

Lucerne-dominated fields recover native grass diversity without intensive management actions

Péter Török^{1*}, András Kelemen¹, Orsolya Valkó¹, Balázs Deák², Balázs Lukács² and Béla Tóthmérész¹

¹Department of Ecology, University of Debrecen, PO Box 71, H-4010 Debrecen, Hungary; and ²Hortobágy National Park Directorate, Sumen út 2, H-4024 Debrecen, Hungary

Summary

1. Spontaneous succession is often underappreciated in restoration after the cessation of intensive agricultural management. Spontaneous succession could improve the success of restoration programmes, and offers a cost-effective option with little active intervention.

2. We studied the spontaneous recovery of loess grasslands in extensively managed lucerne *Medicago sativa* fields mown twice a year using space for time substitutions to highlight the importance of spontaneous processes in grassland restoration.

3. With increasing field age a gradual replacement of lucerne by perennial native grasses and forbs and increase of mean species richness was detected. As the age of fields increased, lucerne decreased from 75% to 2% of total vegetation cover, whereas perennial graminoids increased from 0.5 to 50% cover. Mean total cover showed no significant differences between the age groups; weed cover was less than 10%.

4. The phytomass of lucerne was negatively correlated with graminoid phytomass. As the age of the fields increased, lucerne phytomass decreased and grass phytomass increased. We found a negative correlation between litter and forb phytomass but there was no relationship with the age of the field. There was no litter accumulation and no increase of mean total phytomass as the age of fields increased.

5. *Synthesis and applications.* Native grasses within loess grasslands recovered within 10 years, but characteristic native forbs remained rare. The advantages of spontaneous succession in lucerne fields compared to technical reclamation include: (i) no early stages dominated by weeds, (ii) minimal litter accumulation, (iii) a spontaneous decrease in lucerne over time, and (iv) negligible cost. In addition, the requirement for twice yearly mowing in the early years will guarantee farmer involvement because of the high forage value of lucerne. The complete restoration of species rich grasslands will require more active management such as propagule transfer by hay and/or moderate grazing to encourage the return of native forbs.

Key-words: alfalfa, *Medicago sativa*, old field, phytomass, space for time substitution, succession, weed control

Introduction

The aim of grassland restoration is to recover and/or improve grassland biodiversity and ecosystem functions (Firn 2007; Reid *et al.* 2009). Two contrasting approaches are used most often: technical reclamation or spontaneous succession (Prach & Hobbs 2008). Both methods are generally followed up by site management for weed suppression using techniques such as mowing and/or grazing (Warren, Christal & Wilson 2002; Lepš *et al.* 2007; Kiehl *et al.* 2010). Recovery

can be accelerated and directed by *technical reclamation* methods. In most cases this means adding seeds of desirable species using hay transfer or seed sowing (Pywell *et al.* 2002; Hölzel & Otte 2003). An alternative approach is *spontaneous succession*, where seeds are not added and the system is left to recover naturally (Prach & Pyšek 2001). Technical reclamation is preferred worldwide despite several promising examples of spontaneous recovery of grasslands (e.g. Ruprecht 2006; Prach & Rehouksová 2008). This is especially true when there is an urgent need to heal landscape scars, prevent erosion or suppress weeds (Török *et al.* 2010; Tropek *et al.* 2010).

*Correspondence author. E-mail: molinia@gmail.com

Recently, there have been attempts to link theories of spontaneous succession with direct restoration efforts to mitigate costs and improve the success of restoration (del Moral, Walker & Bakker 2007; Walker, Walker & del Moral 2007). For example, patterns in vegetation dynamics could be used to judge whether or not invasive weed cover will develop rapidly after agriculture ceases or to judge whether active intervention is necessary to eliminate former crops. Spontaneous succession has several advantages over technical reclamation. (i) The natural value of spontaneously regenerated sites is often higher than that of reclaimed ones (Hodačová & Prach 2003). (ii) Spontaneously colonising species are expected to be better adapted to local conditions than species originating from commercial sources or non-local sites (Mijnsbrugge, Bischoff & Smith 2010). (iii) Increased vegetation patchiness at spontaneously regenerated sites provides improved refuges for animals compared to technical reclamation sites (Tropek *et al.* 2010). Finally, (iv) spontaneous succession offers cost-effective restoration with a low rate of active intervention (Prach & Hobbs 2008).

Spontaneous succession also has some drawbacks compared to technical reclamation, concerning (i) the low level of predictability and control of initial vegetation composition, density and pattern, and (ii) the relatively slow development of vegetation towards the target state, especially where proper donor sites for colonisation are missing (Ruprecht 2006; Prach & Hobbs 2008). However, the value of spontaneous succession in restoration programmes is becoming more widely appreciated, which underlines the importance of reporting relevant case (Prach & Pyšek 2001; Prach, Pyšek & Bastl 2001).

There is large scale abandonment in rural areas where productivity is low in Central- and Eastern Europe (Jongepierová, Míthley & Tzanopoulos 2007; Török *et al.* 2010). After the collapse of state owned agricultural cooperatives, the socio-economical changes resulted in large scale abandonment of croplands (Prach, Lepš & Rejmánek 2007; Pullin *et al.* 2009). Between 1990 and 2004, 600 000 ha of croplands have been abandoned in Hungary (Hobbs & Cramer 2007). This has provided an opportunity to use these areas to restore grasslands and improve their continuity for nature conservation (Stevenson, Bullock & Ward 1995; Simmering, Waldhardt & Otte 2006; Lindborg *et al.* 2008).

