



Management effects on the vegetation and soil seed bank of calcareous grasslands: An 11-year experiment

Hans Jacquemyn^{a,*}, Carmen Van Mechelen^a, Rein Brys^b, Olivier Honnay^a

^a Division of Plant Ecology and Systematics, University of Leuven, Arenbergpark 31, B-3001 Heverlee, Belgium

^b Research Institute for Nature and Forest, Kliniekstraat 25, B-1070 Brussels, Belgium

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ABSTRACT

Calcareous grasslands, most of which are man made and therefore depend on some kind of human interference for their maintenance, are among the most species-rich communities on Earth at a small scale. For many centuries, most of these grasslands have been used as extensive pasture. However, after 1900, and particularly from 1940 onwards, livestock grazing has declined throughout Europe leading to the abandonment of low intensity grasslands over large areas. To conserve the remaining grasslands or to restore recently abandoned grasslands, better insights about the effects of grassland management on above and belowground species diversity are needed. Here, we describe the results of an 11-year experiment to investigate the role of grassland management (grazing, mowing and abandonment) in determining species composition and diversity both in the aboveground vegetation and the seed bank of a calcareous grassland in Belgium. Species diversity declined by about 60% 11 years after abandonment, from 29 species m^{-2} to as few as 12 species m^{-2} . Plots that were grazed remained constant in species richness, whereas mown sites lost about 20% of their original species. Abandoned plots were largely dominated by a few grass species, in particular *Festuca rubra*. Concomitant with changes in the aboveground vegetation, both the number of species found in the seed bank and seed density (number of seeds m^{-2}) had changed significantly 11 years after abandonment. Species diversity and seed density were significantly lower in abandoned plots than in grazed or mown plots. We conclude that abandonment of calcareous grasslands may lead to rapid decline of plant species diversity both in the aboveground vegetation and in the seed bank. As a result, seed banks probably have a limited role to play in the restoration of recently abandoned grasslands.

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1. Introduction

Calcareous grasslands are among the most species-rich communities on Earth at a small scale ($<10 m^2$), sometimes containing more than 30–40 plant species m^{-2} (Kull and Zobel, 1991; Jacquemyn et al., 2003). Most calcareous grasslands are man made and therefore depend on some kind of human interference (e.g. grazing, burning or haymaking) for their maintenance (Willems, 2001; Poschlod and Wallis-DeVries, 2002). For many centuries, calcareous grasslands have been used as extensive pasture for livestock grazing. However, after 1900, and particularly from 1940 onwards, livestock grazing has declined throughout Europe leading to the abandonment of low intensity grasslands over large areas (Poschlod et al., 1998; Willems and Bik, 1998). As a result, the extent of these formerly widespread grasslands has greatly diminished during the last century (Keymer and Leach, 1990; Willems, 2001; Poschlod and Wallis-DeVries, 2002), often resulting in the loss of popula-

tions of typical calcareous grassland plant species, many of which are now rare or endangered (Wells, 1968; Stöcklin and Fischer, 1999; Willems, 2001).

To meet the increasing demands to conserve calcareous grasslands as an important part of our natural and cultural heritage, there is a general consensus that restoration and conservation actions are urgently needed to conserve these species-rich habitats [reviewed in Willems (2001) and Poschlod and Wallis-DeVries (2002)]. Whereas conservation of remnant grasslands depends on the management applied (e.g. Jacquemyn et al., 2003), the ultimate success of restoration practices depends on both biotic and abiotic constraints (Bakker and Berendse, 1999). Previous research has shown that reintroduction of traditional management practices in recently abandoned calcareous grasslands could lead to a gradual increase of the number and abundance of typical calcareous grassland species. Willems (2001), for example, showed that clearing of shrubs and mowing resulted in a rapid decline of dominant species (e.g. *Brachypodium pinnatum*), and an associated increase of the number of species characteristic of calcareous grasslands (Willems, 2001). However, the observed increase in species

* Corresponding author. Tel.: +32 16 32 97 73.

