Effect of grassland management on the age and reproduction structure of *Helianthemum nummularium* and *Lotus corniculatus* populations

Vliv obhospodařování travního porostu na populační strukturu druhů *Helianthemum nummularium* a *Lotus corniculatus*

Peter Poschlod[1], John Hoffmann[1] & Markus Bernhardt-Römermann[1,2]

Dedicated to the memory of Leoš Klimeš

[1]*Institute of Botany, Faculty for Biology and Preclinical Medicine, University of Regensburg, D-93040 Regensburg, Germany, e-mail: peter.poschlod@biologie.uni-regensburg.de;* [2]*Institute for Ecology, Evolution and Diversity, University of Frankfurt, D-60438 Frankfurt am Main, Germany*

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Dry calcareous grasslands are among the most species-rich and endangered ecosystems in the Central-European landscape. They are of anthropogenic origin and mainly a result of grazing by domestic animals. Due to land-use changes in the last century, particularly in the 1960s, they were often abandoned or afforested. Therefore, in 1975 long-term experiments were started in the southwestern Germany (Baden-Württemberg) to determine the effectiveness of alternative management treatments in maintaining grasslands and their species composition. The aim of this study was to assess the effect of grazing (reference management treatment), mowing once a year, mulching twice a year, mulching every second year, burning once a year and succession (abandonment) on the population structure (in terms of density, age structure, reproduction mode) and seasonal germination niche of a dwarf shrub, *Helianthemum nummularium*, and a herbaceous plant, *Lotus corniculatus*. To study the age structure, annual ring analyses were applied. The classification of the reproduction mode, either by seed or vegetatively, was carried out by differentiating the central under-ground organ either as a root (in this case the individual has established from seed) or rhizome (the individual has developed from clonal multiplication). The seasonal germination niche was derived from the age structure. Management clearly affected population density and age structure. Highest density of individuals was found in the grazing and the lowest in the succession treatment. In the mulching every second year and succession treatments populations were senescent. Management also affected reproduction mode in *H. nummularium*. Regeneration by seed was especially enhanced by mowing and burning but was inhibited by mulching twice and succession. In the latter treatments *H. nummularium* reproduced only clonally. *Helianthemum nummularium* germinated mainly in autumn but burning by breaking the dormancy of seeds initiated germination in spring. A similar pattern was detected in *L. corniculatus*: burning increased germination rate in spring. Comparing population characters (density, age, reproduction mode) to the traditionally used grazing treatment, mowing was most similar and for *L. corniculatus* additionally burning. This is in contrast to the assessment of the vegetation of the management treatments where mowing and mulching twice per year maintain a similar floristic composition. Finally, the analysis of the population structure revealed important mechanisms behind population and vegetation dynamics.

Keywords: abandonment, ageing of plant populations, burning, calcareous grassland, clonality, conservation, demography, grazing, mowing, mulching, population structure, population viability, seasonal germination niche

Introduction

Calcareous grasslands are among the most species-rich ecosystems in the Central-European landscape. They have developed as a result of different land-use practices such as either grazing – in most cases – or more recently in a few cases, mowing or a combination of both. Fire was used as another management treatment (Poschlod et al. 2009a) since at least the period of the Roman Empire (Poschlod & Baumann 2010). Many calcareous grasslands originated from abandoned arable fields in the 19th and beginning of 20th century (Karlík & Poschlod 2009). However, since the 1960s, grassland areas have markedly declined in size and number due to agricultural intensification (Wallis DeVries et al. 2002). They are only used today for grazing sheep and rarely goats, but not cattle.

This is also true for the Swabian Jurassic Mountains where calcareous grasslands were once widespread (Mattern et al. 1980). In the 1970s, long-term experiments on grassland management were started in the Swabian Jurassic Mountains and the Black Forest (Baden-Württemberg, southwestern Germany) in order to determine the effect of alternative methods of management, like mowing, mulching or burning rather than grazing, on species composition and species richness (Schreiber 2009a, b). To assess the value of the different types of management for nature conservation, species composition and richness were compared between alternative treatments and grazed sites. Moog et al. (2002) and Poschlod et al. (2009b) showed that only mowing and mulching twice per year resulted in a similar diversity to grazing.

This approach, however, does not provide a thorough understanding of the mechanisms resulting in the changes in vegetation. Therefore, functional trait analyses were used to reveal the processes of vegetation changes using the functional identities of favoured or suppressed species (Kahmen et al. 2002, Kahmen & Poschlod 2008a). Römermann et al. (2009) showed that mowing and mulching applied at different frequencies may increase the dominance of clonal species. A comparable affect was recorded in burning treatments by Kahmen & Poschlod (2008a).

In addition, management that favours species with the ability for clonal resprouting also favours those with germination niches appropriate for the current environmental conditions. The denser and thicker the litter layer in autumn (e.g. mulching late in the year, no treatment resulting in succession), the fewer seedlings were detected in autumn (Kahmen & Poschlod 2008b). Burning at the end of winter favoured species with physiological dormancy (Schreiber et al. 2009b, Drobnik et al. 2011).

An alternative but less frequently applied method used to assess the effect of management and understand the processes affecting vegetation and population dynamics is the analysis of the population structure of target species (Rabotnov 1950, Dietz & Ullmann 1998, Schweingruber & Poschlod 2005). However, in all recent studies only assessments of age or size classes are used (Oostermeijer et al. 1994, 1996, Valverde & Silvertown 1998, Bühler & Schmid 2001, Colling et al. 2002, Lienert et al. 2002, Bissels et al. 2004, Endels et al. 2004). Such an approach only allows a very rough and vague assessment of how well populations may regenerate. To understand how management affects the regeneration process, e.g. in which season a species regenerates by seed, or to understand if a clonal species regenerates by seed or vegetatively, populations should be analysed based on their age and individual regeneration status. Schweingruber & Poschlod (2005) demonstrated how to use anatomical features like annual rings to determine the age of 800 woody and herbaceous species of plants in the Central-European flora. Although a single study of the population structure may not replace a demographic study, it can give a deep insight into the extent environmental processes, like disturbance by different management treatments, which may affect reproduction, regeneration and senescence of a population (Watt 1955, Kerster 1968, Dietz & Ullmann 1998, Schweingruber & Poschlod 2005).