Most studies reporting spontaneous succession have focused on abandoned fields formerly cultivated with annual crops or the previous history of the site (e.g. last crop) has been ignored (Csecserits & Rédei 2001; Ruprecht 2006). Generally in these studies, weedy short-lived species are found to dominate in the first years after abandonment (Blumenthal, Jordan & Svenson 2005; Prach, Lepš & Rejmánek 2007). Weed dominance is generally associated with high levels of soil nutrients, which can be difficult and costly to control (Blumenthal, Jordan & Svenson 2003). The dominance of early colonising weedy species can also slow down the regeneration of native vegetation for many years (Collins, Wein & Philippi 2001; Prach & Pyšek 2001). Secondary succession after intensive cultivation of perennial crops has not previously been studied.

One of the most important perennial crops worldwide is lucerne *Medicago sativa* L. Lucerne is often used as silage or hay for cattle forage (Horrocks & Valentine 1999; Li, Xu & Wang 2008). In Hungary more than 130 000 ha of croplands were sown with lucerne although intensity of use has decreased in recent years (2004–2008; K.S.H. 2008). We studied the regeneration of loess grasslands in extensively managed (mown twice a year) lucerne fields using space for time substitutions. We addressed the following questions: (i) How effective is lucerne in weed control? (ii) How quickly does lucerne disappear? (iii) How fast does grassland recover in extensively managed lucerne fields? The overall aim of this study was to examine the value of spontaneous succession in the restoration of grasslands in former lucerne fields as a cost-effective strategy for grassland conservation.

Materials and methods

STUDY AREA

The study area is located in the Hortobágy Puszta (Hortobágy National Park), in East-Hungary. Hortobágy Puszta with an area of 85 000 ha is one of the largest grassland ecosystems in Europe, with vegetation characteristic of alkali and loess grasslands. The climate is moderately continental with a mean annual temperature of 9.5 °C. Mean annual precipitation is about 550 mm. The yearly maximum precipitation falls in June (mean 80 mm) with high year-to-year fluctuations (Pécsi 1989). Historically, loess grassland vegetation (*Festucion rupicolae*) covered the highest elevations in the region (Borhidi 2003). At the lower elevations, loess grasslands were surrounded by dry alkali short grasslands (*Festucion pseudovinae*), alkali wet meadow (*Alopecurion pratensis*) and alkali marsh vegetation (*Bolboschoenetalia maritimi*) (for more details see Molnár *et al.* 2008; Molnár & Borhidi 2003). The loess grasslands have been ploughed up in the last centuries and many of the remaining fragments are degraded by moderate or heavy grazing by cattle and/or sheep. The most degraded loess pastures (*Cynodonti-Poëtum angustifoliae*) are characterised by a high cover of grazing tolerant graminoids [*Cynodon dactylon* (L.) Pers., *Poa angustifolia* L., *Festuca pseudovina* Hack. ex Wiesb., *Festuca rupicola* Heuff. and *Carex stenophylla* Wahlbg.] and forbs [*Galium verum* L., *Euphorbia cyparissias* L., *Cruciata pedemontana* (Bell) Ehrend., *Myosotis stricta* Link, *Achillea collina* L., and *Convolvulus arvensis* L.]. At heavily grazed sites, thistles dominate (*Ononis spinosa* L., *Eryngium campestre* L.). Only small patches of less degraded loess steppe grasslands (*Salvia nemorosae-Festucetum rupicolae*) have remained. The characteristic graminoids for these grasslands are *Festuca rupicola*, *Bromus inermis* Leyss, *Koeleria cristata* (L.) Pers., *Stipa capillata* L., *Alopecurus pratensis* L., and *Poa angustifolia*. They are rich in perennial forb species, and harbour several characteristic loess specialist species (*Salvia nemorosa* L., *Salvia austriaca* Jacq., *Phlomis tuberosa* L., *Thalictrum minus* L., *Thymus glabrescens* Willd.).

In the study region lucerne or alfalfa *Medicago sativa* L. is sown after deep ploughing at the high elevations formerly covered by loess grasslands. Seed sowing density is typically 30 kg ha⁻¹. There are intensively and extensively managed lucerne fields. Intensive management means regular mowing associated with the application of fertilisers and pesticides. After 3 years intensively managed field are re-sown or shallow disked. Extensive management means only regular mowing twice a year. Every year 10–50 ha intensively managed

lucerne fields were replaced by extensively managed ones in the Hortobágy National Park.

SAMPLING

The vegetation of 1-, 3-, 5- and 10-year-old extensively managed lucerne fields (three fields in each age group) was monitored in 2009. The study fields were situated on loess plateaux between 87 and 94 m a.s.l., within a 50 km radius, in the vicinity of the villages of Egyek, Tiszacsege, Karcag and Nádudvar (N47 26'; E21 01'). None of the study fields were directly connected to loess grasslands, which was the most common vegetation at this elevation in the region (Török *et al.* 2010). The fields were mown twice a year but no further management was applied. Small patches of loess grasslands and, at lower elevations, alkali marshes, alkali wet meadows and alkali short grasslands were present in close proximity to most of the fields. In each field three 25-m² sample blocks were chosen randomly. Within each block, the cover of vascular plants was recorded in four 1 m² plots in early June, before the first mowing. In addition, within each block and near to the plots (< 1 m), 10 aboveground phytomass samples were collected (in total 30 per field, 20 × 20 cm, total aboveground green phytomass and litter).

We recorded the vegetation of three variously degraded stands of loess grasslands (*Festucion rupicolae*) for base-line vegetation reference: (i) a formerly heavy grazed *Cynodonti-Poëtum* stand, (ii) a species rich loess balk stand with *Bromus inermis* dominance, and (iii) a regularly mown species rich stand of *Salvio nemorosae-Festucetum rupicolae* grassland (for detailed species lists see Appendix S1 Supporting Information). We used the same sampling design as described above. Phytomass samples were dried (65 °C, 24 h), then sorted to litter, graminoids (Poaceae and Cyperaceae), lucerne and forbs. Dry weights were measured in a laboratory with an accuracy of 0.01 g.