E-mail address: hans.jacquemyn@bio.kuleuven.be (H. Jacquemyn).

diversity was slow despite the fact that the plots discussed in Willemss (2001) were immediately bordered by species-rich calcareous grassland vegetation, which may have facilitated and expedited the rate of recolonization. In spatially isolated grassland remnants, restoration of the original species diversity may be even slower, because influx from seeds is likely to be very limited due to the fact that seed dispersal of species typical of calcareous grasslands is restricted, particularly in highly fragmented landscapes (Honnay et al., 2007; Jacquemyn et al., 2010).

Restoration of calcareous grasslands that experienced a change in land-use practices or that were abandoned for a considerable time is therefore most likely to succeed when remnant populations of calcareous grassland species are still present in the vegetation, or when recruitment from the seed bank can be expected (Bakker and Berendse, 1999). However, gradual decline of species in the seed bank with increasing time after abandonment (Poschlod et al., 1998) suggests that restoration possibilities from the seed bank in calcareous grasslands may be limited, particularly if succession has progressed to the final stage of forest development (e.g. Bossuyt et al., 2006). On the other hand, some studies have not found any differences in species richness and seed density after abandonment and succession towards forests (Milberg, 1995; Maccherini and De Dominicis, 2003). Dutoit and Allard (1995) even found the highest seed densities in grasslands abandoned 40 years ago. Most of these studies, however, are based on space-for-time substitution (chronosequence) methods (but see Milberg, 1995), the use of which has been heavily criticised (Collins and Adams, 1983; Pickett, 1988; Johnson and Miyanishi, 2008), and it remains unclear to what extent results were affected by methodological issues rather than by natural processes related to succession.

To better understand the rate and scale of temporal changes in species diversity in both the aboveground vegetation and soil seed bank of calcareous grasslands after abandonment, an experiment was set up in which different management practices (mowing, grazing, and abandonment) were applied to calcareous grassland vegetation. We describe changes in species richness and diversity of the aboveground vegetation in abandoned plots during the course of the experiment (1999–2009), and compare these with plots that were continuously grazed or mown. We also investigated changes in seed bank density after abandonment by comparing seed bank composition of grazed, mown and undisturbed plots 11 years after the experiment was initiated. Given that seeds of most long-lived grassland species are only moderately long-lived (up to a few years) (Thompson et al., 1997; Bekker et al., 1998), we hypothesize that following changes in the aboveground vegetation due to abandonment both the number of species found in the seed bank and seed density will also change, potentially affecting the restoration possibilities of calcareous grasslands from the seed bank after grasslands have been abandoned for even a limited number of years. Additionally, we were interested in the response of the vegetation to the management type applied (mowing vs. grazing), and on how this response translates into the seed bank composition. The obtained results are likely to provide important insights into the possible role of grassland management in maintaining or restoring species diversity of calcareous grasslands.

2. Materials and methods

2.1. Study site

The study was conducted in the eastern part of Belgium (Limburg) in Voeren. This is one of the few regions in Flanders where calcareous grasslands occur. All experiments (see below) were conducted on a site that showed clear affinities to the Galio-Trifolietum association (Schaminée and Zuidhoff, 1995) and

that was traditionally grazed by cattle for decades. This grassland association occurs on nutrient-poor soils that are relatively well-drained and is characterized by a large frequency of small rosette plants, probably as a result of a long-lasting history of grazing. Typical species of this association include *Primula veris*, *Plantago media*, *Ranunculus bulbosus* and *Cirsium acaule*. The studied grassland is located between 180 and 210 m above sea level on a south-facing slope with an inclination of about 30°. The soil pH is 7.6 with a very low P content (<3 mg P kg⁻¹ dry soil). More details of the study site can be found in Jacquemyn et al. (2003).

