
Effect of Habitat Deterioration on Population Dynamics and Extinction Risks in a Previously Common Perennial

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Abstract: *Habitat deterioration affects population viability and persistence of both plant and animal species. For plants the effect of changes in environmental conditions on population dynamics and extinction risks largely depends on the life span of the species. We used transition matrix models, a life-table response experiment, and stochastic simulations to investigate the overall effects of nitrogen enrichment (9, 6, 3, and 0 g N/m²/year) and grassland management (mowing and grazing) on vital rates, population growth rate (λ), and extinction risks of a previously common perennial herb (*Primula veris* [L.]). We experimentally manipulated 32 permanent plots that were monitored during a 5-year period. To study the effects of nitrogen addition and management on recruitment in more detail and to evaluate the role of seed availability, we experimentally sowed seeds at different densities. Nitrogen addition always resulted in negative population growth rates (range: 0.998 to 0.700), whereas mean population growth rates in the control situation were >1. Interaction effects indicated that the negative effect of increasing nitrogen addition decreased population growth rate more strongly when the vegetation was mown compared with grazing. Besides significantly increased mortality rates, especially in the youngest life stages, decreased population growth rates under nitrogen enrichment were mainly the result of reduced flowering probabilities, seed production rates per plant, recruitment, and establishment of seedlings. Mowing, however, encouraged growth of vegetative adults into a flowering stage and decreased germination and seedling establishment, whereas the reverse was observed under grazing. Under the highest nitrogen levels, mean times to extinction were much shorter than would be expected based on the longevity of the species, especially under mowing. These results demonstrate that even long-lived and formerly common perennial species may quickly respond to habitat deterioration, especially when the deterioration takes place over a short period of time.*

Key Words: LTRE analysis, nitrogen enrichment, population dynamics, *Primula veris*, stochastic simulations, vital rates

Efecto del Deterioro del Hábitat sobre la Dinámica Poblacional y el Riesgo de Extinción de una Perenne Previamente Común

Resumen: *El deterioro del hábitat afecta la viabilidad y persistencia poblacional de especies tanto de plantas como de animales. Para plantas, el impacto de los cambios en las condiciones ambientales sobre la dinámica poblacional y los riesgos de extinción depende en buena medida del tiempo de vida de la especie. Utilizamos modelos matriciales de transición, un experimento de respuesta de tabla de vida y simulaciones estocásticas para investigar los efectos del enriquecimiento de nitrógeno (9, 6, 3, y 0 g N/m²/año) y el manejo de pastizales (siega y pastoreo) sobre las tasas vitales, la tasa de crecimiento poblacional (λ) y el riesgo de extinción de*

una hierba perenne previamente común (*Primula veris* [L.]). Experimentalmente manipulamos 32 parcelas permanentes que fueron monitoreadas durante 5 años. Para estudiar con mayor detalle los efectos de la adición de nitrógeno sobre el reclutamiento y evaluar el papel de la disponibilidad de semillas, experimentalmente sembramos semillas en diferentes densidades. La adición de nitrógeno siempre resultó en tasas de crecimiento poblacional negativas (rango: 0.998 a 0.700), mientras que las tasas de crecimiento poblacional promedio estuvieron por encima de 1 en el tratamiento control. Los efectos de la interacción indicaron que el impacto negativo de la adición de nitrógeno sobre la tasa de crecimiento poblacional fue mayor cuando la vegetación fue segada que cuando fue pastoreada. Además del incremento significativo de las tasas de mortalidad, especialmente en las primeras etapas de vida, la disminución en las tasas de crecimiento poblacional bajo el enriquecimiento de nitrógeno principalmente fue resultado de la disminución de las probabilidades de florecer, de la producción de semillas por planta, del reclutamiento y establecimiento de plántulas. Sin embargo, el segado estimuló el desarrollo de la etapa de floración en adultos vegetativos y disminuyó la germinación y el establecimiento de plántulas, mientras que se observó lo contrario en condiciones de pastoreo. Bajo los niveles más altos de nitrógeno, el tiempo promedio de extinción fue mucho menor al esperado con base en la longevidad de la especie, especialmente en condiciones de segado. Estos resultados demuestran que aun las especies perennes longevas y previamente comunes pueden responder al deterioro del hábitat rápidamente, especialmente cuando esto sucede en un período corto de tiempo.