DATA ANALYSIS

We classified the species into four functional groups using life-form (based on Raunkiaer's life form system, Raunkiaer 1934) and morphological categories (grasses and forbs). These were perennial graminoids, perennial forbs, short-lived graminoids, and short-lived forbs. Annuals and biennials are short-lived, and geophytes, hemikryptophytes, and chamaephytes are perennials. The functional groups of the weed species were classified using Grime C-S-R strategy types

(Grime 1979) which was modified and adapted to local conditions by Borhidi (1995). The cover, species richness and phytomass data of the differently aged fields were compared using General Linear Mixed-Effect Models (GLMM) and Tukey test (Zuur *et al.* 2009). Field age (time) was included as a fixed effect and field/block structure as a random effect. To analyse correlations between the different phytomass groups and sites we used DCA ordination, with square root transformed datasets. DCA was calculated by CANOCO 4.5 (ter Braak & Šmilauer 2002). We used cover based Shannon diversity to characterise vegetation diversity, and Sørensen dissimilarity for vegetation changes. Characteristic species of differently aged lucerne fields and reference grasslands were identified by the IndVal procedure (Dufrene & Legendre 1997); during the calculations 10 000 random permutations were used. The IndVal procedure was executed by a revised version of the R code published as the electronic appendix of Bakker (2008). To explore similarities between restored and reference sites, we used NMDS ordination with Bray-Curtis similarity (Legendre & Legendre 1998). Other statistical analyses were performed using the R statistical environment (version 2.11.1, R Development Core Team 2010). Nomenclature follows Borhidi (2003) for syntaxa, and Simon (2000) for taxa.

Results

VEGETATION AND PHYTOMASS

The vegetation of 1- and 3-year-old lucerne fields was characterized by the high cover of lucerne. Several weed species were present; their mean cover was less than 5% (e.g. *Conyza canadensis* (L.) Cronq., *Lamium amplexicaule* L., *Polygonum aviculare* L., *Stellaria media* (L.) Vill., see Appendix S1 in Supporting Information). The mean cover of lucerne decreased from 75.2 to 2.2% with increasing field age. In the vegetation of 5-year-old fields the cover of lucerne was lower than 50% in all studied plots; moreover in one of the 10-year-old fields no lucerne cover was detected. Conversely, the mean cover of perennial graminoids increased from 0.5 to 50.2% parallel with increasing field age (GLMM, $P < 0.001$, d.f. = 134, $t = 14.30$; Table 1). The mean total cover of differently aged lucerne fields fluctuated between 77.6 and 86.1% (Table 1). Altogether 104 vascular plant species were recorded in the

Table 1. Cover, species richness and Shannon diversity scores of functional species groups

	Age of lucerne fields			
	1-year-old	3-year-old	5-year-old	10-year-old
Cover (%), mean ± SE)				
Total	85.4 ± 0.4	85.8 ± 4.7	86.1 ± 12.9	77.6 ± 12.6
<i>Medicago sativa</i>	75.2 ± 1.1 ^a	72.8 ± 11.0 ^a	24.1 ± 4.9 ^b	2.3 ± 2.3 ^c
Perennial forbs (excl. <i>M. sativa</i>)	0.7 ± 0.2 ^a	6.5 ± 4.5 ^b	10.7 ± 2.7 ^b	16.3 ± 2.2 ^c
Perennial graminoids	0.5 ± 0.2 ^a	0.9 ± 0.1 ^a	29.8 ± 14.1 ^b	50.2 ± 15.0 ^c
Short-lived forbs	8.9 ± 1.6	5.4 ± 2.2	10.6 ± 7.6	6.2 ± 0.5
Short-lived graminoids	0.1 ± 0.1 ^a	0.2 ± 0.1 ^a	11.0 ± 3.9 ^b	2.6 ± 1.5 ^a
Species richness (mean ± SE)				
Perennial species	2.4 ± 0.2 ^a	3.3 ± 0.4 ^a	6.0 ± 1.1 ^b	5.8 ± 0.4 ^b
Short-lived species	6.1 ± 0.7 ^a	5.2 ± 1.6 ^a	8.7 ± 2.1 ^b	8.1 ± 1.0 ^b
Shannon diversity	0.5 ± 0.1 ^a	0.6 ± 0.3 ^a	1.6 ± 0.2 ^b	1.5 ± 0.2 ^b

Different superscripted letters indicate significant differences tested with General Linear Mixed-Effect Models and Tukey test ($P < 0.05$)