2.2. Experimental design

Although the original experiment described in Jacquemyn et al. (2003) was designed to study the effects of different management treatments (mowing, grazing and abandonment) on the response of calcareous grassland vegetation to increased nitrogen, it also allowed us to study the effect of management per se on species composition and richness as several of the original plots were not fertilized (i.e. control treatment). These 3 × 3 m² plots, 15 in total, were monitored in 1999, 2000, 2001, 2002, and finally in 2009, 11 years after the experiment had begun in 1999. To avoid edge effects, only the central area (1 × 1 m²) of each plot was investigated. Grazed plots were grazed periodically throughout the year, meaning that grazing cattle regularly swapped nearby grasslands. Grazing started in late May–early June and lasted until the end of August–the beginning of September. Average cattle density during the study period numbered 15 cows ha⁻¹. Mown plots were mown manually once a year in the second half of August and all litter was immediately removed after mowing. Finally, five plots were left completely undisturbed during the entire experiment, mimicking abandonment of calcareous grasslands.

2.3. Data collection

In each of the four sampling years, the plant community was monitored in mid-May at a time when spring flowers were still present and recognizable and seedlings of summer flowers had already emerged and could be identified. In each plot, presence-absence of species was determined. At the end of the experiment in 2009, the abundance of each species within each plot was surveyed using the Braun-Blanquet scale.

To assess species composition of the seed bank, in November 2009 the soil was sampled 20 times from each plot with a 2.5 cm diameter soil auger. To account for possible differences in seed bank composition between upper and lower soil layers, soil samples were taken to a depth of 10 cm and divided in two parts (0–5 cm and 5–10 cm). All 20 samples were then bulked from each plot, returned to the laboratory and processed using the methodology described by ter Heerdt et al. (1996). Each bulked sample was washed through a coarse (4 mm) and a fine (0.2 mm) sieve in order to remove both coarse and fine soil material, roots and vegetative parts. These concentrated samples were then spread out in a thin layer (2 mm) on 15 × 15 cm trays filled with sterilized potting soil. In addition, a thin layer (1 cm) of expanded clay granules was placed on the bottom of each tray in order to prevent waterlogging. The trays were placed on shelves in a greenhouse with a light regime of 8 h darkness and 16 h light and kept moist. The light was provided by neon tubes, imitating full sunlight conditions. The temperature was not controlled and varied between 14 and 25 °C. Five control trays filled with sterilized potting soil were also placed randomly on the shelves to test for contamination. No seedlings germinated in the control trays.

Seedlings were identified as soon as possible after germination, counted and removed or, if they could not be identified immediately, transplanted in pots to allow further growth. After 8 weeks,

when no further seedlings emerged, the trays were placed in a refrigerator at a temperature of 2 °C for 8 weeks. After this period, they were returned to the shelves for another 8 weeks and newly emerging seedlings were identified and counted again.

2.4. Data analysis

To analyze differences in species richness across the different years of sampling between management regimes, a repeated-measures ANOVA was used with management as fixed factor and species richness (the number of plant species m^{-2}) in 2000, 2001, 2002 and 2009 as the repeated measure. PROC GLM (SAS 2000) with a repeated statement was used to perform the overall analysis, determine sphericity (Mauchly's test) and to generate univariate results. To investigate whether different management regimes resulted in differences in species diversity 11 years after abandonment, we calculated for each plot Shannon's diversity index ($H = -\sum_{i=1}^S p_i \ln p_i$) where p_i is the abundance of the i th species and S the total number of species) and Shannon's equitability ($E_H = H/\ln S$). One-way ANOVA was used to investigate whether diversity indices differed between grazed, mown and abandoned

Table 1

Results of a repeated measures analysis of variance for the effect of management (grazing, mowing or no disturbance) on species richness in $1 \times 1 \text{ m}^2$ plots.

Source	df	MS	F	P
Management	2	885.6	150.6	<0.0001
Error	12	5.9		
Year	4	111.6	54.3	<0.0001
Year $\times$ management	8	56.6	27.5	<0.0001
Error (year)	48	2.1		

Mauchly's $W = 0.482$, $df = 9$, $P = 0.58$. Both the between-subject main effect of management and the within-subject main effect of year and the management $\times$ year interaction are shown.

plots. To investigate whether specific species groups were more sensitive to altered disturbance regimes, species were grouped into four different functional groups: woody plants, rosette plants, other herbs and graminoids. One-way ANOVA was used to investigate whether the average number of species in each group was different among treatments.