Therefore, in this paper an analysis of the population structure and regeneration status of two species in a calcareous grassland, which is part of the grassland management experiments Baden-Württemberg (Schreiber et al. 2009a) is used to address the following questions: (i) Are population density and age structure of the dwarf shrub *Helianthemum nummularium* and the herbaceous plant *Lotus corniculatus* affected by different land use or conservation management practices? (ii) Do different management treatments affect the reproduction mode of *H. nummularium*? (iii) Is it possible to relate differences in the seed germination periods of the two species studied to different management practices?

Materials and methods

Study area and management treatments

This study was carried out in 2002 in a calcareous grassland (*Gentiano-Koelerietum* s.l.) at St. Johann, in the Swabian Jurassic Mountains in Baden-Württemberg (southwestern Germany; 760 m a.s.l., mean annual precipitation 1000 mm, mean temperature 7.6 °C; Schreiber 2009b). Up to 1974, the site was subject to low-intensity grazing by sheep. Since 1975 the suitability of alternative management forms was assessed relative to traditional grazing. The objective was to keep the grasslands open or, in other words, to suppress the establishment of trees and shrubs but maintain the species richness and composition (Schreiber 2009a). In this study the following management treatments were used: grazing (by sheep; GR), mowing once per year (end of August/beginning of September; MO), mulching twice per year (end of June/beginning of July, end of August/beginning of September; 2M), mulching late every second year (end of August/beginning of September; M2), burning once per year (March/beginning of April; 1B) and natural succession (S), which is abandonment. Mowing once per year was the most frequently used alternative management when grazing decreased due to cheap wool imports in the 1970s and has virtually ceased due to financial restrictions. Instead, mulching is now recommended in compliance with the common agricultural policy of the European Commission.

Study species and regeneration

The species studied were *Helianthemum nummularium* subsp. *obscurum* (Čelak.) Holub and *Lotus corniculatus* L. Both are typical and common species in calcareous grasslands but differ in their modes of regeneration. Furthermore, both species produce clearly definable annual rings (Dietz & Fattorini 2002, Schweingruber & Poschlod 2005).

Helianthemum nummularium subsp. *obscurum* is a clonal dwarf shrub. Clonal offspring and individuals established from seed were easily identified either by their growth form or the anatomy of the under-ground organ (Fig. 1). Individuals that developed from seed had a vertically growing taproot, which in cross-section lacks pith. Each seedling consists of only a primary shoot and primary root. After overwintering new shoots are pro-

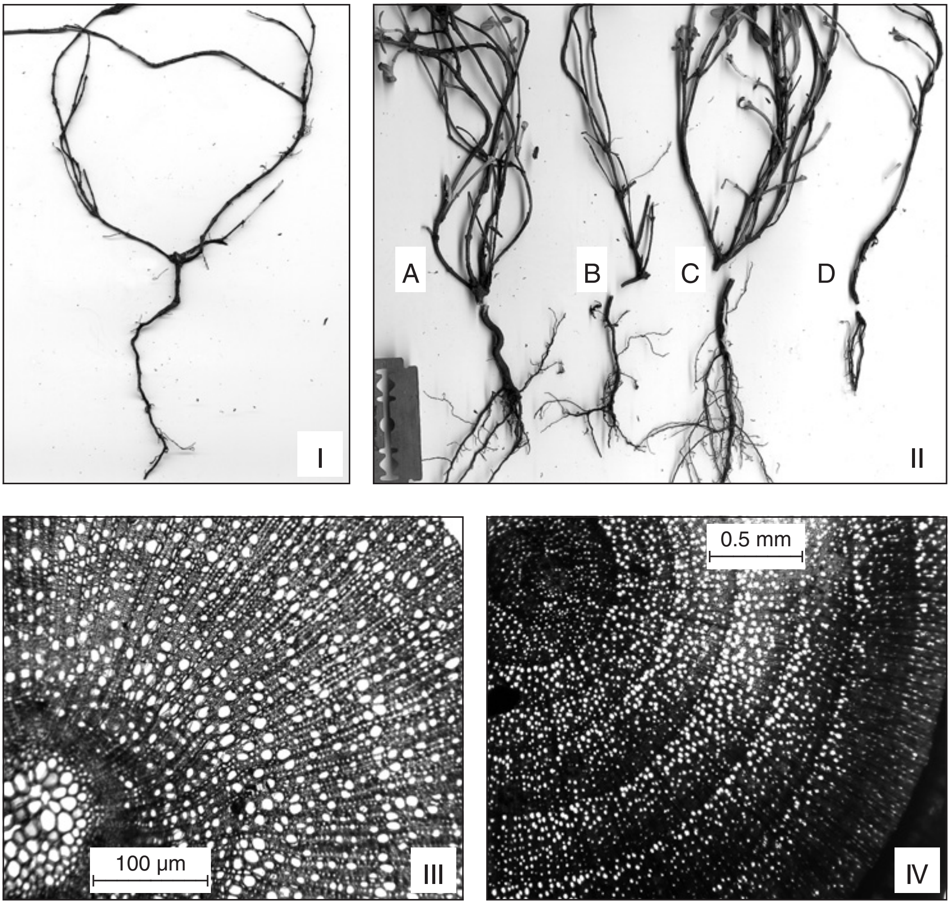

Fig. 1. – Root system of *Helianthemum nummularium*. I – individual established from seed, 2-years old with primary taproot; II – individuals established by clonal mutliplication with rhizomes and adventitious roots (A, B: 3-years old; C: 2-years old; D: 1-year old individuals); III – cross-section of the rhizome with pith in the centre and annual rings; IV – cross-section of the root collar without pith in the centre and with visible annual rings.