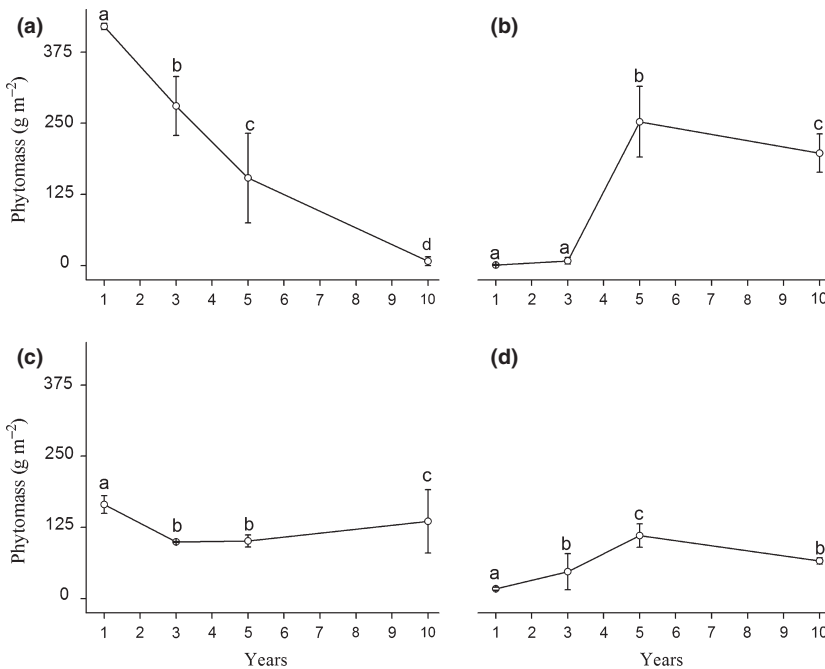


Fig. 1. Phytomass scores of *Medicago sativa* and three functional groups in different aged lucerne fields. Notations: a = *Medicago sativa*, b = graminoids, c = litter, d = other forbs. Different letters indicate significant differences within a phytomass group between years (General Linear Mixed-Effect Models and Tukey test, $P < 0.05$; tests were executed on 20×20 cm samples).

vegetation of the studied lucerne fields. The mean total species richness (from 8.5 to 13.9–14.7), the mean species richness of perennials (from 2.4 to 5.8–6.0), and the mean Shannon diversity scores (from 0.5 to 1.5–1.6) were increased with field age (GLMM, $P < 0.001$, d.f. = 134, $t = 11.04$ and 11.17 , respectively; Table 1).

No significant differences were found between the total phytomass of differently aged lucerne fields (means ranged between 286 and 689 g m^{-2}). As for cover, the phytomass of lucerne decreased with increasing field age (GLMM, $P < 0.001$, d.f. = 350, $t = 17.17$). The phytomass of graminoids was highest in the 5- and 10-year-old fields (Fig. 1). A negative correlation was detected between the phytomass of lucerne and that of graminoids. Litter and forb phytomass were also negatively correlated, but no clear temporal trend was detected. A decreasing lucerne phytomass and an increasing grass phytomass were detected with increasing field age (Fig. 2).

LUCERNE FIELDS AND REFERENCE GRASSLANDS

Characteristic grass species for reference grasslands (e.g. *Festuca rupicola* and *Bromus inermis*) were found at low levels of cover in 5- and 10-year-old lucerne fields. Conversely, some common grasses were dominant (e.g. *Festuca pseudovina*, *Poa angustifolia*, *Agropyron intermedium* (Host) P.B., *Alopecurus pratensis*; see Appendix S1). Decreasing mean dissimilarity of species composition was detected with increasing field age (from a mean of 0.96 in 1-year-old fields to a mean of 0.76 in 10-year-old fields). Characteristic forb species of native loess grasslands were only present in 5- and 10-year-old lucerne fields (e.g. *Vicia hirsuta* (L.) S.F., *V. angustifolia* L., *Galium verum*, *Medicago minima* (L.) Grufbg., *Trifolium angulatum* W. et Kit., *T. retusum* Höjer, *Lathyrus tuberosus* L.). Several other characteristic perennial forbs were not detected even in the

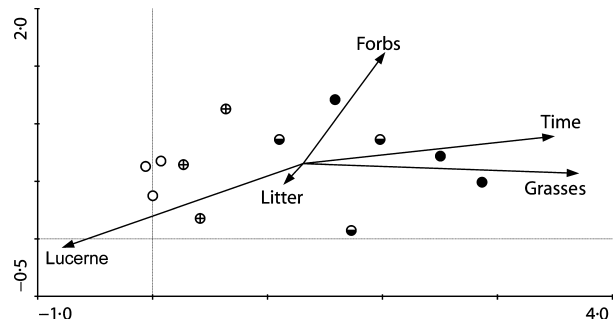


Fig. 2. The relationship between the various phytomass fractions and time using DCA. The points (main data) were based on mean species percentage cover. All data were pooled at the field's level. Notations for the lucerne fields: 1-year-old – ○; 3-year-old – ⊕; 5-year-old – ●; 10-year-old – ●. Notations for the background variables (arrows): Lucerne = phytomass of alfalfa; Forbs = forb phytomass; Grasses = graminoid phytomass, Time = field age; Litter = litter phytomass. Eigenvalues are 0.52 and 0.08 for axis 1 and 2, respectively.

vegetation of 10-year-old lucerne fields (e.g. *Ajuga genevensis* L., *Salvia nemorosa*, *S. austriaca*, *Pimpinella saxifraga* L., *Thymus degenianus* Lyka, *Euphorbia cyparissias*, *Veronica prostrata* L.; see Appendix S1). Several disturbance tolerant and weedy perennial forbs were more frequent in the lucerne fields than in reference grasslands (e.g. *Cirsium arvense* (L.) Scop., *Convolvulus arvensis*, *Taraxacum officinale* Weber ex Wiggers). Species composition in the lucerne fields showed a clear shift along the first axis in the NMDS ordination (Fig. 3). Time is represented by the first axis, and the age groups are separated along it. The vegetation of the 1 and 3-year-old fields showed low variability, while the variability of plots of the older fields was much higher (Fig. 3). The vegetation of the 10-year-old fields showed the most similarity with the vegetation of reference grasslands.