For each plot, the total number of species found in the seed bank in November 2009 and the average seed density were calculated. We also calculated the number of species and seed density in the upper 5 cm and lower 5 cm of the soil. A one-way ANOVA was used to investigate whether the total number of species found in the seed bank and seed density was affected by management regime. To investigate the effect of soil depth and management regime on species number and seed density, a two-way ANOVA was used with soil depth and management as fixed factors. For each plot, Shannon's diversity and equitability index were calculated and compared between treatments using a one-way ANOVA. For species with at least five seedlings, individual seed density was calculated and compared between grazed, mown and undisturbed plots using non-parametric ANOVA (Kruskal–Wallis χ^2). To compare similarity between above ground vegetation and the seed bank, for each plot the Jaccard similarity index was calculated as $J = \frac{a}{a+b+c}$ with a the number of species occurring both in the vegetation and the seed bank, b the number of species occurring solely in the vegetation and c the number of species found exclusively in the seed bank. Differences in similarity between grazed, mown and abandoned plots were tested using one-way ANOVA.

3. Results

3.1. Vegetation

At the end of the experiment in 2009, a total of 44, 32 and 20 species was found in the grazed, mown and abandoned plots, respectively. Results from the repeated-measures ANOVA showed

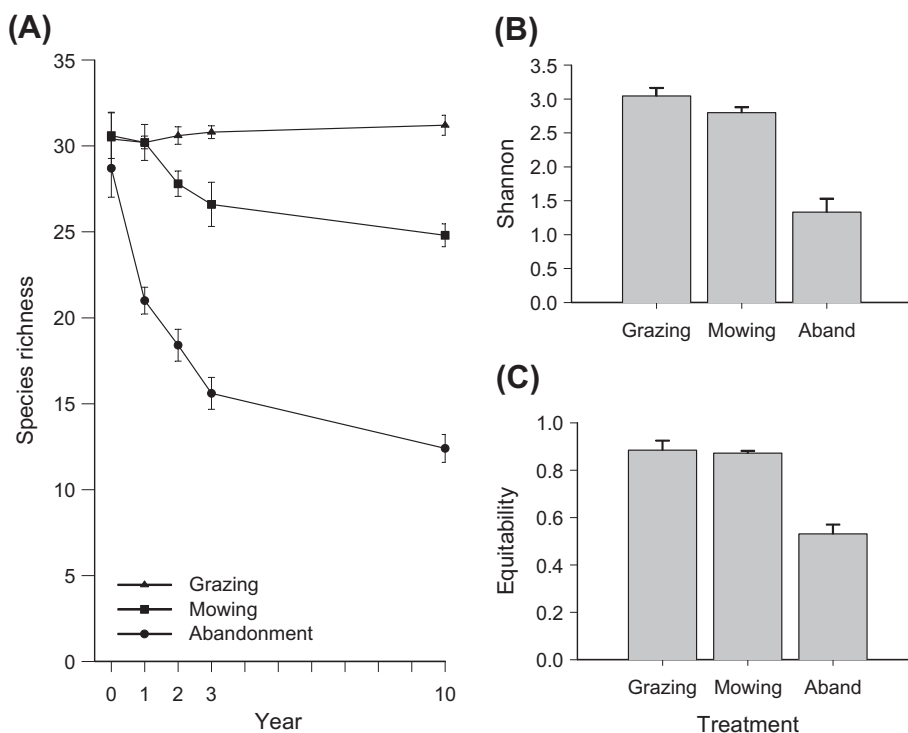


Fig. 1. (A) Evolution of species diversity in mown, grazed and abandoned plots 1, 2, 3 and 10 years after the experiment was initiated (1999). (B) Shannon diversity index and (C) equitability index of vegetation plots 10 years after the experiment was initiated. Values represent averages and standard errors of five $1 \times 1 \text{ m}^2$ plots.