duced in the form of horizontal above- or below-ground branches from the base of the primary shoot. On below-ground stems adventitious roots may develop. Branches can separate from the parent plant producing physically independent clonal offspring (ramet), which can be recognized by horizontal below-ground stem with adventitious roots (rhizome), which in cross-section lacks pith. These branches may also form new shoots. Annual rings are clearly visible in cross-sections of the shoot base, rhizome, root collar (transition zone between root and shoot) and taproot (Fig. 1).

Lotus corniculatus is a non-clonal herbaceous plant with a central vertical tap root. Annual rings in cross-sections of the shoot base or root collar are easily measured (Fig. 2). Regeneration is by seed only. The seeds of both species have a hard seed coat and undergo a physical dormancy (Thanos et al. 1992, Baskin & Baskin 1998).

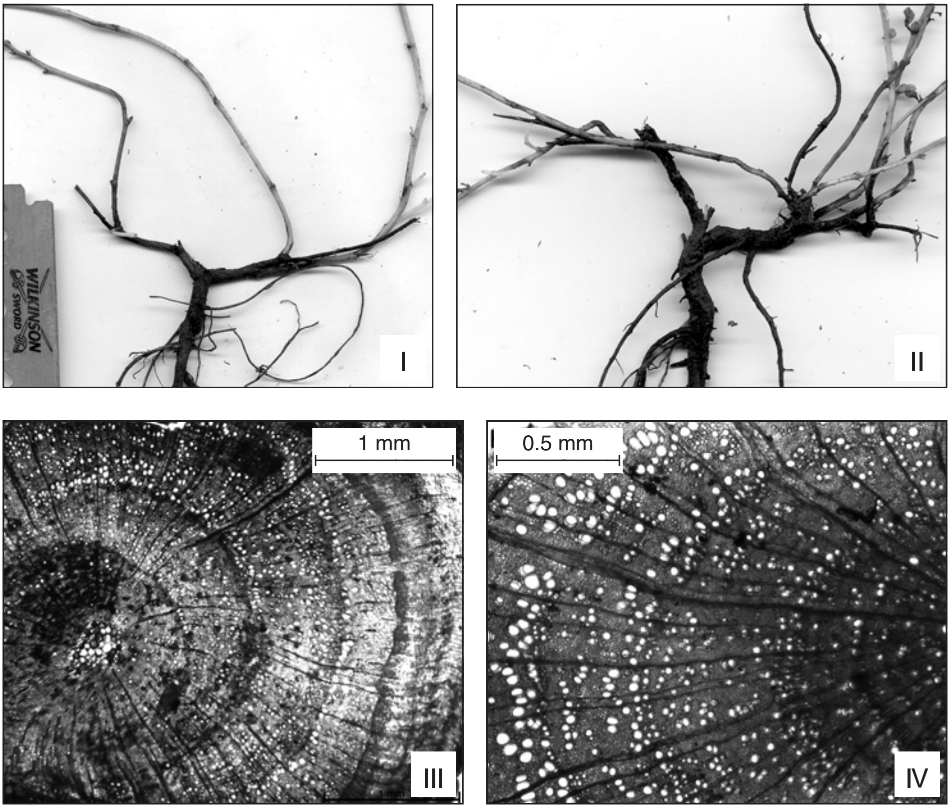

Fig. 2. – Root system of *Lotus corniculatus* with primary taproot. I – 4-years old plant; II – 5-years old plant; III – cross-section of the shoot base with pith in the centre and annual rings; IV – cross-section of the root collar without pith in the centre and with annual rings.

Seed germination

Soil was excavated in June 2002. If seedlings from the same year were found, germination may have occurred in spring or over the whole season. If no seedlings were found, but only one-year old juveniles, it is assumed that germination occurred in autumn (see e.g. Kahmen & Poschlod 2008b).

Data collection

In each treatment (for a detailed description see Schreiber 2009a) 12 to 44 plots 1m^2 in size were randomly established. The number of plots sampled depended on the density of individuals per m^2 in each treatment. The aim was to analyse at least 100 individuals per treatment. For *H. nummularium* the following numbers of individuals were sampled: GR – 259, MO – 142, 2M – 210, M2–132, 1B – 114, S – 56. For *L. corniculatus* the numbers were: GR – 219, MO – 116, 2M – 152; M2–41, 1B – 223, S – 4.

On all 1 m^2 plots all individuals (including seedlings) of the respective species were cautiously excavated and separated from the soil. In the case of *H. nummularium* an individual was defined as a physically independent plant either established from seed (generative regeneration – with a taproot) or by clonal multiplication (with a rhizome) with no traces indicating that the rhizome was severed during excavation. Plants were kept in 30% ethanol solution until the origin (generative regeneration or clonal multiplication) and age were determined.

To assess the age of each individual thin cross-sections of either, the shoot base, root collar or rhizome were prepared and stained with FCA (fuchsin, chryosidine, astral blue). The method followed Schweingruber & Poschlod (2005).

The following parameters were assessed: (i) number of individuals established per plot by generative regeneration or clonal multiplication (only *H. nummularium*) and (ii) the age of each individual based on the number of annual rings.

Data analyses

The effects of different types of management on population density (number of individuals per m^2), and mean population age were tested using one-way analysis of variance (ANOVA) with subsequent Tukey-tests (data for both species were normally distributed with homogeneous variances).

