The effects of grassland management on plant performance and demography in the perennial herb *Primula veris*

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Summary

1. Because of changing land-use practices and abandonment, many European calcareous grasslands are under increasing threat. In order to protect those grasslands that remain, better insights into how plant populations respond to different management scenarios are needed.

2. Using transition matrix models and life-table response experiment (LTRE) analysis, the effects of different management strategies (grazing, summer and autumn mowing, and no management) on plant performance and population dynamics of the perennial herb *Primula veris* (Primulaceae) were experimentally studied. Data were collected between 1999 and 2003 in a species-rich calcareous grassland.

3. Early grazing (May) resulted in low population growth rates ($\lambda < 0.860$) and a mean annual population decline of 11%. Under these conditions, both the proportion of flowering individuals and flower and seed production per plant were low, resulting in seed limitation overall. However, when grazing started later in the growing season (early July) flowering probability and overall seed set increased, as did population growth rates ($\lambda > 1$).

4. Mowing in autumn (October) was the most favourable management scenario (mean $\lambda = 1.213$), resulting in high proportions of flowering individuals and a large seed output. Furthermore, this management yielded optimal conditions for recruitment and seedling establishment during the next growing season.

5. Summer mowing (mid-July) resulted in a similar increase of flowering and overall seed shed to autumn mowing, but recruitment rates were lower because of a dense and tall vegetation structure at the time of germination. Consequently, population growth rates (mean $\lambda = 1.045$) were lower compared with the autumn mowing regime.

6. No management of the grassland resulted in low growth rates ($\lambda < 0.843$) and a mean annual population decline of 35%, because of high mortality rates of each life stage and a lack of recruitment. Recruitment rates were strongly reduced by lowered flowering probabilities and limited germination possibilities.

7. *Synthesis and applications*. This study may enable conservation managers to understand better the effects of time and type of management on population dynamics of *P. veris*. In order to preserve the remaining populations of this long-lived species, management interventions can promote flowering and seed shed and reduce productivity of the vegetation by mowing in autumn. Finally, this study has clearly shown that the lack of any management, which is the fate of many abandoned calcareous grassland relicts, will seriously restrict the long-term survival of *P. veris*.

Key-words: elasticities, LTRE, population dynamics, recruitment, seed production, transition matrix models, vital rates

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Introduction

In central and northern Europe, calcareous grasslands are extraordinarily species-rich and diverse habitats (Willems 1982; Fischer & Stöcklin 1997). As a consequence of their dependency on human-induced disturbance, the distribution of many characteristic plant species is often related to traditional management practices. During recent decades, however, management strategies of these grasslands have often changed drastically because of intensification of agricultural land use or abandonment of small habitat patches (Fischer & Stöcklin 1997; Willems 2001; Dolek & Geyer 2002). Despite the relatively well-known effects of different management regimes and disturbance on community organization and species diversity (Bullock *et al*. 1994, 2001; Huber 1994; Schlapfer, Zoller & Korner 1998; Jacquemyn, Brys & Hermy 2003; Landsberg *et al*. 2003), their effects on individual plant populations have received far less attention. Consequently, there is an urgent need for studies that examine the effects of different management options with varying intensities of human-induced interference on individual plant performance and demography of plant populations in calcareous grasslands (Bullock *et al*. 1994; Lennartsson & Oostermeijer 2001). Long-term experiments may provide an excellent way to identify optimal management strategies that will guarantee the persistence of often small and isolated remnant plant populations (Kaye *et al*. 2001; Oostermeijer *et al*. 2002).

In general, dynamics of plant populations are determined by their vital rates (i.e. recruitment, death and growth rates; Schemske *et al*. 1994). As disturbances may affect each rate differently, it is essential to investigate different stages of the life cycle, and effects on life-cycle transitions and overall population growth. Phenological variation in reproductive individuals may have consequences for population dynamics (Pico, de Kroon & Retana 2002). Indeed, differences in environmental conditions may variably affect reproductive individuals, as was found in *Primula veris* L. (cowslip) and the related *Primula vulgaris* (Whale 1984; Brys *et al*. 2004).

Transition matrix models are appropriate tools with which to evaluate population dynamics and life histories of structured populations (de Kroon *et al*. 1986; van Groenendael, de Kroon & Caswell 1988; Horvitz & Schemske 1995; Ehrlén & van Groenendael 1998; Caswell 2001). Matrix models attempt to identify and quantify demographic processes of natural populations and to interpret the influence of environmental factors (Bastrenta, Lebreton & Thompson 1995). In general, two approaches can be used to explore how population statistics respond to changes in the life-cycle transitions. The first, 'prospective' analysis (sensitivity and elasticity), explores the functional dependence of the population growth rate (λ) on each life-cycle transition in the future, while the second, 'retrospective'

analysis, expresses variation in λ due to different environmental conditions as a function of variation in the life-cycle stage transitions (Caswell 2000). As de Kroon, van Groenendael & Ehrlén (2000) concluded, prospective analysis cannot be used as the sole tool to identify where population-management efforts should be directed. Moreover, one needs to know whether the actual causes of variation are random (due to environmental stochasticity) or manageable (e.g. related to habitat quality that may be manipulated), which clearly is a retrospective question. Although only rarely done (but see García & Ehrlén 2002; Kiviniemi 2002), both approaches need to be considered if the importance of variation in life-stage transitions is to be determined and efficient guidelines for management interventions formulated (Caswell 2000).

Primula veris is a characteristic species of calcareous grasslands. This species has shown a sharp decline, not only in the study area of Voeren (Belgium) but in larger parts of western Europe as well (Zoller & Wagner 1986; Kéry, Matthies & Spillmann 2000). In this study, the short-term effects of different management strategies on the population viability of *P. veris* were studied. We evaluated (i) the effect of four management scenarios on the performance of reproductive individuals, and (ii) the sensitivity of population growth rates to changes in life-cycle stage transitions of this species. The results allowed us to identify important life cycle transitions explaining observed differences in population growth as a result of the different management scenarios. This could then contribute to the maintenance or restoration of calcareous grasslands in general and *P. veris* populations in particular.