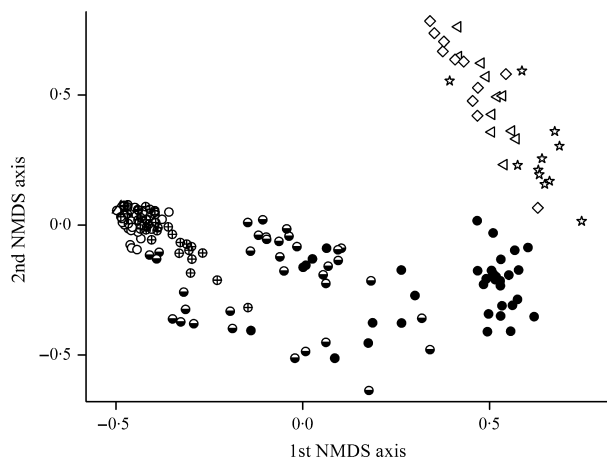


Fig. 3. Vegetation composition of different aged lucerne fields and reference grasslands. Ordination plot was based on percentage cover data of the sample plots using NMDS ordination and Bray–Curtis similarity (Stress = 15.91). Lucerne fields: 1-year-old – ○; 3-year-old – □; 5-year-old – ●; 10-year-old – ●; Species poor Cynodonti-Poëtum loess grassland – ◇; Loess balk with high cover of *Bromus inermis* – ☆; Species rich Salvia-Festucetum loess grassland – ★.

Discussion

WEED CONTROL

Previous studies have reported high weed cover after abandonment of intensively managed crop fields, e.g. weed cover of 5–40% for sandy fields abandoned for 1–10 years (Central-Hungary; Csécsécsérts & Rédei 2001; Csécsécsérts *et al.* 2007), and 10–60% for 1- to 12-year-old abandoned loess fields (Ruprecht 2005, 2006). Low weed cover was found after abandonment only where crop production lasted just a few years, and no mineral fertilizers had been applied (e.g. Jongepierová, Jongepier & Klimes 2004). It has been suggested that the rapid development of weed cover can be avoided by sowing mixtures of seeds of characteristic late successional species (Prach & Pyšek 2001; Pywell *et al.* 2002; Warren, Christal & Wilson 2002) or cover crop grasses (Hansson & Fogelfors 1998).

In our study weedy species did not dominate in the early years. The total cover of weeds was low at less than 5% cover, regardless of the age of the fields. Our results support the findings of Li, Xu & Wang (2008), where lucerne and other legume species were found to aid in suppressing weeds. It is well known that seeds of weed species are present in the soils of croplands in high density (Hutchings & Booth 1996; Manchester *et al.* 1999). Török *et al.* (2010) detected a high cover of short-lived weeds after ploughing and sowing of perennial graminoids in former lucerne fields (1–3 years old), which suggests a high amount of weed seeds in the soil of lucerne fields. The low cover of weeds detected in the present study is most likely to be explained by the presence of lucerne, than by the absence of weed seeds in the soil. The high cover and phytomass of lucerne in the first years caused weed suppression by increased shading of the soil surface (Güsewell & Edwards 1999), and/or the competitive exclusion of short-lived weeds (Bischoff, Auge

& Mahn 2005). An allelopathic effect of lucerne may be responsible for low weed cover: Ells & McSay (1991) showed that lucerne leaf extract (containing phenolic allelochemicals) was detrimental to germination and differentiation of susceptible plants.

COVER AND PHYTOMASS OF LUCERNE

In our study the cover of lucerne was over 70% in 1- and 3-year-old lucerne fields. A sharp decline was detected after the third year. This is in accordance with the common agricultural practice in this region, where the lucerne is re-sown after 3–4 years of cultivation. In a sowing experiment conducted by Li, Xu & Wang (2008) in loess plateaux in China, the mean cover of lucerne decreased after the first year of sowing (about 50% of cover in the first, and 29% in the third year after sowing, respectively). The more rapid decrease in lucerne cover can be explained by the lower sowing density than in our study (22.5 kg ha⁻¹, in our region 30 kg ha⁻¹ is typical). Our results suggest that lucerne could disappear within a decade from grasslands under extensive management by mowing. The disappearance of lucerne could also be facilitated by low intensity grazing, which would select for leguminous species (Stroh *et al.* 2002).

In previous studies a significant increase in total vegetation cover (Ruprecht 2005; Li, Xu & Wang 2008) or an increase of cover and/or phytomass of perennials (Štolcová 2002; Feng *et al.* 2007a,b; Török *et al.* 2008) has been found during secondary succession. In our study, no such trend was detected. The total cover and also the total phytomass scores remained stable during secondary succession. This was caused by the gradual replacement of lucerne by perennial grasses. Török *et al.* (2010) found litter accumulation of one order of magnitude higher between the first and second years after restoration of grasslands with low diversity mixtures in former lucerne fields (first year litter: 28–37 g m⁻²; second year litter: 280–289 g m⁻²). The litter scores in the second and the third year of this study were about two to three times higher than that detected in the present study. Accumulated plant litter was identified as negatively affecting vascular plant species richness in several studies (Huhta *et al.* 2001; Enyedi, Ruprecht & Deák 2007). Therefore, high amounts of litter with high perennial cover are especially effective in weed suppression (Török *et al.* 2010). Litter accumulation can also be negative as litter can reduce the micro-topographical heterogeneity (Tropek *et al.* 2010), and decrease the availability of colonisation sites (Jensen & Gutekunst 2003), which can stabilise the community in an undesirable state (Hobbs *et al.* 2006). High amounts of litter could also hamper the immigration and establishment of several target species by limiting microsite availability (Foster & Gross 1998; Bissels *et al.* 2006). In this study, there was no litter accumulation detected and, as a result, germination and colonisation was not hampered and species richness increased with field age. Other studies reporting spontaneous grassland succession have found similar links with litter accumulation and reduction in germination and colonisation (Jongepierová, Jongepier & Klimes 2004; Ruprecht 2006; Feng *et al.* 2007a).

