g/m^2 to 280–290 g/m^2 in the Year 1 to Year 2, respectively. The detected litter scores in the second year are in line with former findings where litter scores up to 700 g/m^2 were found in abandoned and sown fields (Touzard et al. 2002; Foster et al. 2007). The litter accumulation was positively correlated with the increase of graminoid biomass production of sown grasses. The litter accumulation was probably caused by the decay of secondary sprouting of mown graminoids. This is well in accordance with Hrevušová et al. (2009), where almost the same amount of biomass was harvested during the first and second cut in fertilised nutrient-rich grasslands. Further, long-term monitoring of changes after restoration is necessary to explore sophisticated details of the processes in biomass changes (Virágh et al. 2008). We found a strong negative correlation between litter and forbs (both biomass and richness). These results support the findings of Eckstein & Donath (2005), where suppressive effect of litter was confirmed in recovered grassland, if the amount of litter exceeds 200 g/m^2.

Implications for restoration

One of the research hypotheses was that the evenness and amount of graminoids and litter is higher in sown grasslands than in native grasslands. This was only partly supported by our findings. Much higher litter and graminoid biomass was detected in restored fields than in native grasslands, but the evenness of both scores was similar in restored and native grasslands. The detected scores of litter and graminoid biomass in Year 3 were higher than scores in native grasslands. The detected litter (Year 3: 130–466 g/m^2) and graminoid biomass scores (Year 3: 701–905 g/m^2) were also higher than scores detected in a grassland recovery in variously aged extensively managed alfalfa fields in this region (up to 165 g/m^2 litter and up to 253 g/m^2 graminoid biomass in one to 10 years old fields, Török et al. 2011a). This higher biomass and litter production was probably supported by the residual surplus of soil nutrients typical after the termination of agricultural cultivation, found also in our region and other studies of grassland restoration (Pywell et al. 2002; Foster et al. 2007; Török et al. 2010). This increased level of biomass production is beneficial for the suppression of early weedy forbs found in the present study and also suggested by others (Lepš et al. 2007). However, the increased levels of litter and graminoid biomass can also hamper the establishment of several characteristic grassland species by (i) competitive exclusion (Foster & Tilman 2000; Anderson 2007) and/or by (ii) decreasing gap availability (Facelli & Pickett 1991; Ruprecht et al. 2010). To facilitate the development of a natural species composition typical in target native grasslands, the reduction of litter and graminoid biomass may be necessary. Several studies suggested that the recovery of low levels of nutrients characteristic to native grasslands in restoration sites can last several decades (Knops & Tilman 2000; Foster et al. 2007, Hrevušová et al. 2009). Our results indicate that a higher biomass production can be foreseen in restored than in reference grasslands. The total biomass scores of restored grasslands exceeded 700 g/m^2 in most of the sites every studied year. These biomass scores are very similar to scores sampled in high productive fertilised meadows (Hrevušová et al. 2009), improved calcareous grasslands (Bonanomi et al. 2009), and fen-meadows (Török et al. 2009); but lower than sampled in reference grasslands in this study and in other alkali grasslands in Hungary (Tasi et al. 2009). Therefore, introducing traditional levels of management characteristic to native alkali and loess grasslands may not be the most appropriate option to decrease biomass in sites with improved productivity (e.g. mowing once a year, or low intensity grazing, Török et al. 2010). Reintroduction of the traditional management with increased frequency and/or intensity can be the proper management option (e.g. mown twice a year, high intensity grazing by cattle and/or sheep). However, it may suitable if only low intensity management is applied in the first several years because of the seed bank weeds (Renne & Tracy 2007).

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