Methods

STUDY SPECIES

Primula veris (Primulaceae) is a small perennial herb typical of nutrient-poor grasslands, with a distribution ranging from Spain to eastern Asia (Hegi 1975). Early in spring, plants produce a rosette of several leaves and one (rarely two or more) flowering stalk that bears 5–15 yellow distylic flowers disposed in an umbel. Flowering usually begins in April and ends 3–4 weeks later in May. Seeds ripen in June–July. Flowers are mainly pollinated by *Hymenoptera* and *Diptera* (Woodell 1960). The seeds of this species have no special features facilitating dispersal, and the plant is therefore considered a barochorous species. Seedling emergence and survival rate are generally low (Tamm 1972) but vegetative propagation through side rosettes sometimes occurs (Tamm 1972; M. Kéry, personal communication). Under favourable conditions, adults can live for several decades (Inghe & Tamm 1988; Ehrlén & Lehtilä 2002). Leaves, inflorescences and flowers are sometimes damaged by insects or molluscs and are often destroyed by cattle grazing, which may affect future plant performance (García & Ehrlén 2002).

STUDY POPULATION

The study was conducted at the site of a large *P. veris* population in the eastern part of Belgium (Voeren) where the vegetation shows clear affinities with the Galio-Trifolietum. This community has a very restricted distribution range in western Europe (Schaminée & Zuidhoff 1995) and is characterized by species such as *P. veris*, *Plantago media* L., *Circium acaule* L. and *Ranunculus bulbosus* L. Traditional management consists of periodic cattle grazing, which is restricted to short periods (< 2 weeks) during the growing season (Schaminée & Zuidhoff 1995). This allows a large number of rosette plants to survive in this community (e.g. *Bellis perennis* L., *Leontodon hispidus* L., *Leucanthemum vulgare* Lam., *Succisa pratensis* Moench, *Prunella vulgaris* L., *Plantago lanceolata* L.; Schaminée & Zuidhoff 1995; Jacquemyn, Brys & Hermy 2003). The study site was a species-rich grassland, on a south-facing slope, with an inclination of 30° at an altitude of 180–210 m a.s.l. The soil is well buffered and poor in phosphorus (for details see Jacquemyn, Brys & Hermy 2003). About 10 000 plants (adults) of *P. veris* are present in the actual grassland. However, during the last decade site managers have noticed a remarkable decrease of the overall viability of the population.

EXPERIMENTAL DESIGN

In an experimental factorial design, temporal variation in population dynamics and plant performance was investigated over a 5-year period from 1999 to 2003 in permanent plots. Four different management regimes were applied to five plots measuring 3 × 3 m: (i) grazing; (ii) summer mowing (mid-July); (iii) autumn mowing (mowing after the growing season in early October); and (iv) no management. Plots were laid out in the central and most homogeneous part of the grassland. Except for plots that were grazed, all others were fenced. To avoid edge effects as a result of fencing and/ or trampling during data collection, only the central 1 × 1-m area of each plot was sampled. In the mown treatments, the vegetation was clipped 2–4 cm above the ground and litter was removed. Grazed plots received the same periodical grazing regime as the rest of the whole grassland as described above. Grazing too early in the growing season was thought to cause an overall decline in viability of the studied *P. veris* population, so the reserve managers restricted grazing to later in the growing season from 2001 onwards (early July).

Plots were monitored at the end of May from 1999 to 2003, resulting in a total of 1083 monitored *P. veris* plants over the whole study period (mean number of individuals per plot 51, range 24–90). At that time all plants had developed to their full size and seedlings had emerged. To avoid damage, plants were not tagged individually but were located by using a 10 × 10-cm grid. Each year all plants and newly observed seedlings
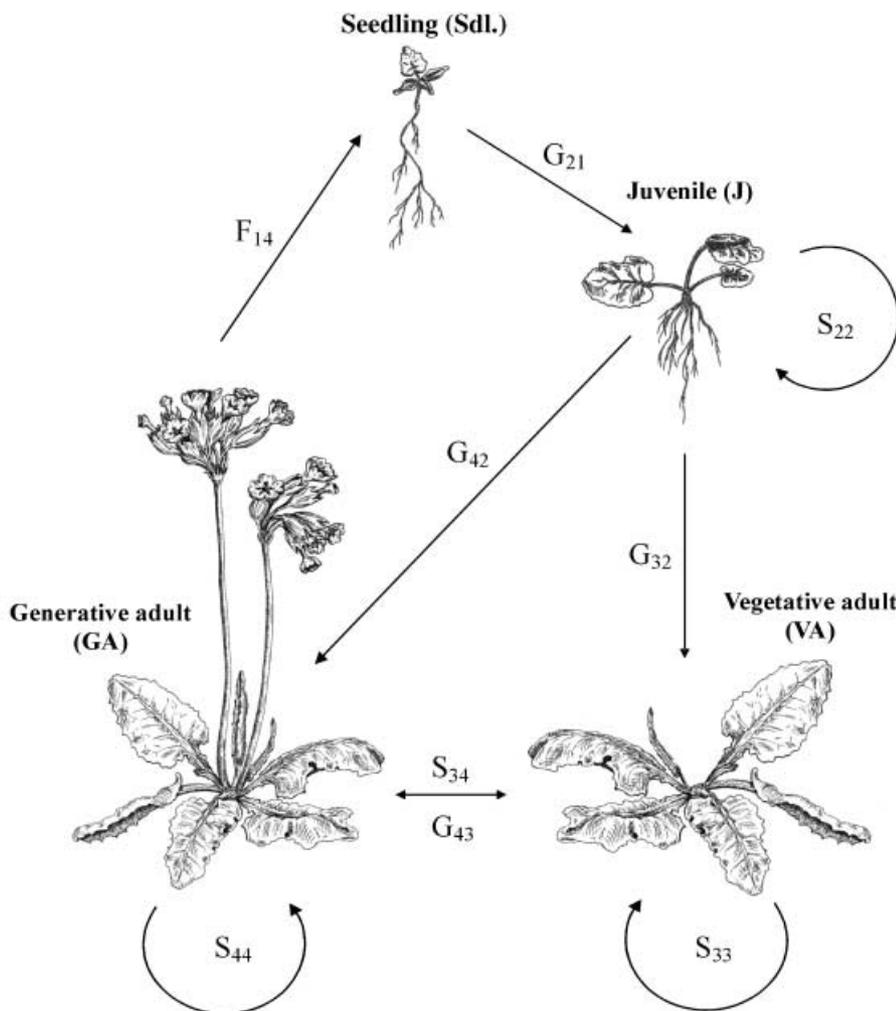
were mapped. With these time series, the fate of each individual plant in the sample was assessed, yielding population projection matrices for four growth periods: 1999–2000, 2000–01, 2001–02 and 2002–03.