RECOVERY OF GRASSLANDS

We found that the recovery of species poor loess grasslands dominated by perennial native species in former lucerne fields was possible within 10 years. Other old-field studies found 6–23 years after abandonment was sufficient time for the spontaneous succession of loess grasslands (Molnár & Botta-Dukát 1998; Ruprecht 2005; Csécséris *et al.* 2007; Feng *et al.* 2007a,b). The dissimilarity in species composition between lucerne fields and reference grasslands has continuously decreased with increasing field age. Dissimilarity scores were, however, high even between 5 and 10-year-old fields and reference grasslands. Several perennial forbs found at high frequency in loess grasslands were not detected in lucerne fields; and several short-lived weeds detected with low cover but high frequency in lucerne fields were missing from reference grasslands (see Appendix S1). Previous studies have reported that the spontaneous immigration of desirable target species is a diaspore limited process (Donath *et al.* 2007; Kiehl *et al.* 2010). There are two reasons for diaspore limitation: (i) limited spatial dispersal (e.g. missing dispersal agents and heavy seeds) reduces the movement of seeds into target sites (Simmering, Waldhardt & Otte 2006); (ii) long-term agricultural use often depletes the local seed bank, and also increases the amount of weed seeds in the soil (Coulson *et al.* 2001). Therefore, spontaneous recovery will be most effective where native grassland sites are located nearby (Öster *et al.* 2009). A further explanation for the persistent differences in species composition between the old fields and reference grasslands is that the perennial forbs may require more time to establish in extensively managed fields (e.g. Prach, Lepš & Rejmánek 2007).

PRACTICAL IMPLICATIONS FOR POLICY

Our results suggest that the recovery of initial loess grasslands may not require technical reclamation methods (i.e. sowing competitor grasses and/or forbs) in lucerne fields where nearby grasslands are present as a seed source. We found that after a decade of regular mowing, lucerne fields were transformed into loess grasslands dominated by native perennial grasses. However, most of the characteristic loess grasslands forbs are missing. Similar results were found under the more common technical reclamation method of sowing low diversity seed mixtures (Hansson & Fogelfors 1998; Lepš *et al.* 2007; Török *et al.* 2010). The full recovery of loess grasslands requires more time and/or should be facilitated by technical introduction of some of the target species (Kirmer *et al.* 2008; Kiehl *et al.* 2010). The transfer of hay and/or low intensity grazing combined with continued mowing can be another option to facilitate the establishment of desirable species.

Our results suggest that sowing lucerne in abandoned fields and following this with extensive management can combine the advantages of both spontaneous succession and technical reclamation in grassland restoration. It offers a cost effective solution from the economic (agricultural) and conservation management point of view. The method has several advantages over technical reclamation. In particular, there is no weed

dominated stage and no intensive litter accumulation. Lucerne gradually decreases in abundance once re-sowing and/or fertilizing stop so we there will be a lower microsite limitation rate compared to technical reclamation sites where competitor grasses are sown. Finally, spontaneous succession is cheaper than technical reclamation, and provides a high value hay harvest in the first few years in lucerne fields.

Acknowledgments

We thank I. Kapocsi, L. Gál, S. Újfalusi, S. Tóth from the Hortobágy National Park for their help. We are indebted to T. Miglécz, K. Tóth, Sz. Tasnády graduate students for their help in field and laboratory works. We are grateful to J. Memmott, and J. Firn for improving the former draft of the paper.

References

- Bakker, J.D. (2008) Increasing the utility of indicator species analysis. *Journal of Applied Ecology*, **45**, 1829–1835.
- Bischoff, A., Auge, H. & Mahn, E.-G. (2005) Seasonal changes in the relationship between plant species richness and community phytomass in early succession. *Basic and Applied Ecology*, **6**, 385–394.
- Bissels, S., Donath, T.W., Hölzel, N. & Otte, A. (2006) Effects of different mowing regimes on seedling recruitment in alluvial grasslands. *Basic and Applied Ecology*, **7**, 433–442.
- Blumenthal, D.M., Jordan, N.R. & Svenson, E.L. (2003) Weed control as a rationale for restoration: the example of tallgrass prairie. *Conservation Ecology*, **7**, [online] URL: <http://www.consecol.org/vol7/iss1/art6/>
- Blumenthal, D.M., Jordan, N.R. & Svenson, E.L. (2005) Effects of prairie restoration on weed invasions. *Agriculture, Ecosystems & Environment*, **107**, 221–230.
- Borhidi, A. (1995) Social behaviour types, the naturalness and relative indicator values of the higher plants in the Hungarian Flora. *Acta Botanica Hungarica*, **39**, 97–181.
- Borhidi, A. (2003) Magyarország Növénytársulásai (Plant associations of Hungary). Akadémiai Kiadó, Budapest, Hungary. (in Hungarian).
- ter Braak, C.J.F. & Šmilauer, P. (2002) CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power Ithaca, NY, USA.
- Collins, B., Wein, G. & Philippi, T. (2001) Effects of disturbance intensity and frequency on early old-field succession. *Journal of Vegetation Science*, **12**, 721–728.
- Coulson, S.J., Bullock, J.M., Stevenson, M.J. & Pywell, R.F. (2001) Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology*, **38**, 204–216.
- Csécséris, A. & Rédei, T. (2001) Secondary succession on sandy old-fields in Hungary. *Applied Vegetation Science*, **4**, 63–74.
- Csécséris, A., Szabó, R., Halassy, M. & Rédei, T. (2007) Testing the validity of successional predictions on an old-field chronosequence in Hungary. *Community Ecology*, **8**, 195–207.
- Donath, T.W., Bissels, S., Hölzel, N. & Otte, A. (2007) Large scale application of diaspore transfer with plant material in restoration practice – impact of seed and microsite limitation. *Biological Conservation*, **138**, 224–234.
- Dufréne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- Ells, J.E. & McSay, A.E. (1991) Allelopathic effects of alfalfa plant residues on emergence and growth of cucumber seedlings. *HortScience*, **26**, 368–370.
- Enyedi, M.Z., Ruprecht, E. & Deák, M. (2007) Long-term effects of the abandonment of grazing on steppe-like grasslands. *Applied Vegetation Science*, **11**, 55–62.
- Feng, D., Hong-Bo, S., Lun, S., Zong-Suo, L. & Ming-Ana, S. (2007a) Secondary succession and its effects on soil moisture and nutrition in abandoned old-fields of hilly region of Loess Plateau, China. *Colloids and Surfaces B: Biointerfaces*, **58**, 278–285.
- Feng, D., Zongsuo, L., Xuexuan, X., Lun, S. & Xingchang, Z. (2007b) Community biomass of abandoned farmland and its effects on soil nutrition in