that species richness was significantly affected by management, year, and the interaction between year and management (Table 1). Species richness declined significantly in abandoned plots from ca 29 species m^{-2} in 1999 to only 12 m^{-2} species in 2009 (Fig. 1A). In contrast, species richness in grazed plots remained constant (on average 30 species m^{-2}), whereas in mown plots it decreased from 30 species m^{-2} in 2000 to 25 m^{-2} species in 2009, indicating that mowing could not prevent species to be lost from the vegetation (Fig. 1A). Both the Shannon diversity index and equitability index were significantly ($F_{2,12} = 703.0$ and 606.1 , respectively, $P < 0.0001$) different between the different management regimes. In particular, abandoned plots were dominated by a few species leading to small diversity and equitability indices (Fig. 1B and C). The average number of species was significantly different between grazed, mown and abandoned plots for all functional groups,

except for woody plants (Fig. 2). In particular, the loss of rosette plants and herbs in abandoned plots was very obvious, whereas graminoids showed less pronounced declines (Fig. 2).

3.2. Seed bank

A total of 444 seedlings from 32 species germinated from the soil samples, corresponding to an average seed density of 2994 seedlings m^{-2} over all plots. The most abundant species in the seed bank were *Leucanthemum vulgare* (26% of the seedlings), *Bellis perennis* (10%), *Ranunculus repens*, *Arrhenatherum elatius*, *Plantago lanceolata* and *Daucus carota* (all 8%). Three species (*Glechoma hederacea*, *Cardamine hirsuta* and *Poa pratensis*) were found in the soil seed bank, but not in the aboveground vegetation. Nonetheless, the densities of these species in the seed bank were

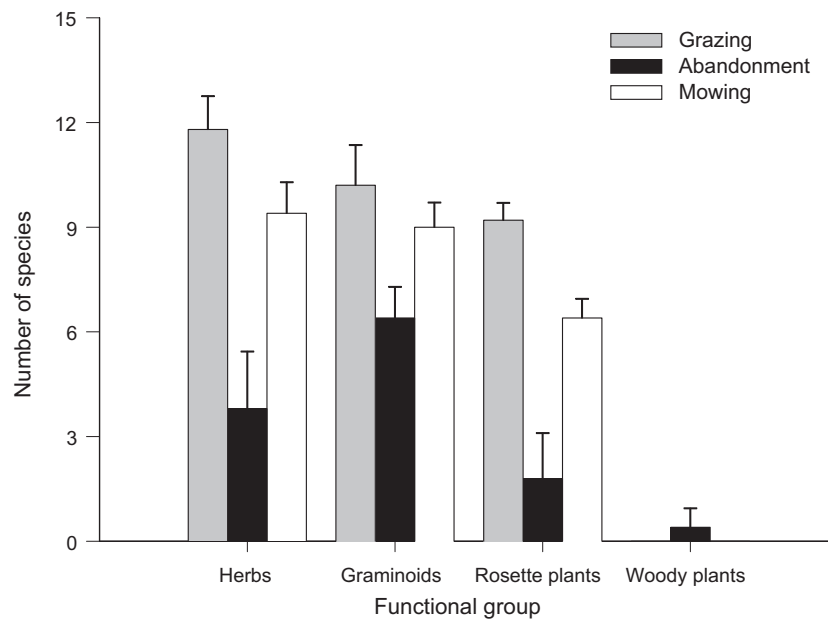


Fig. 2. Total number of species within different functional groups in grazed, mown and abandoned plots at the end of the experiment.