To study the effect of different management scenarios on the performance of reproductive individuals, 30 suitable plants were randomly selected per treatment (six individuals per plot) in 1999, 2000, 2002 and 2003. The numbers of leaves, flower stalks and flowers of those individuals were recorded in early June. Leaf area was calculated using the formula of Syrjänen & Lehtilä (1993) and was used as an estimate of plant size, after multiplying by the total number of leaves per plant.

Mean seed production was estimated per management regime and year by collecting mature intact fruits from 15 individuals in the buffer area around the monitored 1 × 1-m plots. Seeds were counted in the laboratory and mean seed number per capsule was multiplied by total flower number to give per capita fecundity for flowering plants under each management regime.

PROJECTION MATRICES

Monitored plants were classified into different categories in order to build projection matrices. Three criteria were used to group plants: age (younger or older than 1 year), reproductive status of individuals (reproductive or vegetative) and size. This classification yielded four different classes: seedlings (younger than 1 year); juveniles (more than 1 year and number of leaves ≤ 3 and/or length of the largest leaf < 2 cm); vegetative individuals (more than 1 year and number of leaves > 3 and/or length of the largest leave ≥ 2 cm); and reproductive individuals (more than 1 year and bearing flowers; Fig. 1). Fecundity was calculated as the number of emerging seedlings partitioned according to the proportion of flowering individuals during the previous year. We assumed that seed quality was equal among individuals, management regimes and years. As a seed germination experiment showed no or very poor germination rates of *P. veris* seeds from the seed bank (R. Brys and H. Jacquemyn, unpublished results), a seed bank was not included as a matrix element. Thus, this model assumes that seeds do not remain in the soil for more than 1 year without germinating or dying. Furthermore, elasticity analysis on a hypothetical matrix projection model in which 25% of the produced seeds entered the seed bank revealed that this had only a marginal impact on population growth rates (< 3%; R. Brys and H. Jacquemyn, unpublished results). Finally, it was assumed that, once a seed enters the seed bank, the probability is high that it will stay in a dormant state, because *P. veris* seeds do not germinate in darkness (Milberg 1994). Because the soil of the grassland was not drastically disturbed under the management regimes applied, conditions for germination of buried seeds would not improve considerably. Hence, we concluded that the impact of a persistent seed bank on future recruitment and population growth

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Seedling (Sdl.)

F_{14}

G_{21}

Juvenile (J)

S_{22}

**Generative adult
(GA)**

G_{42}

G_{32}

**Vegetative adult
(VA)**

S_{34}

G_{43}

S_{44}

S_{33}

Stage at time *t*

		Sdl.	J	VA	GA
Stage at time *t* +1	Sdl.	0	0	0	F_{14}
	J	G_{21}	S_{22}	0	0
	VA	0	G_{32}	S_{33}	S_{34}
	GA	0	G_{42}	G_{43}	S_{44}

Fig. 1. Life-cycle graph of *P. veris* and its correspondence with the basic population projection matrix. Arrows represent the possible transitions between stages, and letters show the connection between each transition and its corresponding matrix entry. Matrix entries are subdivided into fecundity (F, i.e. number of seedlings per reproductive adult), growth (G, i.e. transition to higher stages) and survival (S, i.e. remaining at the same or retrogression to a lower stage).

rate would be small in these grasslands, and the model thus realistically represents the life cycle of *P. veris*.

A transition frequency matrix (4×4) of state at time *t* vs. state time *t* + 1 was constructed to calculate the a_{ij} entries of individual transition matrices. Dividing each entry of the frequency matrix by its column total yielded a maximum likelihood estimate of the transition probabilities (Caswell 2001). The power method was used to calculate the main demographic parameters of each population from the projection matrices: the dominant right eigenvector of the matrix and its associated eigenvalue correspond with the stable-stage

distribution and the finite rate of increase (λ) of the population, respectively, whereas the left eigenvector represents the stage-specific reproductive values (Caswell 2001). Transitions from the five plots per treatment were pooled before analysis to achieve a larger number of individuals in each age class, which yielded a more robust matrix (see the Appendix).

STATISTICAL ANALYSIS

Repeated-measures GLM was used, with management (grazing, autumn mowing, summer mowing and no

management), year (1999, 2000, 2002 and 2003) and the interaction term as fixed factors, to examine their effects on different plant traits (flowers per plant, seeds per plant and plant size). PROC GLM with a repeated statement was used to perform the overall analysis, to determine sphericity (Mauchly's test) and to generate univariate results. Plot means were used as repeated measures, resulting in five replicates per treatment. Variables were log-transformed to achieve normality and homoscedasticity of residuals.

A Kruskal–Wallis test was used to test for differences in proportional seedling emergence in year $t + 1$ per seed produced in year t, among the four management regimes.

Differences between mean proportional survival per life category in different management regimes and years were evaluated using a likelihood ratio test (*G*-test), which is a more robust test than χ^2 to evaluate goodness-of-fit (Sokal & Rohlf 1995).

Elasticity analysis was conducted in order to obtain the relative contribution of non-zero transition probabilities (a_{ij}) to λ and were scaled such that the sum of all values equalled 1; small perturbations to a_{ij} with high elasticity values would have strong impacts on population growth (de Kroon *et al.* 1986).

Non-parametric permutation tests were used to test for differences in population growth rates (λ) and elasticities of the transition elements between management regimes within years (Manly 1997). The observed assortment of individuals in the populations under the different management scenarios produced an observed difference (θ) in population growth rate and elasticity values (e_{ij}). The null hypothesis was that each management scenario received by an individual had no effect on its fate, thus: $\theta = |\lambda_1 - \lambda_2| = 0$ and $\theta = |e_{ij1} - e_{ij2}| = 0$. We calculated the distribution of θ under the null hypothesis by permuting individuals, with their history, among management treatments, maintaining the sample sizes for each management scenario. For each permutation, we repeated the whole series of calculations, from life table to transition matrix model to λ and the elasticity of each transition element, and then calculated the test statistic θ. A total of 2000 permutations was performed. If the observed value of the test was greater than $(1 - \alpha)\%$ of the value in the permutation distribution, then it was considered significantly different at the $\alpha\%$ level (Manly 1997). As multiple tests were conducted, Bonferroni corrections were applied. A Spearman rank correlation coefficient was assessed to determine the association between the calculated population growth rate and the observed proportional population increase or decrease.