To compare the age structures recorded in the six different types of management, the data were separated into five age classes: (i) seedlings; (ii) 1-year old plants; (iii) 2-years old plants; (iv) 3–10-years old plants; and (v) plants older > 10 years. This classification represents crucial stages in the life-cycle of individual plants; seedlings and one-year old individuals have just become established and first flowering occurs in the second year. The class 3–10 years contained adult plants (about 80% flowering), while plants of the class >10 years can be characterized as "old". (Schweingruber & Poschlod 2005). Because age-class data were not normally distributed, differences between treatments were tested using Kruskal-Wallis H-tests with subsequent Mann-Whitney U-tests. P-values of the U-test were corrected for multiple comparisons using the procedure proposed by Holm (1979). This method (sometimes also called Bonferroni-Holm correction) is known to be less restrictive than the frequently applied Bonferroni correction, and is therefore more suitable for ecological studies.

All statistical tests were done using R 12.0.1 (R Development Core Team 2010).

Results

Effects of the different types of management on population density and age structure

The type of management affected the number of plants per m^2 and mean age of the populations of both species significantly (Tables 1, 2). For *H. nummularium* the highest densities per m^2 were recorded in the grazing treatment, followed by mowing and the other treatments (Table 1). The lowest density was recorded in the succession and the mulching every second year treatments. In contrast, the mean age of the population was highest in the succession treatment, followed by mulching every second year and burning treatments. In addition to population density and mean population age, the age structure was also significantly affected by management (Table 3).

Table 1. – Effect of different types of management on density and age of individuals of *Helianthemun nummularium*. (i) Results of ANOVA for all individuals per m^2 and separately for plants established by clonal multiplication (veg) and generative regeneration (gen) are shown: df – degrees of freedom, F-values and corresponding levels of significance (*** P < 0.001). (ii) Results of post-hoc Tukey-tests of the effects of individual treatments; those that do not differ significantly (P < 0.05) are indicated by the same superscripts following means. SE – standard errors, N – number of plots sampled. Management treatments: GR – grazing; 2M – mulching twice a year; MO – mowing with removing of litter once a year; M2 – mulching every second year; 1B – burning once a year; SU – succession.

	Plants/m^2						Age	
	Gen & veg		Veg		Gen			
ANOVA	df	F-value	df	F-value	df	F-value	df	F-value
	5	27.51***	5	31.27***	5	13.02***	5	30.47***
Treatment	Mean±SE	N	Mean ± SE	N	Mean±SE	N	Mean±SE	N
GR	21.6±2.12^{a}	12	15.7±1.85^{a}	12	5.9±0.76^{a}	12	3.6±0.20^{ac}	12
2M	9.5±1.38^{bd}	15	8.5±1.26^{b}	15	0.9±0.30^{b}	15	3.5±0.34^{ac}	15
MO	13.1±1.51^{b}	16	6.3±0.96^{b}	16	6.9±1.18^{a}	16	3.2±0.18^{a}	16
M2	3.6±0.54^{c}	28	1.9±0.35^{c}	28	1.7±0.38^{b}	28	6.4±0.42^{b}	25
1B	7.1±1.63^{cd}	16	2.5±0.56^{c}	16	4.6±1.12^{a}	16	5.5±0.82^{bc}	14
SU	3.3±0.73^{c}	17	2.5±0.61^{c}	17	0.8±0.32^{b}	17	10.9±0.69^{d}	13

Table 2. – Effect of different types of management on density and age of individuals of *Lotus corniculatus*. (i) Results of ANOVA are shown: df – degrees of freedom, F-values and corresponding levels of significance (*** P < 0.001). (ii) Results of post-hoc Tukey-tests of the effects of individual treatments; those that do not differ significantly (P < 0.05) are indicated by the same superscripts following means. SE – standard errors, N – number of sampled plots. Management treatments: GR – grazing; 2M – mulching twice a year; MO – mowing with removing of litter once a year; M2 – mulching every second year; 1B – burning once a year; SU – succession.

	Plants/m^2		Age	
ANOVA	df	F-value	df	F-value
	5	38.18 ***	5	6.53 ***
Treatment	Mean ± SE	N	Mean ± SE	N
GR	13.9±2.92^{a}	12	4.0±0.48^{ab}	12
2M	7.7±1.73^{b}	15	3.2±0.31^{ac}	14
MO	3.8±0.44^{c}	40	3.1±0.25^{ac}	37
M2	1.3±0.46^{cd}	29	5.1±0.58^{b}	10
1B	13.9±1.78^{a}	16	2.2±0.15^{c}	16
SU	0.1±0.05^{d}	44	4.8±1.42^{b}	3

The highest population density of *L. corniculatus* was recorded in the grazing and burning treatments (Table 2) and the lowest in the succession and mulching every second year treatments, in which only a few individuals survived. Mean age was highest in the mulching every second year, succession and grazing treatments.