- the Loess hilly region of Northern Shaanxi, China. *Acta Ecologica Sinica*, **27**, 1673–1683.
- Firn, J. (2007) Developing strategies and methods for rehabilitating degraded pastures using native grasses. *Ecological Management & Restoration*, **8**, 183–187.
- Foster, B.L. & Gross, K.L. (1998) Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, **79**, 2593–2602.
- Grime, J.P. (1979) *Plant strategies and Vegetation Processes*. Wiley, Chichester.
- Güsewell, S. & Edwards, P. (1999) Shading by *Phragmites australis*: a threat for species-rich fen meadows? *Applied Vegetation Science*, **2**, 61–70.
- Hansson, M. & Fogelfors, H. (1998) Management of permanent set-aside on arable land in Sweden. *Journal of Applied Ecology*, **35**, 758–771.
- Hobbs, R.J. & Cramer, V.A. (2007) Why Old Fields? Socioeconomic and ecological causes and consequences of land abandonment. *Old Fields: Dynamics and Restoration of Abandoned Farmland* (eds V.A. Cramer & R.J. Hobbs), pp. 1–15. Island Press, Washington.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
- Hodačová, D. & Prach, K. (2003) Spoil heaps from brown coal mining: technical reclamation vs. spontaneous re-vegetation. *Restoration Ecology*, **11**, 385–391.
- Hölzel, N. & Otte, A. (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science*, **6**, 131–140.
- Horrocks, R.D. & Valentine, J.F. (1999) *Harvested Forages*. Academic Press, San Diego, CA, USA.
- Huhta, A.-P., Rautio, P., Tuomi, J. & Laine, K. (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. *Journal of Vegetation Science*, **12**, 677–686.
- Hutchings, M.J. & Booth, K.D. (1996) Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *Journal of Applied Ecology*, **33**, 1171–1181.
- Jensen, K. & Gutekunst, K. (2003) Effects of litter on establishment of grassland plant species: the role of successional status. *Basic and Applied Ecology*, **4**, 579–587.
- Jongepierová, I., Jongepier, J.W. & Klimes, L. (2004) Restoring grassland on arable land: an example of a fast spontaneous succession without weed-dominated stages. *Preslia*, **76**, 361–369.
- Jongepierová, I., Mitchley, J. & Tzanopoulos, J. (2007) A field experiment to recreate species rich hay meadows using regional seed mixtures. *Biological Conservation*, **139**, 297–305.
- Kiehl, K., Kirmer, A., Donath, T.W., Rasran, L. & Hölzel, N. (2010) Species introduction in restoration projects – evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology*, **11**, 285–299.
- Kirmer, A., Tischew, S., Ozinga, W.A., von Lampe, M., Baasch, A. & Groenendaal, J.M. (2008) Importance of regional species pools and functional traits in colonisation processes: predicting re-colonization after large-scale destruction of ecosystems. *Journal of Applied Ecology*, **45**, 1523–1530.
- K.S.H. (Hungarian Central Statistical Office) (2008) Economic Accounts for Agriculture in Hungary, 2008. *Statistical Reflections*, **26**, [online] <http://portal.ksh.hu/portal/>
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Elsevier Science, Amsterdam, The Netherlands.
- Lepš, J., Doležal, J., Bezemer, T.M., Brown, V.K., Hedlund, K., Igual Arroyo, M., Jörgensen, H.B., Lawson, C.S., Mortimer, S.R., Peix Geldart, A., Rodríguez Barrueco, C., Santa Regina, I., Šmilauer, P. & van der Putten, W.H. (2007) Long-term effectiveness of sowing high and low diversity seed mixtures to enhance plant community development on ex-arable fields. *Applied Vegetation Science*, **10**, 97–110.
- Li, J.-H., Xu, D.-H. & Wang, G. (2008) Weed inhibition by sowing legume species in early succession of abandoned fields on Loess Plateau, China. *Acta Oecologica*, **33**, 10–14.
- Lindborg, R., Bengtsson, J., Berg, A., Cousins, S.A.O., Eriksson, O., Gustafsson, T., Per Hasund, K., Lenoir, L., Pihlgren, A., Sjödin, E. & Stenske, M. (2008) A landscape perspective on conservation of semi-natural grasslands. *Agriculture, Ecosystems & Environment*, **125**, 213–222.
- Manchester, S.J., McNally, S., Treweek, J.R., Sparks, T.H. & Mountford, J.O. (1999) The cost and practicality of techniques for the reversion of arable land to lowland wet grassland – an experimental study and review. *Journal of Environmental Management*, **55**, 91–109.
- Mijnsbrugge, K.V., Bischoff, A. & Smith, B. (2010) A question of origin: where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, **11**, 300–311.
- Molnár, Zs. & Borhidi, A. (2003) Hungarian alkali vegetation: origins, landscape history syntaxonomy, conservation. *Phytocoenologia*, **33**, 377–408.
- Molnár, Zs. & Botta-Dukát, Z. (1998) Improved space-for-time substitution for hypothesis generation: secondary grasslands with documented site history in SE-Hungary. *Phytocoenologia*, **28**, 1–29.