Finally, life-table response experiment (LTRE) analysis with a fixed, factorial design was conducted to examine between-management and year variation in population growth rate. This analysis quantified the contribution of each matrix element on the observed difference in λ between management regimes and years. Following Caswell (2001), data from all manage-

ment regimes during the study period were pooled to calculate the overall mean matrix ($\mathbf{A}^{..}$). Consequently:

$$\lambda^{(my)} = \lambda^{(..)} + \alpha^{(m)} + \beta^{(y)} + (\alpha\beta)^{(my)}$$

where $\alpha^{(m)}$ and $\beta^{(y)}$ are the main effects of the *m*th level of management and the *y*th level of year, and $(\alpha\beta)^{(my)}$ is the interaction effect. $\lambda^{(..)}$ refers to the population growth rate of the overall mean matrix ($\mathbf{A}^{..}$). Following the methods of Horvitz, Schemske & Caswell (1997) and Caswell (2001) these effects can be decomposed into contributions from each matrix element:

$$\alpha^{(m)} = \sum(a_{ij}^{(m.)} - a_{ij}^{(..)})s_{ij}$$

$$\beta^{(y)} = \sum(a_{ij}^{(.y)} - a_{ij}^{(..)})s_{ij}$$

$$(\alpha\beta)^{(my)} = \sum(a_{ij}^{(my)} - a_{ij}^{(..)})s_{ij} - \alpha^{(m)} - \beta^{(y)}$$

Here, s_{ij} are the sensitivities of the *ij* transitions. To control for changes in the sensitivity structure that may occur from one treatment to another, sensitivity matrices were evaluated as a matrix that was intermediate between the particular management or year being considered and the overall mean matrix. Similar to Horvitz, Schemske & Caswell (1997), the mean matrix of the relevant pooled management or year matrix and the overall mean matrix ($\mathbf{A}^{..}$) were used for these calculations.

Results

PLANT TRAITS

The mean number of flowers and seeds per plant differed significantly between the management regimes applied ($P \leq 0.001$; Table 1 and Fig. 2a,b). Flowering

Table 1. Results of a repeated-measures analysis of variance for the effect of management (summer mowing, autumn mowing, grazing and no management) on plant traits in *P. veris* (1×1-m plots)

Source	d.f.	MS	F	P
Flowers per plant				
Management	3	0·151	7·03	0·003
Error	16	0·021		
Year	3	0·183	13·28	< 0·001
Year × management	9	0·041	2·95	0·007
Error (year)	48	0·014		
Seeds per plant				
Management	3	1·175	24·96	< 0·001
Error	16	0·047		
Year	3	0·453	10·77	< 0·001
Year × management	9	0·383	9·09	< 0·001
Error (year)	48	0·042		
Plant size				
Management	3	0·079	27·42	< 0·001
Error	16	0·028		
Year	3	1·588	464·30	< 0·001
Year × management	9	0·023	6·59	< 0·001
Error (year)	48	0·003		

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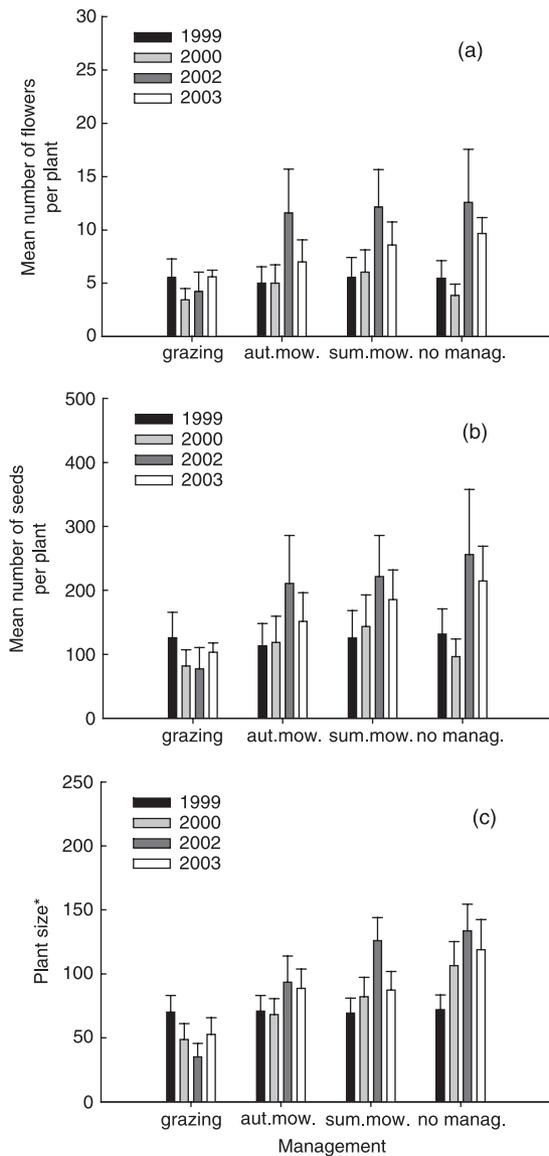*Plant performance
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Fig. 2. Mean (± SE) of (a) number of flowers, (b) number of seeds and (c) size of generative individuals (*for the formula see Syrjänen & Lehtilä 1993) in 1999, 2000, 2002 and 2003, under four management regimes, in *P. veris*.

Fig. 3. Mean (± SE) proportional number of seedlings per seed in year *t* + 1 in relation to mean (± SE) seed shed per m² the previous year *t*, under four management regimes in *P. veris* (number of years = 4; number of 1 × 1-m plots = 5).

Fig. 4. Mean proportion of individuals surviving each year (± SE) in the different life stages (S, seedlings; J, juveniles; VA, vegetative adults; GA, generative adults) in *P. veris* during the years 1999–2000, 2000–01, 2001–02 and 2002–03. *G*, likelihood ratio statistic.