The type of management affected the age structure of the *L. corniculatus* populations significantly. Regeneration by seed was strongly reduced by mulching every second year and did not occur in the succession treatment. The population in the first treatment was clearly overaged, but only four individuals of different ages were recorded in the latter treatment. In all other treatments most of the individuals or ramets were 3–10 years old

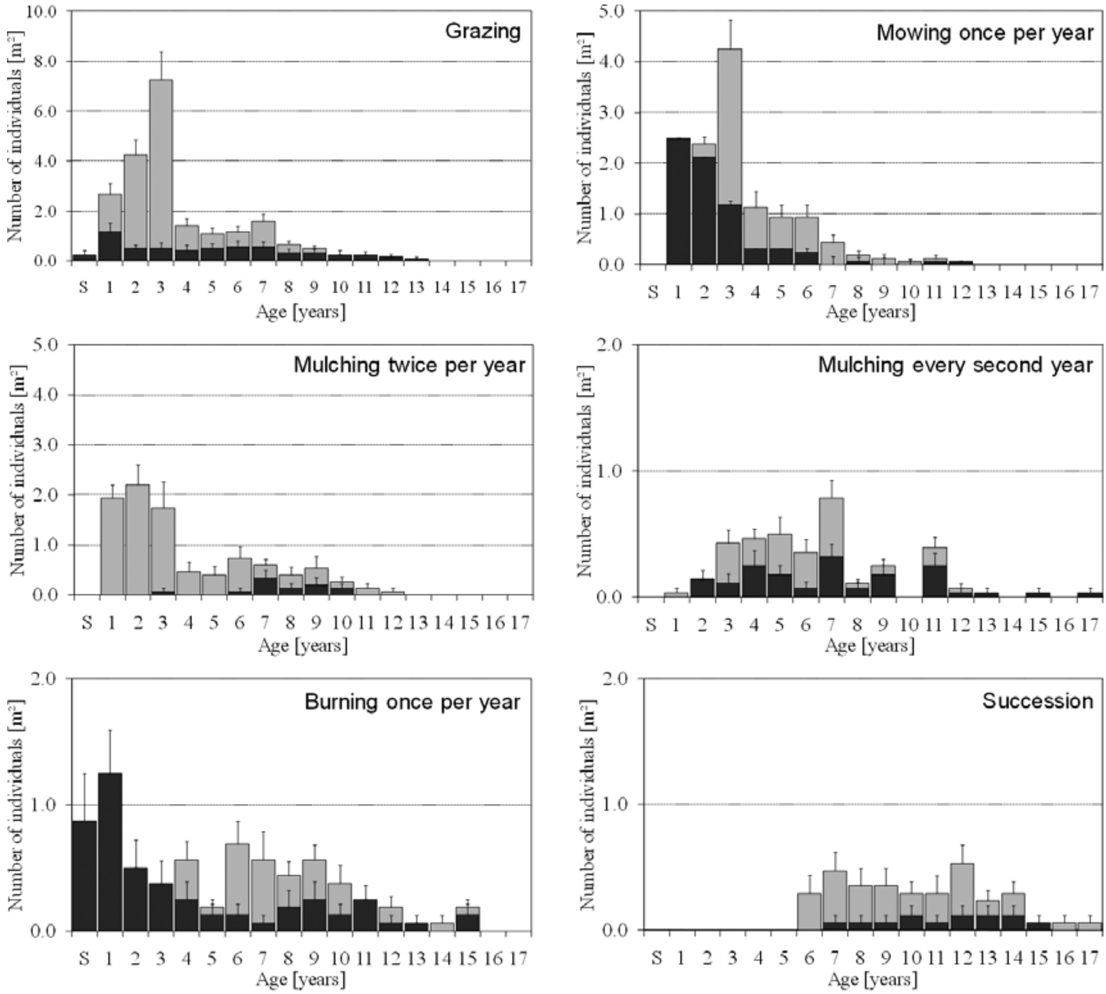

Fig. 3. – Comparison of age structures of *Helianthemum nummularium* in the six treatments. Mean numbers of individuals per m^2 are given separately for plants established by clonal multiplication (grey) and generative regeneration (black).

(Table 3). In *H. nummularium*, however, reduced regeneration by seed was associated with an increase in clonal reproduction (Table 3, Fig. 3).

Effects of type of management on clonal reproduction in Helianthemum nummularium

Treatments significantly affected the type of regeneration in *H. nummularium*. Generative regeneration was highest in the mowing, burning and grazing treatments and did not occur in the mulching twice and succession treatments (Table 1, Fig. 3). The youngest individual established from seed in the mulching twice treatment was 3 years old. All other individuals established from seed were between 6 and 10 years old (Table 3, Fig. 3).

Table 3. – Effect of the different types of management on density of different age classes of *Helianthemum nummularium* and *Lotus corniculatus*.(i) Results of Kruskal-Wallis H-tests. Age classes: S – Seedlings; 1-year old plants; 2-years old plants; 3–10 years old plants; >10 – plants older than 10 years. Veg – plants established by clonal multiplication, gen – plants established by generative regeneration. ** P < 0.01; *** P < 0.001; n.s. – not significant. (ii) Post-hoc U-tests with adjusted P-values for multiple comparisons. Treatments that do not differ significantly are indicated by the same superscript following means. SE – standard error, N – number of plots sampled. Management treatments: GR – grazing; 2M – mulching twice a year; MO – mowing with removing of litter once a year; M2 – mulching every second year; 1B – burning once a year; SU – succession.