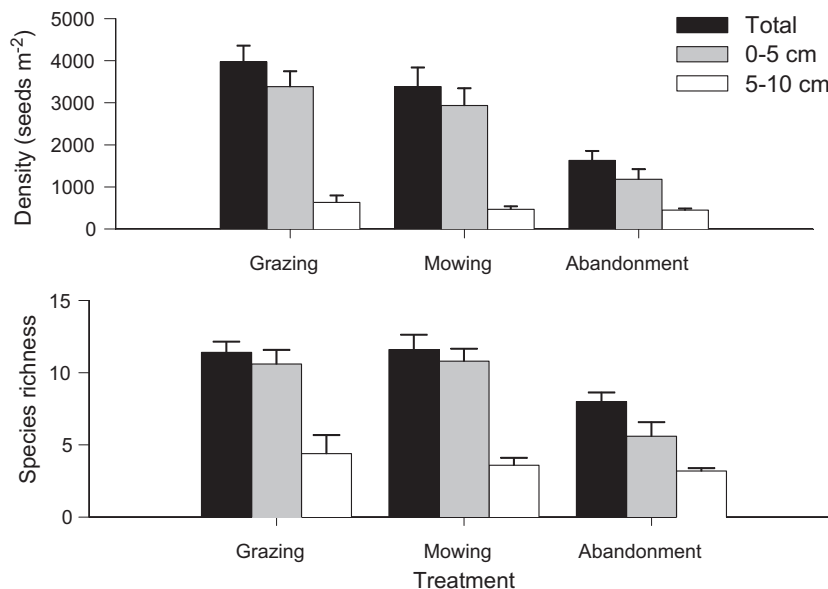


Fig. 3. Seed bank composition of mown, grazed and undisturbed plots 11 years after different management regimes were installed.

Table 2

Two-way ANOVA investigating the effects of soil layer and disturbance regime affecting the number of species found in the seed bank and seed density (seeds m⁻²).

Source	df	MS	F	P
<i>Species number</i>				
Soil layer	1	208.0	6.2	0.007
Management	2	24.0	54.0	<0.001
Soil layer × management	2	21.2	5.5	0.011
Error	24	3.9		
<i>Seed density</i>				
Soil layer	1	2.9 × 10 ⁷	87.4	<0.001
Management	2	3.8 × 10 ⁶	11.4	<0.001
Soil layer × management	2	2.9 × 10 ⁶	8.8	0.001
Error	24	0.3 × 10 ⁶		

Table 3

Average seed bank density (seeds m⁻²) of 16 species with more than five seedlings emerging in grazed, mown and abandoned grassland plots.

Species	Grazing	Mowing	Abandonment	Kruskal–Wallis
<i>Agrostis capillaris</i>	2.0	10.2	0.0	4.63 (*)
<i>Arrhenatherum elatius</i>	2.0	46.9	20.4	7.37 *
<i>Bellis perennis</i>	50.9	38.7	4.1	9.36 **
<i>Cerastium fontanum</i>	8.1	0.0	6.1	3.38 ns
<i>Crepis capillaris</i>	4.1	8.1	0.0	2.53 ns
<i>Cynosurus cristatus</i>	2.0	0.0	12.2	4.86 (*)
<i>Daucus carota</i>	34.6	2.0	34.6	8.98 *
<i>Holcus lanatus</i>	28.5	6.1	10.2	4.63 (*)
<i>Leucanthemum vulgare</i>	110.0	87.6	34.6	5.88 *
<i>Lolium perenne</i>	0.0	6.1	10.2	3.76 ns
<i>Medicago lupulina</i>	30.6	6.1	2.0	5.29 (*)
<i>Plantago lanceolata</i>	18.3	48.9	2.0	6.63 *
<i>Primula veris</i>	10.2	16.3	4.1	3.72 ns
<i>Prunella vulgaris</i>	6.1	10.2	6.1	1.17 ns
<i>Ranunculus repens</i>	59.1	14.3	2.0	9.34 **
<i>Senecio jacobaea</i>	0.0	12.2	0.0	6.90 *

ns: $P > 0.1$.

(*) $0.1 \leq P < 0.05$.

* $0.05 \leq P < 0.01$.

** $P \leq 0.01$.

very low (<100 seeds m⁻²). There were significant differences in the number of species found in the seed bank and seed densities between grazed, mown and abandoned plots ($F_{2,12} = 6.08$ and 10.8 ; $P = 0.002$ and 0.015 , respectively). Average seed densities ranged from 3972 seeds m⁻² over 3382 seeds m⁻² in mown plots to 1630 seeds m⁻² in abandoned plots (Fig. 3a). The average number of species varied between 12 in grazed and mown plots and 8 in abandoned plots (Fig. 3b). In addition, there were significant ($P < 0.001$) differences in the number of species and seed density between the upper 0–5 cm of the seed bank and the seed bank at 5–10 cm depth (Table 2, Fig. 3a and b). Moreover, this effect was significantly dependent upon disturbance type, as indicated by the significant interaction effect (Table 2). On the other hand, there were no significant ($P > 0.05$) differences in diversity indices between disturbance types, indicating that abundances of species in the seed bank were relatively equally distributed among disturbance regimes and that there were no species that dominated one of the different treatments.