RECRUITMENT AND LIFE-STAGE TRANSITIONS

Mean proportional germination was significantly related to the management regime applied (Kruskal–Wallis χ^2 = 14·12, d.f. = 3, $P = 0·003$; Fig. 3). Autumn mowing resulted in the highest germination rates, which was on average two-fold higher than under the grazing regime (mean proportional germination ± SE = 0·027 ± 0·002 and 0·014 ± 0·002, respectively), whereas summer mowing and no management resulted in strongly lowered germination rates (mean proportional germination ± SE = 0·007 ± 0·001 and 0·003 ± 0·001, respectively).

Annual survival varied significantly between different management regimes for the seedling and juvenile life stages (Fig. 4). Seedlings showed by far the lowest annual survival, and survival was very low in the undisturbed plots (< 20%). Grazing and autumn mowing, on the other hand, resulted in the highest annual survival

individuals under the no management treatment produced increasing numbers of flowers and seeds during the experiment, while grazing resulted in the lowest reproductive success per plant. Tests of within-subjects showed that year significantly determined both reproductive factors ($P < 0·001$; Table 1 and Fig. 2a,b) and interacted significantly with management ($P < 0·01$; Table 1). Significant management, year and interaction effects were also found for the mean size of *P. veris* adults (Table 1 and Fig. 2c). Furthermore, the results showed that 2002 was a very good year for overall plant performance of *P. veris*, except under the grazing treatment (Fig. 2). However, in 2003 individuals seemed to recover slightly from the high grazing pressures in 1999 and 2000 and earlier, while under the other management regimes plant performance was lower compared with the year before (Fig. 2).
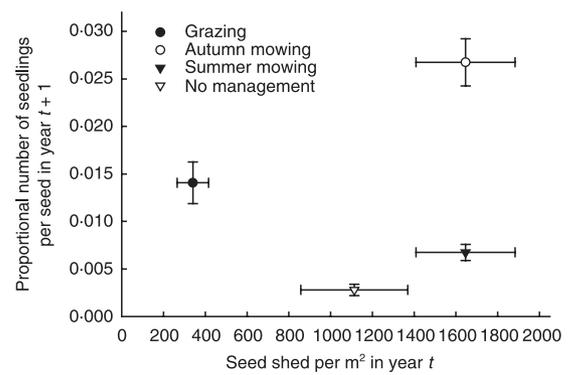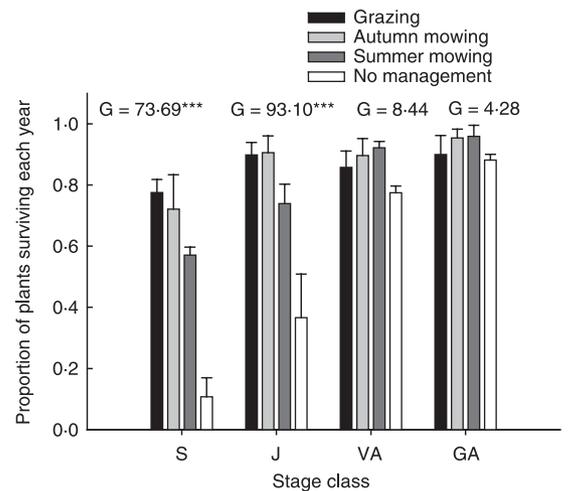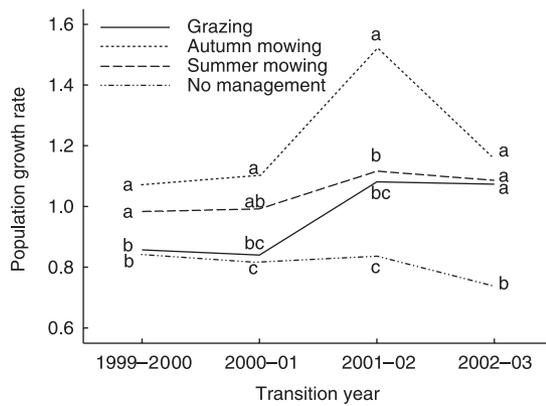
Fig. 5. Population growth rate (λ) for each management regime (grazing, autumn mowing, summer mowing and no management) and year (1999–2000, 2000–01, 2001–02 and 2002–03) in *P. veris*. Results of a non-parametric randomization test (Manly 1997) to test for the statistical significance of management regime on population growth rate per year, are presented by subscripts (a, b, c and d). Population growth rates with different subscripts in each year differ significantly from each other ($P < 0.005$).

rates of this stage. Juvenile mortality, again, was highest in the unmanaged situations (< 50%), while the other management scenarios resulted in a much higher survival rate, varying from 70% up to 90%. For both adult stages, annual survival was quite high (mostly > 80%; Fig. 4) and no significant differences between the management types applied were found (Fig. 4).

POPULATION PROJECTION ANALYSIS

Population growth rates varied from 0·739 to 1·523 (Fig. 5 and Table 2). Autumn mowing resulted in the highest growth rates, whereas the no management situation resulted in the lowest growth rates. During the first year, population growth rates were significantly different between both mowing regimes on the one hand, and the no management and grazing treatments on the other hand ($P < 0.05$). Apart from summer mowing not differing significantly from grazing anymore, a similar pattern was observed the following year. The third year was characterized by a remarkable increase in the population growth rates for all regimes except for the no management treatment. In this year, autumn mowing resulted in a population growth rate that differed significantly from all other population growth rates, while differences between summer mowing vs. grazing and grazing vs. no management were not significant. In the last year, however, population growth rates decreased under both mowing regimes and in the no management situation. Finally, population growth rates and the annual observed proportion of population increase or decrease were significantly and positively correlated ($r_s = 0.938$, $n = 16$, $P < 0.001$).