		Helianthemum nummularium						*Lotus corniculatus*	
		Plants/m^2 (gen & veg)		Plants/m^2 (veg)		Plants/m^2 (gen)		Plants/m^2	
Age class	df	chi^2-value		chi^2-value		chi^2-value		chi^2-value	
S	5	–		–		22.77***		72.87***	
1	5	66.89***		76.50***		69.15***		73.68***	
2	5	63.92***		80.88***		40.16***		71.92***	
3–10	5	42.67**		41.15***		23.99***		91.75***	
> 10	5	17.17**		18.62**		10.24 n.s.		5.96 n.s.	
	Treatment	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N
S	GR	–	–	–	–	0.2±0.18^{a}	12	0.6±0.34^{a}	12
	2M	–	–	–	–	0.0±0.00^{a}	15	0.5±0.17^{a}	15
	MO	–	–	–	–	0.0±0.00^{a}	16	0.8±0.16^{a}	40
	M2	–	–	–	–	0.0±0.00^{a}	28	0.1±0.05^{b}	29
	1B	–	–	–	–	0.9±0.38^{b}	16	3.8±0.83^{c}	16
	SU	–	–	–	–	0.0±0.00^{a}	17	0.0±0.00^{b}	44
1	GR	2.7±0.54^{a}	12	1.5±0.44^{a}	12	1.2±0.34^{a}	12	2.2±0.89^{ac}	12
	2M	1.9±0.27^{a}	15	1.9±0.27^{a}	15	0.0±0.00^{b}	15	1.2±0.38^{ac}	15
	MO	2.5±0.38^{a}	16	0.0±0.00^{b}	16	2.5±0.38^{a}	16	0.4±0.11^{a}	40
	M2	0.0±0.04^{b}	28	0.0±0.04^{b}	28	0.0±0.00^{b}	28	0.0±0.03^{b}	29
	1B	1.2±0.35^{b}	16	0.0±0.00^{b}	16	1.2±0.35^{a}	16	3.4±0.75^{c}	16
	SU	0.0±0.00^{b}	17	0.0±0.00^{b}	17	0.0±0.00^{a}	17	0.0±0.00^{b}	44
2	GR	4.2±0.59^{a}	12	3.8±0.62^{a}	12	0.5±0.15^{a}	12	3.3±1.04^{a}	12
	2M	2.2±0.40^{ab}	15	2.2±0.40^{a}	15	0.0±0.00^{b}	15	1.3±0.41^{a}	15
	MO	1.8±0.41^{bd}	16	0.2±0.14^{b}	16	2.1±0.60^{a}	16	0.3±0.09^{b}	40
	M2	0.1±0.07^{c}	28	0.0±0.00^{b}	28	0.1±0.07^{b}	28	0.2±0.12^{b}	29
	1B	0.5±0.22^{cd}	16	0.0±0.00^{b}	16	0.5±0.22^{ab}	16	2.2±0.44^{a}	16
	SU	0.0±0.00^{c}	17	0.0±0.00^{b}	17	0.0±0.00^{b}	17	0.0±0.02^{b}	44
3–10	GR	13.9±1.69^{a}	12	10.4±1.37^{a}	12	3.5±0.60^{a}	12	7.8±1.19^{a}	12
	2M	5.1±1.12^{bc}	15	4.2±1.06^{bc}	15	0.9±0.30^{bc}	15	4.7±1.20^{ab}	15
	MO	8.1±1.07^{ab}	16	5.9±0.86^{b}	16	2.1±0.69^{ab}	16	2.2±0.29^{b}	40
	M2	2.9±0.45^{c}	28	1.7±0.32^{c}	28	1.2±0.31^{bc}	28	1.0±0.35^{c}	29
	1B	3.8±0.89^{bc}	16	2.2±0.48^{c}	16	1.5±0.52^{bc}	16	4.6±0.70^{a}	16
	SU	1.8±0.52^{c}	17	1.5±0.44^{c}	17	0.3±0.19^{c}	17	0.1±0.05^{d}	44
>10	GR	0.5±0.26^{ab}	12	0.0±0.00^{a}	12	0.5±0.26^{a}	12	0.1±0.08^{a}	12
	2M	0.2±0.11^{a}	15	0.2±0.11^{a}	15	0.0±0.00^{a}	15	0.0±0.00^{a}	15
	MO	0.2±0.14^{a}	16	0.1±0.06^{a}	16	0.1±0.12^{a}	16	0.0±0.02^{a}	40
	M2	0.6±0.22^{ab}	28	0.2±0.09^{a}	28	0.4±0.16^{a}	28	0.0±0.00^{a}	29
	1B	0.8±0.27^{ab}	16	0.2±0.14^{a}	16	0.5±0.20^{a}	16	0.1±0.06^{a}	16
	SU	1.5±0.39^{b}	17	1.1±0.34^{a}	17	0.5±0.17^{a}	17	0.0±0.00^{a}	44