Palabras Clave: análisis LTRE, dinámica poblacional, enriquecimiento de nitrógeno, *Primula veris*, simulaciones estocásticas, tasas vitales

Introduction

Understanding the consequences of habitat deterioration for population viability and long-term persistence of both plant and animal species is a central theme in conservation research (Harrison & Bruna 1999; Debinski & Holt 2000). In most cases, degradation of habitat quality, mostly due to an increased impact of the surrounding landscape matrix on habitat patches, has been invoked as the most important determinant of the viability and long-term persistence of plant populations (Saunders et al. 1991; Harrison & Bruna 1999). Changes in habitat quality may be due to eutrophication (especially N) (Gotelli & Ellison 2002), edge effects (Jules 1998; Jules & Rathcke 1999; Moen & Jonsson 2003), or changes in disturbance regimes (Eisto et al. 2000; Lennartsson & Oostermeijer 2001). Nitrogen is unique among nutrients not only as a widespread air, soil, and water pollutant but also as the predominant limiting nutrient in terrestrial ecosystems (Fenn et al. 1998). In most cases, the deterioration of local habitat conditions due to increases in N deposition has resulted in decreased species diversity and local extinction of plant populations (e.g., Endels et al. 2002; Jacquemyn et al. 2003b, 2005).

The effects of habitat deterioration on long-term persistence of plant populations may strongly differ from one species to another (Fischer & Stöcklin 1997; Eriksson & Ehrlén 2001). Especially long-lived perennials may show a slow response to changing environmental conditions (Fischer & Stöcklin 1997; Eriksson & Ehrlén 2001). For these species, it may take some time before they reach their new equilibrium corresponding to the new environmental conditions (Eriksson et al. 2002; Hanski

& Ovaskainen 2002). Consequently, for perennials it is important to follow plants long enough to detect delayed responses. As a result, the question whether distribution patterns of plant species reflect persistent populations or populations that are in a steady state of decline cannot be answered based on patch occupancy patterns of plant species alone (Eriksson & Ehrlén 2001). These patterns may not be in equilibrium with the current landscape configuration, which may generate a so-called extinction debt (Hanski & Ovaskainen 2002). This implies that to comprehend plant distribution patterns in modern, cultural landscapes, the existence and magnitude of possible time delays in population responses to habitat deterioration should be determined (Eriksson & Ehrlén 2001; Hanski & Ovaskainen 2002; Hooftman et al. 2004).

To fully understand the effects of habitat deterioration on plant population demography and extinction risks, detailed descriptive demographic information is needed (Schemske et al. 1994; Menges 2000). Moreover, because changes in the environment may affect each vital rate differently, it is essential to analyze the effects on different parts of the life cycle to understand life-cycle transitions and overall population growth (e.g., Horvitz & Schemske 1995; Caswell 2001). For plants, however, most demographic studies consider only one or a few populations without taking habitat quality into account (Menges 2000; but see, e.g., Oostermeijer et al. 1996; Lennartsson & Oostermeijer 2001) or they have not adequately separated habitat quality effects between populations from those resulting from genetic or reproductive processes (Oostermeijer et al. 2003). Detailed demographic studies in combination with experimentally manipulated habitat

conditions offer a powerful way to unravel the mechanisms that govern population dynamics and their variability but are even more scarce (Lindborg & Ehrlén 2003).

To investigate the effect of changing environmental conditions on the population viability of a long-lived perennial, we selected *Primula veris* (Linnaeus) as our study species. Once a common grassland herb, this species has become rare in many regions of its original distribution area as a consequence of changed land-use practices (e.g., Fischer & Stöcklin 1997; Kéry et al. 2000; Brys et al. 2003). We examined how population dynamics of *P. veris* vary under different habitat conditions. Specifically, we (1) evaluated population responses to different levels of nitrogen addition under two management regimes; (2) determined the population-level consequences of alteration of seed production, survival, and vital rates; (3) examined whether recruitment success is determined by seed density or microsite availability or both; and (4) estimated extinction risks under these different conditions.