ELASTICITIES

For all management regimes, λ was found to be most sensitive to perturbations in the matrix element representing the likelihood of vegetative adults remaining in

Table 2. Comparisons of population growth rates (λ) and elasticity values of each life-cycle transition among management scenarios (summer mowing, autumn mowing, grazing and no management) per year in *P. veris*

	Sm	Am	G	Nm		Sm	Am	G	Nm
1999–2000					**2000–01**				
λ	0·98[a]	1·07[a]	0·86[b]	0·84[b]		0·99[ab]	1·10[a]	0·84[bc]	0·82[c]
F_{14}	0·09[ab]	0·15[a]	0·06[b]	0·01[c]		0·06[a]	0·07[a]	0·08[a]	0·00[b]
G_{21}	0·09[ab]	0·15[a]	0·06[b]	0·01[c]		0·06[a]	0·07[a]	0·08[a]	0·00[b]
S_{22}	0·00[b]	0·03[a]	0·01[ab]	0·00[b]		0·00[a]	0·00[a]	0·00[a]	0·00[a]
G_{32}	0·09[ab]	0·15[a]	0·06[b]	0·01[c]		0·06[a]	0·07[a]	0·08[a]	0·00[b]
S_{33}	0·30[c]	0·27[c]	0·58[b]	0·73[a]		0·53[b]	0·59[b]	0·53[b]	0·90[a]
S_{34}	0·11[a]	0·04[c]	0·06[bc]	0·10[ab]		0·09[a]	0·05[a]	0·05[a]	0·05[a]
G_{42}	0·00[a]	0·00[a]	0·00[a]	0·00[a]		0·00[a]	0·00[a]	0·00[a]	0·00[a]
G_{43}	0·20[a]	0·19[a]	0·13[b]	0·12[b]		0·15[a]	0·12[a]	0·13[a]	0·05[b]
S_{44}	0·12[a]	0·01[b]	0·04[ab]	0·02[b]		0·05[a]	0·02[a]	0·06[a]	0·00[b]
2001–02					**2002–03**				
λ	1·12[b]	1·52[a]	1·08[bc]	0·83[c]		1·09[a]	1·16[a]	1·07[a]	0·74[b]
F_{14}	0·12[a]	0·15[a]	0·09[a]	0·00[b]		0·08[b]	0·14[a]	0·08[b]	0·00[c]
G_{21}	0·12[a]	0·15[a]	0·09[a]	0·00[b]		0·08[b]	0·14[a]	0·08[b]	0·00[c]
S_{22}	0·00[a]	0·00[a]	0·00[a]	0·00[a]		0·00[a]	0·00[a]	0·02[a]	0·00[a]
G_{32}	0·12[a]	0·15[a]	0·09[a]	0·00[b]		0·08[b]	0·14[a]	0·08[b]	0·00[c]
S_{33}	0·06[b]	0·08[b]	0·52[a]	0·35[a]		0·26[c]	0·22[c]	0·50[b]	0·91[a]
S_{34}	0·09[b]	0·00[c]	0·08[b]	0·25[a]		0·14[a]	0·08[ab]	0·08[ab]	0·04[b]
G_{42}	0·06[a]	0·00[b]	0·03[ab]	0·00[b]		0·00[a]	0·02[a]	0·00[a]	0·00[a]
G_{43}	0·15[a]	0·15[a]	0·12[b]	0·11[b]		0·23[a]	0·21[a]	0·15[b]	0·04[c]
S_{44}	0·27[a]	0·30[a]	0·00[b]	0·28[a]		0·12[a]	0·06[ab]	0·03[b]	0·00[c]

Values followed by different letters are significantly different ($P < 0.01$).
Sm, summer mowing; Am, autumn mowing; G, grazing; Nm, no management.

this stage (S_{33}; Table 2), while the second most influential transition stage appeared to be growth of vegetative adults entering the flowering stage (G_{43}). Elasticity values of stasis of vegetative adults were significantly smaller under both mowing regimes compared with the undisturbed and grazed situation for all years, except in the year 2000–01 (Table 2), whereas the opposite was found for growth of vegetative adults into a flowering stage (Table 2). Elasticities for fecundity (F_{14}), seedling growth to a juvenile stage (G_{21}) and growth of juveniles to vegetative adults (G_{32}) were significantly larger under both mowing regimes and grazing compared with the undisturbed situation. Moreover, autumn mowing mainly resulted in the highest elasticity values of these life-cycle stage transitions. Stasis of flowering individuals (S_{44}), and survival (S_{22}) as well as growth of juveniles into a flowering stage (G_{42}), resulted in the lowest elasticity values overall (Table 2).

LIFE-TABLE RESPONSE EXPERIMENTS

LTRE analysis showed that mowing in autumn had the largest positive effect on variation of λ, whereas a lack of management gave the largest negative effect (Fig. 6a). Compared with autumn mowing and no management, the contribution of grazing was more than four-fold smaller and negative, while summer mowing had a slightly larger but positive influence on λ. Year 2001–02 had the largest impact and was the only year that showed a positive contribution to the difference in λ within years (Fig. 6b), while the first 2 years appeared to be the most negative for λ. Furthermore, temporal patterns differed among management treatments, as demonstrated by management-by-year interactions (Fig. 6c). Positive interactions indicated that λ increased faster than predicted by the additive model. This was found under autumn mowing for all years, and grazing and summer mowing for the years 2001–02 and 2002–03. Strongly negative interactions were observed under grazing and no management for the first 2 years and all years, respectively.