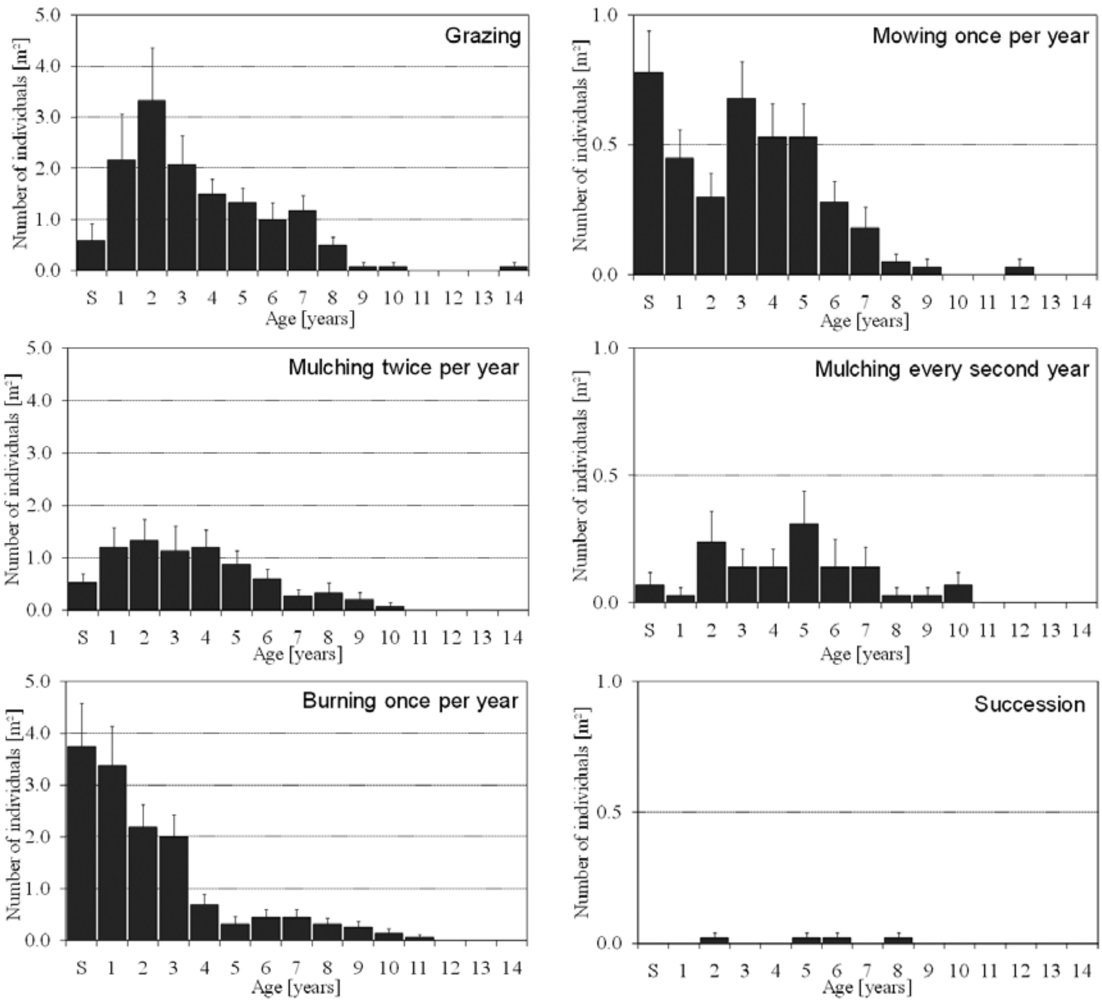

Fig. 4. – Comparison of the age structures of *Lotus corniculatus* in the six treatments. Mean numbers of individuals per m^2 are shown.

Clonal offspring were detached from the mother plant when the ramet was only one year old (Table 3, Fig. 3). In the succession treatment the youngest physically independent ramet was 6 years old.

Effects of management treatment on the time of germination

Germination in both species occurred in all treatments in autumn. One exception was *H. nummularium* in the burning treatment (Fig. 3) in which most of the seeds germinated in spring. Germination of *L. corniculatus* was recorded in both autumn and spring, but was significantly higher in spring in the burning and mowing treatments. Germination in both species was strongly reduced for mulching every second year and succession (Fig. 4).

Discussion

Effects of type of management on population density and age structure

Management had an obvious effect on population density and mean age. The total number of individuals decreased with decreasing frequency of disturbance. In contrast, mean age increased with decreasing frequency of disturbance. Differences in population density caused by management are also recorded for other grassland plants like *Primula veris* and *Succisa pratensis* (Bühler & Schmid 2001, Endels et al. 2004). Total plant density of *P. veris* was higher in populations managed by mowing or ditch clearing than in unmanaged populations at the edges of forests (Endels et al. 2004). Densities of seedlings and vegetative adults of *S. pratensis* are higher in mown than in grazed fens (Bühler & Schmid 2001). This supports the hypothesis that many open habitat species need small gaps for regeneration by seed. A denser vegetation structure resulting from less frequent management or abandonment, however, often results not only in lower population densities but also in older populations (Ooostermeijer et al. 1994).

The occurrence of senescent populations in less frequently managed or abandoned grasslands is reported for several non-clonal species like *Gentiana pneumonanthe* (Ooostermeijer et al. 1994) and *Trollius europaeus* (Schweingruber & Poschlod 2005). These populations are referred to as either senescent (Endels et al. 2004) or senile (Ooostermeijer et al. 1994). A reduction in the numbers of seedlings and juveniles relative to the number of adults is also reported in populations of *Primula vulgaris* in more closed forests (Valverde & Silvertown 1998). However, not only abandonment but also fertilization may affect the ageing of a population. In *Scorzonera humilis* senescent populations are found in more fertile grasslands where competition prevents the establishment of seedlings (Colling et al. 2002). This again is related to density, which was lower in old than in regenerating populations.

The question is if populations eventually become extinct when growing in unsuitable conditions like abandonment. For *L. corniculatus*, this is expected because the production of offspring ceases; even though single individuals can survive for up to 14 years. However, how long will a clonal species like *H. nummularium* survive? Will it go extinct because clones become senile or the conditions become unsuitable for growth? At the study site, the latter is more probable since succession in calcareous grasslands to closed shrub or forests after abandonment is rapid and *H. nummularium* is unable to survive when shaded (Kiefer 1998, Poschlod et al. 1998).

Type of management and clonal reproduction in Helianthemum nummularium

The more frequent disturbance by management (like mowing or mulching), the lower the probability that a species produces seeds. Therefore, only clonally reproducing species survive under such conditions (Kleijn & Steinger 2002). Phenological surveys of calcareous grasslands have shown that *H. nummularium* starts flowering in June and maturing seeds in July (Grunicke & Poschlod 1991). Seed dispersal starts at the earliest at the end of July. Therefore, management by mowing or mulching twice with the first cut at the end of June/beginning of July prevents successful seed set and accounts for the dominance of clonal reproduction under this type of management. Later flowering and successful seed set after the first cut is prevented by the second cut. The individuals within the population in this type of treatment are survivors from former seed regeneration and are with two exceptions at least 7 years old. Their continued occurrence 20 years after this form of management started maybe due to regeneration from a persistent seed bank although seed dispersal or successful seed set cannot be ruled out. Comparative studies of the seed bank along a successional sere have shown that the seeds of *H. nummularium* may persist for up to 20 years (Kiefer 1998, Poschlod et al. 1998).