Methods

Study Species and Site

P. veris (Primulaceae) is a long-lived, perennial herb typically from nutrient-poor seminatural grasslands. Because of changes in management practices and habitat deterioration it has declined sharply in distribution in Belgium (Brys et al. 2003) and large parts of Western Europe (Zoller & Wagner 1986; Kéry et al. 2000; Kiviniemi & Eriksson 2002). Historically, the habitat of the species is closely associated with grazing and mowing. In Belgium, *P. veris* occurs sparsely in calcareous grassland relicts and nutrient-poor grassland patches such as road verges and ditch banks (Brys et al. 2003). In early spring, adults develop a rosette of several leaves and produce one or more flowering stalks with an umbel of 5–15 yellow, self-incompatible, and heterostylous flowers. Flowering starts in April and ends 3–4 weeks later. Seeds ripen in June–July. Flowers are mainly visited by Hymenoptera, Diptera (mainly pollen-gathering bees), and Lepidoptera (e.g., Woodell 1960; León-Cortés et al. 2003). The seeds have no special dispersal features. Seedling emergence and survival are generally low (Brys et al. 2004a) and vegetative propagation through side rosettes sometimes occurs (M. Kéry, personal communication). Under favorable conditions adults can live for several decades (Ehrlén & Lehtilä 2002).

The demographic study was performed in a large *P. veris* population (about 10,000 plants) in the eastern part of Belgium (Voeren). The population was situated in a species-rich calcareous grassland reserve. The conventional management of these grasslands is intermittent cattle grazing, restricted to short periods of 1 or 2 weeks during the growing season.

Experimental Design and Data Collection

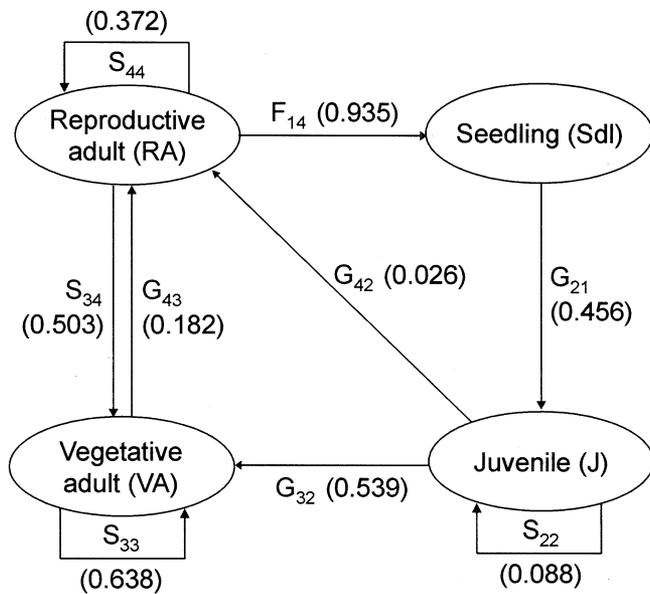
To examine the effects of nitrogen enrichment and management on the demography of *P. veris*, nitrogen concentrations and vegetation management were manipulated over a 5-year period, from 1999 to 2003. During the experiment 32 permanent plots, 3 × 3 m, were defined. Half the plots were mowed annually (early July) and the others were grazed by cattle. Under both management regimes, nitrogen was added annually in early April as commercial solid NH₄NO₃ at 9, 6, 3, and 0 g N/m², resulting in eight plots per N treatment (four per management regime). Plots received the same treatment during the entire study period and were laid out in the central and most homogeneous part of the grassland and the *P. veris* population. The mown plots were fenced off from grazing. In these plots, the vegetation was clipped 2–4 cm above the ground surface with scissors and litter was removed. Grazed plots were conventionally managed by cattle grazing from the end of June to the end of September.

To avoid edge effects we monitored only the central area (1 × 1 m) of the defined plots. Within these 1 × 1 m plots, all *P. veris* individuals within 10 × 10 cm grids were monitored annually at the end of May. With these time-series the fate of each individual plant in the sample could be assessed, allowing us to calculate annual transition probabilities of recruitment, growth, stasis, reproduction, and mortality for the four growth periods (1999–2003).

Seed Production and Seed-Sowing Experiment

To estimate annual seed production per flowering plant, each year we randomly selected 16 reproductive individuals per treatment and recorded their flowering and fruiting status. We collected five mature, intact fruits per individual (four per plot) in the buffer area around the monitored 1 × 1 m plots and determined the mean seed number per capsule. We multiplied this mean by the total number of fruits per plant to determine per capita seed production rate per flowering plant under the different treatments.