The transitions in the life cycle of *P. veris* that contributed most to the variation of λ because of management effects were growth of vegetative adults (G_{43}), fecundity (F_{14}) and growth of seedlings to a juvenile stage (G_{21}) (Table 3). For all these transitions, autumn mowing affected them most strongly and in a positive way, while the reverse was true for the impact of no management. Under grazing and summer mowing, fecundity and growth of seedlings to a juvenile stage were, respectively, negatively and positively affected. In contrast to grazing, summer mowing affected flowering of vegetative adults positively, resulting in higher population growth rates than under grazing. Matrix entries that have been most influential in determining the temporal variation in λ within management regimes were flowering of vegetative adults (G_{43}), stasis in the flowering stage (S_{44}) and stasis in the vegetative stage (S_{33}) (Table 3). It appeared that the positive year effect
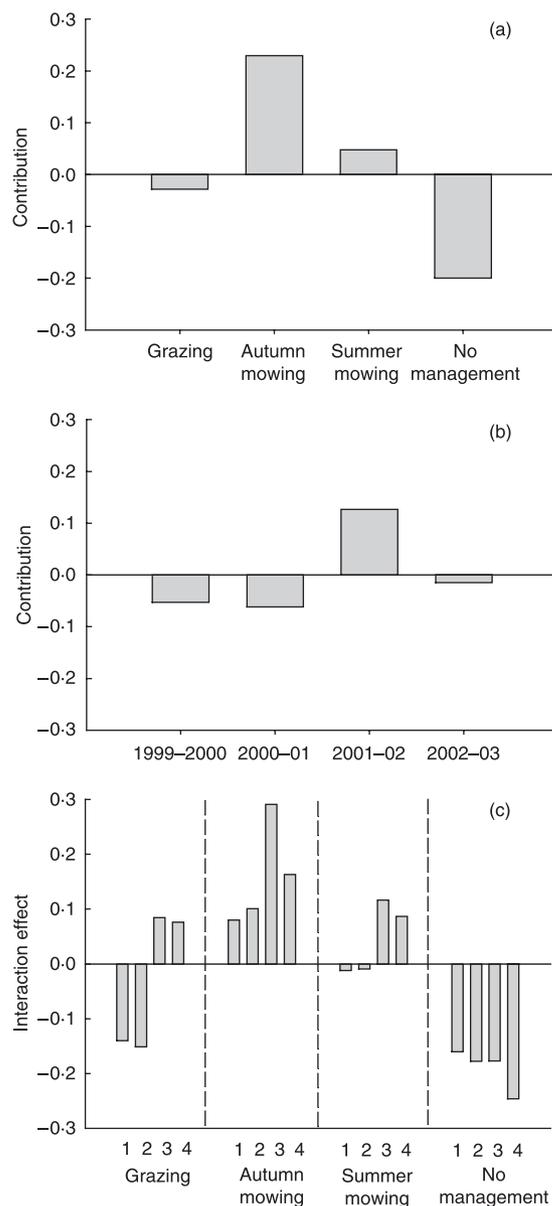
Fig. 6. Results of the LTRE analysis. The main effects of (a) management (grazing, autumn mowing, summer mowing and no management), (b) years (1999–2000, 2000–01, 2001–02 and 2002–03) and (c) interaction effects, in which years (1, 1999–2000; 2, 2000–01; 3, 2001–02; 4, 2002–03) are shown within each management regime, in *P. veris*.

of 2001–02 was mainly the result of increased probabilities of vegetative individuals entering the flowering stage and of reproductive individuals continuing flowering.

Discussion

This experimental study documents the impact of different management scenarios on the response of a typical long-lived grassland herb, *P. veris*. Although the observed population dynamics under the changing management scenarios (both mowing regimes and no management) are in a transitory phase, this work has provided clear insights into how management affects

Table 3. Contribution of each life-cycle transition to the management, year and management by year interaction effect on the observed variation in population growth as obtained by LTRE analysis in *P. veris*. Life-cycle transitions are subdivided into fecundity (F, i.e. number of seedlings per reproductive adult), growth (G, i.e. transition to higher stages) and survival (S, i.e. remaining at the same or retrogression to a lower stage)

	Management effects				Year effects			
	Sm	Am	G	Nm	1999–2000	2000–01	2001–02	2002–03
F_{14}	−0·039	0·105	−0·022	−0·035	−0·007	−0·004	0·023	−0·009
G_{21}	0·005	0·036	0·031	−0·042	0·015	−0·010	0·000	−0·005
S_{22}	−0·004	−0·001	0·004	0·001	0·005	−0·001	−0·005	0·001
G_{32}	0·003	0·035	0·014	−0·023	0·011	0·009	−0·013	−0·012
S_{33}	−0·036	−0·008	0·048	0·006	−0·010	0·067	−0·037	−0·004
S_{34}	−0·029	−0·008	0·011	0·017	0·000	0·013	−0·038	0·015
G_{42}	0·006	−0·005	0·002	−0·003	−0·006	−0·005	0·018	−0·003
G_{43}	0·101	0·048	−0·090	−0·096	−0·039	−0·111	0·093	0·021
S_{44}	0·040	0·026	−0·025	−0·024	−0·020	−0·020	0·084	−0·019

	Interaction effects							
	1999–2000	2000–01	2001–02	2002–03	1999–00	2000–01	2001–02	2002–03
	Sm				Am			
F_{14}	−0·054	−0·042	−0·017	−0·037	0·114	0·075	0·156	0·059
G_{21}	0·012	−0·005	0·001	0·011	0·065	−0·029	0·067	0·041
S_{22}	−0·004	−0·003	−0·005	−0·004	0·017	−0·004	−0·006	−0·006
G_{32}	0·020	0·021	−0·048	0·002	0·031	0·038	0·041	0·018
S_{33}	−0·045	0·059	−0·076	−0·054	−0·028	0·142	−0·053	−0·041
S_{34}	−0·030	−0·004	−0·087	−0·009	0·016	0·019	−0·118	0·007
G_{42}	−0·005	−0·004	0·053	−0·006	−0·012	−0·006	−0·013	0·010
G_{43}	0·067	−0·026	0·164	0·151	−0·074	−0·113	0·182	0·085
S_{44}	0·028	−0·004	0·132	0·033	−0·048	−0·021	0·274	−0·010
	G				Nm			
F_{14}	−0·076	−0·023	0·007	−0·007	−0·045	−0·042	−0·038	−0·016
G_{21}	0·036	0·023	0·040	0·020	−0·040	−0·020	−0·076	−0·036
S_{22}	0·003	0·000	−0·004	0·016	0·004	0·002	−0·002	−0·001
G_{32}	0·012	0·013	0·015	0·015	−0·006	−0·017	−0·027	−0·034
S_{33}	0·015	−0·002	0·095	0·084	0·031	0·074	−0·078	0·020
S_{34}	−0·013	−0·006	0·039	0·024	0·013	0·039	−0·033	0·022
G_{42}	−0·005	−0·006	0·024	−0·006	−0·003	−0·002	−0·003	−0·002
G_{43}	−0·096	−0·150	−0·074	−0·045	−0·081	−0·168	0·006	−0·158
S_{44}	−0·015	−0·001	−0·056	−0·025	−0·032	−0·043	0·075	−0·042

Sm, summer mowing; Am, autumn mowing; G, grazing; Nm, no management.

plant performance, life-cycle stage transitions and population growth rates (λ) in the short term.