Clonal multiplication is also enhanced in the grazing and succession treatments. Similar to the preceding case, this may be due to frequent disturbance and the selective removal of generative reproductive structures by sheep (Pakeman 2004). Kahmen & Poschlod (1998) show that an increased clumping in *Arnica montana* populations in abandoned *Nardus stricta* grasslands is caused by clonal growth but no regeneration by seed. Similarly Bissels et al. (2004) claim there is a shift from generative to vegetative reproduction in *Serratula tinctoria*. As shown experimentally for species occurring either in forests or abandoned land, lack of regeneration can often be related to microsite limitation (Eriksson & Ehrlén 1992, Eriksson & Froeborg 1996). Prach & Pyšek (1994) and Bernhardt-Römermann et al. (2008) report an increase of clonal plants in several successional seres (as long as sites redevelop to forest, Dölle et al. 2008).

Management treatment and seasonal germination niche

The seasonal germination niche was affected by the type of management. Seeds with a hard seed coat and/or physical dormancy either germinate directly after seed dispersal in autumn when the seed coat is not completely hardened or when high temperatures soften the seed coat (Baskin & Baskin 1998). This also occurs in *H. oelandicum*, which is closely related to *H. nummularium* (Widén 1982). Seeds were capable of germinating immediately after maturation. Therefore, management that does not result in gaps in the sward canopy but in an accumulation of a thick litter layer may result in reduced germination rates and seedling numbers as observed in the mulching every second year and succession treatments. This confirms the findings of Kahmen & Poschlod (2008b) who showed that a dense litter layer decreases the germination and seedling establishment rate of species that mainly germinate in autumn while those that only germinate in spring are unaffected.

However, not only gaps but also fire may increase the germination rate in certain species. In both species germination on the burned plot occurred in spring, which accords with their physical dormancy. In the family *Cistaceae* the effect of heat on germination was reported for several Mediterranean *Cistus* (Roy & Sonié 1992, Herranz et al. 1999, Moreira et al. 2010) and two *Helianthemum* species (Perez-García & González-Benito 2006). The increase in the germination rates of *L. corniculatus* in spring in the mowing treatment and little germination recorded in other treatments may be explained by the fact that *L. corniculatus* not only produces hard coated but also soft coated seeds (Jones & Turkington 1986).

Conclusions

A comparison of the treatments shows that for *H. nummularium* only mowing results in a similar population structure (density, age, proportion of seed to clonal regeneration) to grazing. For *L. corniculatus*, burning is also recommended as it is equivalent to grazing. A comparison of vegetation composition, however, revealed that mowing and mulching twice was similar to grazing (Poschlod et al. 2009b). The population structure analysis revealed a different pattern to the floristic analysis. This is especially striking in the reproduction mode in *H. nummularium*. In contrast to the floristic analysis, the assessment of the population structure gives a deeper insight into the processes acting at the population level which, however, may finally result in the future in another vegetation pattern.

Based on this study a more frequent use of age-structure analysis based on the annual rings of woody and herbaceous species is recommended for studies in nature conservation. Even if such analyses are destructive, they may allow deeper insights into demographic processes, which cannot be replaced by simple classification of age classes. Especially for clonal plants, it is stressed that annual-ring analysis should be used as it allows the reconstruction of the mechanism of population dynamics based on a single sample.

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Souhrn

Suché vápencové trávníky náleží mezi druhově nejbohatší a současně nejohroženější ekosystémy středoevropské krajiny. Vznikly činností člověka a byly udržovány především pastvou. Kvůli změnám v obhospodařování krajiny v minulém století, obzvlášť v šedesátých letech, byly často opuštěny nebo zalesněny. Proto byl v roce 1975 založen dlouhodobý experiment v jihozápadním Německu (Bádensko-Würtembersko) za účelem testovat různé alternativní způsoby obhospodařování pro udržení trávníků a jejich druhového složení. Cílem této studie bylo zjistit vliv různého obhospodařování (pokračující pastva, kosení jednou v roce, mulčování dvakrát v roce, mulčování každý druhý rok, vypalování jednou v roce a opuštění) na populační strukturu (hustota, věková struktura, způsob reprodukce) a sezónní průběh klíčení u polokeře devaterníku penízkovitého (*Helianthemum nummularium*) a byliny štírovníku růžkatého (*Lotus corniculatus*). Pro studium věkové struktury byla využita analýza letokruhů. Způsob reprodukce (generativní nebo vegetativní) byl určován u devaterníku podle morfologie podzemního orgánu: v případě, že se jednalo o kořen, jedinec vznikl ze semene, pokud o oddenek, jedinec vznikl klonálním růstem. Sezónní průběh klíčení byl určen podle věkové struktury populace. Obhospodařování ovlivnilo populační hustotu a věkovou strukturu. Nejvyšší hustota jedinců byla nalezena na pasených plochách, nejnižší na opuštěných plochách. Na plochách mulčovaných každým druhým rokem a na plochách opuštěných byly populace složeny jen ze starých jedinců. Způsob obhospodařování ovlivnil také způsob obnovování populace *H. nummularium*. Generativní regenerace převažovala v kosených a vypalovaných plochách, ale byla potlačena v mulčovaných a opuštěných plochách, kde se druh rozmnožoval pouze klonálním růstem. Devaterník klíčil většinou na podzim, ale vypalování mělo za následek ukončení dormance a klíčení na jaře. Podobný efekt, zvýšení klíčení na jaře ve vypalovaných plochách, byl zjištěn u štírovníku. Srovnáním vlivu všech typů obhospodařování na populační strukturu studovaných druhů se ukázalo, že kosení, a u štírovníku také vypalování, jsou rovnocennými náhradami pastvy. Tento závěr je v rozporu s vegetační studií, kde se ukázalo, že pro zachování složení celého společenstva jsou vhodnými typy obhospodařování kosení a mulčování dvakrát ročně.

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