- Molnár, Zs., Biró, M., Bölöni, J. & Horváth, F. (2008) Distribution of the (semi)-natural habitats in Hungary I. Marshes and grasslands. *Acta Botanica Hungarica*, **50**, Suppl. 1, 59–106.
- del Moral, R., Walker, L.R. & Bakker, J.P. (2007) Insights gained from succession fort he restoration of landscape structure and function. *Linking Restoration and Ecological Succession* (eds L.R. Walker, J. Walker & R.J. Hobbs), pp. 19–45. Springer-Verlag, New York, USA.
- Öster, M., Ask, K., Römermann, C., Tackenberg, O. & Eriksson, O. (2009) Plant colonization of ex-arable fields from adjacent species-rich grasslands: the importance of dispersal vs. recruitment ability. *Agriculture, Ecosystems & Environment*, **130**, 93–99.
- Pécsi, M. (eds) (1989) Magyarország Nemzeti Atlasza (National Atlas of Hungary). Kartográfiai vállalat, Budapest (in Hungarian).
- Prach, K. & Hobbs, R.J. (2008) Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology*, **16**, 363–366.
- Prach, K., Lepš, J. & Rejmánek, M. (2007) Old field succession in Central Europe: local and regional patterns. *Old Fields: Dynamics and Restoration of Abandoned Farmland* (eds V.A. Cramer & R.J. Hobbs), pp. 180–201. Island Press, Washington.
- Prach, K. & Pyšek, P. (2001) Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. *Ecological Engineering*, **17**, 55–62.
- Prach, K., Pyšek, P. & Bastl, M. (2001) Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. *Applied Vegetation Science*, **4**, 83–88.
- Prach, K. & Řehouňková, K. (2008) Spontaneous vegetation succession in gravel-sand pits: a potential for restoration. *Restoration Ecology*, **16**, 305–312.
- Pullin, A.S., Báldi, A., Can, O.E., Dieterich, M., Kati, V., Livoreil, B., Lövei, G., Mihók, B., Nevin, O., Selva, N. & Sousa-Pinto, I. (2009) Conservation focus on Europe: major conservation policy issues that need to be informed by Conservation Science. *Conservation Biology*, **23**, 818–824.
- Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294–309.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Raunkiaer, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*, Being the Collected Papers of C. Raunkiaer. Oxford University Press, Oxford.
- Reid, A.M., Morin, L., Downey, P.O., French, K. & Virtue, J.G. (2008) Does invasive plant management aid restoration of natural ecosystems? *Biological Conservation*, **142**, 2342–2349.
- Ruprecht, E. (2005) Secondary succession in old-fields in the Transylvanian Lowland (Romania). *Preslia*, **77**, 145–157.
- Ruprecht, E. (2006) Successfully recovered grassland: a promising example from Romanian old-fields. *Restoration Ecology*, **14**, 473–480.
- Simmering, D., Waldhardt, R. & Otte, A. (2006) Quantifying determinants contributing to plant species richness in mosaic landscapes: a single- and multi-patch perspective. *Landscape Ecology*, **21**, 1233–1251.
- Simon, T. (2000) *A magyarországi edényes flóra határozója* (Vascular Flora of Hungary). Nemzeti Tankönyvkiadó, Budapest, Hungary (In Hungarian).
- Stevenson, M.J., Bullock, J.M. & Ward, L.K. (1995) Re-creating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. *Restoration Ecology*, **3**, 279–289.
- Štolcová, J. (2002) Secondary succession on an early abandoned field: vegetation composition and production of biomass. *Plant Protection Science*, **38**, 149–154.
- Stroh, M., Storm, C., Zehm, A. & Schwabe, A. (2002) Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. *Phytocoenologia*, **32**, 595–625.
- Török, P., Matus, G., Papp, M. & Tóthmérész, B. (2008) Secondary succession in overgrazed Pannonian sandy grasslands. *Preslia*, **80**, 73–85.

- Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, Sz. & Tóthmérész, B. (2010) Restoring grassland biodiversity: sowing low diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation*, **143**, 806–812.
- Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, I., Banar, P., Tuf, I.H., Hejda, M. & Konvicka, M. (2010) Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *Journal of Applied Ecology*, **47**, 139–147.
- Walker, L.R., Walker, J. & del Moral, R. (2007) Forging a new alliance between succession and restoration. *Linking Restoration and Ecological Succession* (eds L.R. Walker, J. Walker & R.J. Hobbs), pp. 1–19. Springer-Verlag, New York, USA.
- Warren, J., Christal, A. & Wilson, F. (2002) Effects of sowing and management on vegetation succession during grassland habitat restoration. *Agriculture, Ecosystems & Environment*, **93**, 393–402.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.

Received 9 June 2010; accepted 20 October 2010

Handling Editor: Jennifer Finn

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Characteristic species of target loess grasslands and extensively managed lucerne fields identified by an IndVal procedure; 10,000 random permutations were used.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.