The life-cycle transition that contributed most to the observed variance in λ under different management regimes was growth of vegetative individuals into the flowering stage. This transition showed the second highest elasticity value in the studied population, and was significantly larger under both mowing regimes compared with the grazing and no disturbance regime. The transition probability, however, with the highest elasticity value appeared to be stasis of vegetative adults, especially under a lack of disturbance and grazing. Surprisingly, the contribution of this transition stage on the observed population growth rates under the different management regimes was relatively small. This is in accordance with findings of Horvitz, Schemske & Caswell (1997) and Caswell (2000), who reported that transitions contributing most to the difference in population growth were not necessarily the ones with the

highest elasticity values. Thus, after stasis of vegetative adults, growth to reproductive individuals represents a critical life-history stage influencing population growth rate. Moreover, increasing flowering probabilities allows this long-lived perennial to expand rapidly under optimal environmental conditions, as recruitment depends strongly on seed production of the previous year.

Grazing applied early in the growing season resulted not only in the destruction of flowering stalks and fruits but also in reduced flowering probabilities and performance of adult individuals the following growing season. This is in accordance with observations of García & Ehrlén (2002), who reported that defoliation of *P. veris* at an early stage of plant development negatively affected current reproductive performance and future growth. Because *P. veris* invests considerable effort in above-ground growth and carbohydrate production each summer (Syrjänen & Lehtilä 1993), damage of above-ground tissue (such as leaves and/or flower

stalks) during the growing season may thus alter future performance of those individuals. Similar results have been found in *Hepatica nobilis*, where leaf removal in spring and early summer strongly reduced flowering during the following year (Inghe 1989). Given that destruction of *P. veris* flower stalks and fruits does not result in compensatory flower and fruit production later in the growing season, this inevitably results in reduced seed set and therefore in lower seedling recruitment. In the long run, a lack of seedlings may lead to reduced population size, as demonstrated by the low population growth rates and a mean annual population decrease of 11% observed under the early grazing regime. Similar reductions in recruitment, because of destruction of flowering adults by early grazing and/ or mowing, have also been reported in populations of other grassland herbs, such as *Gentiana pneumonanthe* (Oostermeijer, van't Veer & den Nijs 1994), *Succisa pratensis* (Bühler & Schmid 2001), *Salvia pratensis* (Hegland, van Leeuwen & Oostermeijer 2001) and *Gentianopsis ciliata* and *Gentianella germanica* (Oostermeijer *et al.* 2002). However, if grazing was applied later in the growing season (early July), it appeared that the population growth rate of *P. veris* increased (mean $\lambda = 1.08$), resulting in a mean annual population increase of 6%.

Strongly reduced population growth rates under a lack of management were partly the result of largely diminished flowering probabilities of adult plants. This was mainly because of increased competition with the surrounding vegetation and reduced light penetration through the vegetation canopy (Whale 1984; Valverde & Silvertown 1998; Jacquemyn, Brys & Hermy 2003; Endels *et al.* 2004). Under such conditions, only a limited number of individuals appeared to be able to flower and shed seed. Although those few flowering individuals produced proportionally more seeds per plant compared with reproductive individuals under the other management regimes, the absolute number of seeds was small. Besides the reduced seed density under no management, seed germination and seedling establishment were also limited, indicating that the process of recruitment was also reduced by a lack of suitable microsites. Reduced recruitment, together with elevated mortality rates of established individuals, resulted in a 35% annual decrease of population size and in skewed population structures with an excess of old adults. Similar 'regressive' population structures have also been reported in small and remnant populations of *P. veris* (Brys *et al.* 2003) and *P. vulgaris* (Jacquemyn *et al.* 2003) growing in small landscape elements deprived of any disturbance regime in the western part of Belgium. Oostermeijer, van't Veer & den Nijs (1994) and Colling, Matthies & Reckinger (2002) have observed similar population structures in *Gentiana pneumonanthe* and *Scorzonera humilis*, respectively, located in unmanaged grasslands.

Finally, summer (July) and autumn (October) mowing clearly had a positive impact on the probability that vegetative adults started flowering. Mowing not only increased the density of flowering plants, but flower and seed production per plant were also significantly larger compared with that of flowering individuals under the grazing regime. Both mowing regimes, however, affected the process of recruitment in a different way. Autumn mowing created ideal conditions and gaps in which seedlings could escape competition from established plants. Summer mowing, on the other hand, allowed vegetation recovery during the growing season resulting in a more dense vegetation structure the following spring, conditions that reduce recruitment in *P. veris*.

IMPLICATIONS FOR CONSERVATION MANAGEMENT

Changes in land use or abandonment are a major threat to the maintenance of high species diversity in calcareous grasslands (Hillier 1990; Fischer & Stöcklin 1997; Dolek & Geyer 2002). We have shown how changes in management affect plant performance and population demography of a long-lived perennial herb in the short term, as indicated by the significant correlation between the calculated population growth rate and the observed population increase or decrease. Our study revealed that the population growth rate of *P. veris* is most strongly affected by variation in the probability that vegetative adults start flowering. Moreover, this life-cycle transition responds strongly and in a different way to the time and type of the disturbance regime applied, making it a manageable life-cycle phase on which to focus population management efforts. Other important life-cycle transitions to maintain or restore populations of *P. veris* are seedling emergence and establishment, transitions that appeared to be positively affected by autumn mowing and grazing. However, grazing too early in the growing season reduced flowering probabilities of this rosette herb, and resulted in low population growth rates because of limited seed shed. Finally, it should be stressed that lack of any managed disturbance of the vegetation appeared to be very disadvantageous to this species. Traditional grazing or additional mowing has ceased on many of the steep slopes in the study area. Consequently, there are serious doubts regarding the long-term population viability of *P. veris* and other characteristic plant species in many abandoned calcareous grasslands. It is clear that habitat quality needs to be improved by adequate management intervention to avoid further extinction of this once locally abundant species. Many perennial rosette herbs with a similar life-history strategy find their optimum occurrence in nutrient-poor grasslands, suggesting that the processes and interactions between population demography and management reported in this work are relevant for other species too.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE981/JPE981sm.htm.

Appendix. Transition probabilities of each life-cycle transition under different management scenarios

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