Seven species had significantly ($P < 0.05$) different seed bank densities between the disturbance types (Table 3), four of them having the highest seed densities in the grazed plots (*B. perennis*, *D. carota*, *L. vulgare* and *R. repens*), whereas *A. elatius*, *P. lanceolata* and *Senecio jacobaea* had significantly higher seed densities in mown plots. Seed densities for the four functional groups were also significantly different between the three disturbance types, with rosette plants having much and significantly higher seed densities

in grazed plots. Finally, the congruence between seed bank and vegetation was significantly ($F_{2,12} = 5.97$, $P = 0.016$) different between the different disturbance types and was highest for grazed plots ($J = 0.27$) and lowest for the abandoned plots ($J = 0.12$).

4. Discussion

4.1. Species decline following abandonment

It is widely agreed that the maintenance of high plant species diversity in calcareous grasslands cannot be guaranteed without some kind of disturbance (Willems, 2001; Poschlod and Wallis-DeVries, 2002). Similar to previous studies (Willems, 1990; Kahmen et al., 2002), abandonment of grazing resulted in a dramatic decline in species richness and a significant change in floristic composition. Within a decade, average species richness on a small scale (m⁻²) declined by about 60% when plots received no disturbance, whereas plots that were grazed maintained their high species diversity. In mown plots, on the other hand, small-scale species diversity had declined by about 20%. The total number of species had also declined from 44 species in grazed plots to 32 and 20 species in mown and abandoned plots, respectively.

The observed decline in species richness after abandonment was most likely the result of competition for light (Mitchley and Grubb, 1986; Mitchley and Willems, 1995) and decreased germination possibilities resulting from the loss of gap formation (Grubb, 1977; McConnaughay and Bazzaz, 1987). In abandoned plots, a few tall grass species gained dominance in aboveground biomass and, moreover, overtopped most of the accompanying subordinate species, resulting in a dramatic decrease in light penetration to the soil. Jacquemyn et al. (2003) already showed that 4 years after abandonment canopy height had increased to more than 60 cm, while in grazed and mown plots canopy height varied between 20 and 40 cm, respectively. Similarly, light penetration to the soil had decreased to <1% in abandoned plots, whereas in mown and grazed plots 5% and 30% of the incoming radiation still reached the soil. As a result of the decreased light availability, several small herbs and rosette plants were quickly lost in the abandoned plots. The role of light in determining maintenance of species diversity has recently also been shown experimentally by Hautier et al. (2009). Using experimental species mixtures and light conditions, they showed that decline in light penetration resulted in a significant decline of species richness. The decrease in light penetration and the resulting decline in species richness observed in our plots can be mainly attributed to increased dominance of *Festuca rubra*. This grass species forms thick tufts, reducing light penetrating to the soil and diminishing the availability of bare soil necessary for the establishment of many species. As a result, very little seedling recruitment occurred and small species were the first to disappear.

Besides, the lack of disturbance also limited creation of suitable micro-sites, which in turn may have hampered seedling establishment and survival. The repeated periods of grazing and treading by cattle, on the other hand, result in repeated periods of gap formation, which provide space and favorable light conditions for germination and seedling recruitment (Grubb, 1977). Its absence may also explain the significant decline in small-scale species richness in mown plots. Whereas grazing took place throughout the vegetation season, creating suitable micro-sites during a longer period of time, mowing only occurred at the end of the growing season. Because seed set and dispersal vary across species during the growing season, the temporal unavailability of micro-sites may have prevented some species from becoming established in mown plots, leading to their gradual decline and finally disappearance.