We examined the effect of different environmental conditions and seed production rates on seedling emergence with a sowing experiment. These experimental plots were established at the same site but outside the demographic study plots. Per treatment (N level and management type), we added three seed densities (15, 50, and 250 seeds) randomly to permanently marked 20 × 20 cm plots. Each density was replicated three times per treatment, resulting in a total of 72 plots. The sowing densities represented the normal range of the natural seed range in the studied grassland: from 21 up to 291 seeds per 20 × 20 cm (mean = 123; *n* = 160 permanent 1 × 1 m plots). Fruits were randomly collected in July 2002 from 150 plants growing in the same population outside the



| | | Stage at time t | | | |
|---------------------|------|-------------------|----------|----------|----------|
| | | Sdl. | J | VA | RA |
| 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} |
| | RA | 0 | G_{42} | G_{43} | S_{44} |

Figure 1. Life-cycle graph and associated projection matrix of *Primula veris*. 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, number of seedlings per reproductive adult), growth (G, transition to higher stages), and survival (S, remaining at the same or retrogression to a lower stage). Values between the brackets represent the overall mean transition value between stages.

treatment plots. After seeds were counted, they were immediately sown in the experimental plots. To determine the number of recruits per seed density, the experimental 20 × 20 cm plots were monitored at the end of May 2003.

Stage-Based Matrix Model

We constructed a matrix model of population growth in which individuals were classified in four well-defined stages: seedlings (<1 year), juveniles (>1 year and < 3 leaves and/or length of the largest leaf <2 cm), vegetative individuals (>1 year and > 3 leaves and/or length of the largest leaf >2 cm), and reproductive individuals (flowering individuals) (Fig. 1). The number of emerging seedlings was partitioned according to the proportion of flowering individuals in the previous year. Since a seed-

germination experiment, in which the seed bank of *P. veris* was investigated, showed no or very poor germination rates (R. Brys & H. Jacquemyn, unpublished results), a seed bank was not included as a life-cycle stage in the model.

Total fitness effects of different treatments were estimated through changes in population growth rate (λ). Population growth rates for each treatment were calculated by transition-matrix models of the form

$$\mathbf{n}(t+1) = \mathbf{A} * \mathbf{n}(t),$$

where $\mathbf{n}(t)$ is the vector of the number of plants in each stage at time t and \mathbf{A} is the 4 × 4 transition matrix (Caswell 2001). We used the power method to calculate the main demographic parameters of each population from the projection matrices. The dominant eigenvalue and the right eigenvector of the matrix correspond with the finite rate of increase (λ) and the stable-stage distribution of the population, respectively, whereas the left eigenvector represents the stage-specific reproductive values (Caswell 2001). Transitions from the four plots per treatment were pooled before analysis to achieve a larger number of individuals in each stage class, which yields a more robust matrix.

Statistical Analyses

A two-way analysis of variance (ANOVA) was used to test for significant differences in annual survival of the different life-stages (seedlings, juveniles, vegetative adults, and reproductive adults) under different N application and management regimes. Nitrogen addition, management, and the interaction term were fixed factors, whereas annual survival rate per life stage was the dependent variable. For each life stage, annual survival estimated per plot each year resulted in 16 replicates per treatment. To examine the effects of N addition, management, and the interaction of both factors on seed production rates per flowering plant, we again used a two-way ANOVA.

We used a three-way ANOVA to test for significant differences in proportional recruitment rates when seeds were added under different densities. Seed density, N addition, and management were the fixed factors, whereas the proportional number of recruits was the dependent variable. Before statistical analysis, dependent variables were transformed by arc-sine square root if they represented proportions or log transformed if they represented count data to achieve normality and homoscedasticity of residuals.

A life-table response experiment (LTRE) with a fixed factorial design was conducted to examine the effect of year, management, and fertilization measured as a deviation from the growth rate of a reference overall mean matrix (\mathbf{A}^{\dots}). Following Caswell (2001), data from all treatments during the study period were pooled to calculate

the overall mean matrix (\mathbf{A}^{\dots}). Consequently,

$$\lambda^{(mny)} = \lambda^{(\dots)} + \alpha^{(m)} + \beta^{(n)} + \gamma^{(y)} + (\alpha\beta)^{(mn)} + (\alpha\gamma)^{(my)} + (\beta\gamma)^{(ny)} + (\alpha\beta\gamma)^{(mny)},$$

where $\lambda^{(\dots)}$ is the population growth rate of the overall mean matrix (\mathbf{A}^{\dots}) and the effects $\alpha^{(m)}$, $\beta^{(n)}$, and $\gamma^{(y)}$ are the main effects of the i th level of management, the j th level of fertilizer, and the k th level of year, respectively, on λ . Consequently, they incorporate all differences in survival and fertility between the treatment matrix and the overall mean matrix. Following Caswell (2001), the contribution of the transition a_{ij} to the effect of management, fertilizer, and year on population growth can be decomposed in