4.2. Density and composition of the seed bank

The average seed bank density found across all treatments (2994 seeds m^{-2}) was similar to that reported for other grasslands (Bossuyt and Honnay, 2008). However, when comparing seed bank densities with those reported for other calcareous grasslands, we found relatively high seed bank densities. For example, Willems and Bik (1998) reported seed bank densities of 770 seeds m^{-2} , Bossuyt et al. (2006) 930 seeds m^{-2} , Akinola et al. (1998) 2549 seeds m^{-2} and Kalamees and Zobel (2002) 2362 seeds m^{-2} . There are numerous factors that can affect seed bank density. Because the soil in this grassland community is relatively deep compared to other calcareous grasslands on rocky substrate, it can be assumed that many seeds can accumulate in the soil. However, seed bank density quickly declined with increasing depth, indicating that soil depth had no major impact on seed density. Soil depth is therefore unlikely to be an important factor determining seed bank density in this grassland. More likely, high seed production, low rates of seed predation and presence of a few species with a long-lived seed bank explain the relatively higher seed bank densities than in other studies. In addition, the time of sampling could also have affected seed density. Because samples were taken in November, most plants had shed their seeds. Species with the highest seed bank densities (*B. perennis*, *D. carota*, *L. vulgare*, *P. lanceolata*) were also very common in the vegetation. On the other hand, many species typical of calcareous grasslands (*Carex caryophylla*, *Centaurea scabiosa*, *Crepis biennis*, *Pimpinella saxifraga*, *P. media*, *P. veris*) had very low seed bank densities. For some of these species, low seed bank densities can be explained by low abundances in the vegetation, but for others that were quite common, low seed bank densities are probably related to the short-lived, transient nature of their seed banks (Thompson et al., 1997; Bekker et al., 1998).

4.3. Effects of management on seed bank density and composition

We found strong differences in seed bank density and composition 11 years after different management treatments (grazing, mowing and abandonment) were installed. Grazed plots showed the highest seed bank densities, whereas seed bank densities were lowest in abandoned plots. These results strongly contrast with findings of Bossuyt et al. (2006), who could not find a decline in seed bank densities in recently abandoned calcareous grassland that were developing into scrub vegetation. Similarly, Milberg (1995) and Bakker et al. (1996) could also not find significant differences in seed bank density and species richness between grassland and spontaneously established forest or scrub 18 years after grazing abandonment. Milberg (1995) explained his findings by the occurrence of one or two species that make up 80–90% of the seed bank. Because in our case Shannon's diversity and equitability indices were not significantly different between grazed, mown or abandoned plots, dominance of one or a few species in one of the treatments cannot explain the strong differences in seed bank densities between the different treatments. More likely, the swift response of the aboveground vegetation to changes in management, the strong decline in species richness and reduced flowering performance of the remaining plants in abandoned plots (Brys et al., 2004), in combination with the short-lived, transient nature of the seed banks of the observed species, explain the strong decline in species richness and density in abandoned plots.

4.4. The role of seed banks in mediating restoration of calcareous grasslands after abandonment

Because in our highly fragmented landscapes, seed flow between remnant calcareous grassland patches has been shown to

be limited (Honnay et al., 2007; Jacquemyn et al., 2010), seed banks can play an important role in restoring plant diversity in calcareous grasslands. However, because most perennial grassland species have only relatively short-lived seeds, restoration possibilities from the seed bank are very limited (Bossuyt et al., 2006). Our data clearly indicate that species richness both in the aboveground vegetation and the seed bank quickly declined after plots were abandoned. Because some species (e.g. *Leontodon hispidus*, *Lotus corniculatus*, *Medicago lupulina*, *C. biennis*) were no longer present in the seed bank after abandonment, whereas others only occurred in very low abundances (e.g. *P. veris*, *C. scabiosa*, *C. caryophylla*), other possibilities need to be considered to restore recently abandoned calcareous grasslands. Artificial introduction of species as seed mixtures, green hay or turf transplants have been proposed as possible means to introduce seeds of calcareous grassland species in these fields (Rosén and van der Maarel, 2000; Walker et al., 2004). Because maintenance of species diversity significantly depends on management, it is clear that restoration can only succeed when the traditional management practices such as grazing and mowing are re-installed.

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