$$\begin{aligned} \alpha^{(m)} &= \sum_{ij} t_{ij}^{(m\cdot\cdot)} - a_{ij}^{(\dots)} \{ s_{ij} \}, \\ \beta^{(n)} &= \sum_{ij} t_{ij}^{(\cdot n \cdot)} - a_{ij}^{(\dots)} \{ s_{ij} \}, \\ \gamma^{(y)} &= \sum_{ij} t_{ij}^{(\cdot\cdot y)} - a_{ij}^{(\dots)} \{ s_{ij} \}, \\ (\alpha\beta)^{(mn)} &= \sum_{ij} t_{ij}^{(mn\cdot)} - a_{ij}^{(\dots)} \{ s_{ij} - \alpha^{(m)} - \beta^{(n)} \}, \\ (\alpha\gamma)^{(my)} &= \sum_{ij} t_{ij}^{(m\cdot y)} - a_{ij}^{(\dots)} \{ s_{ij} - \alpha^{(m)} - \gamma^{(y)} \}, \text{ and} \\ (\beta\gamma)^{(ny)} &= \sum_{ij} t_{ij}^{(\cdot n y)} - a_{ij}^{(\dots)} \{ s_{ij} - \beta^{(n)} - \gamma^{(y)} \}. \end{aligned}$$

Here, s_{ij} is the sensitivity of the ij transition. To control for changes in the sensitivity structure that may occur from one treatment to another, we evaluated sensitivity matrices halfway between the particular treatment matrix and the reference matrix. Similar to Horvitz et al. (1997), the overall mean matrix (\mathbf{A}^{\dots}) was used as reference matrix for these calculations. The decomposition analysis thus gives the contribution of each life-cycle transition to each treatment effect. Important life-cycle transitions are those with large positive contributions at some treatment levels and large negative contributions at others. Analogous to analysis of variance, the mean of the treatment effects is approximately zero. Despite this structural analogy with ANOVA and other approaches based on linear models, the LTRE approach does not constitute a formal statistical analysis of variation; in other words, there is no underlying null hypothesis being tested (see Caswell 2001). Each interaction term ($(\alpha\beta)^{(mn)}$, $(\alpha\gamma)^{(my)}$, and $(\beta\gamma)^{(ny)}$) is calculated as the difference between the actual contribution of a_{ij} to $\lambda^{(mny)}$ and the difference predicted on the basis of the additive model. Hence, a positive contribution indicates that this interaction has increased $\lambda^{(mny)}$ above the value predicted by the additive model (Caswell 2001).

We used a Spearman rank correlation coefficient to determine the association between calculated population growth rates and the observed “real” proportional population increase or decrease under the different treatments.

Stochastic simulations were assessed to estimate extinction risks under both management regimes and different N levels. The four transition matrices per treatment were sampled with equal probability. Time to extinction

was estimated for an initial population size of 100 and 10,000 individuals distributed among the nonseed stages as the initial stable stage distribution of the studied population. The criterion for population extinction was defined as < 1 individual. We calculated the extinction rate from 2,000 simulations of 200 years each with a specific Visual Basic program written by K. Lehtilä and X. Picó

Results

For all life stages, annual survival rates decreased significantly with increasing N levels (Table 1). Annual survival rates of seedlings and juveniles were significantly lower under mowing than under the grazing regime (Ta-

ble 1). For the juvenile life stage there was a marginally significant interaction between N application and management ($p = 0.072$), in which mortality increased more with increasing N addition under mowing than with graz-

ing. Management did not significantly affect survival rates in either adult stage (Table 1).

Seed set per flowering plant was significantly affected by N enrichment ($F_{3,460} = 106.84; p < 0.001$) and management ($F_{1,460} = 112.93; p < 0.001$). Compared with the

control treatment, the highest N application reduced seed production per plant by an average of 36% and 19% under the mowing and grazing regimes, respectively. In general, grazing resulted in significantly lower seed production rates per plant than mowing, but the significant interaction between N addition and management indicated that seed production per plant decreased more strongly with increasing N under the mowing regime ($F_{3,460} = 18.73; p = 0.001$).

In the seed-sowing experiment recruitment was significantly reduced under increasing N enrichment ($F_{3,48} =$

Table 1. The effects of nitrogen application (0, 3, 6, and 9 g N/m²/year) and management (mowing and grazing) on survival of different life stages (seedlings, juveniles, vegetative adults, and reproductive adults) during the year transitions 1999–2003 in *P. veris* (examined with analysis of variance).

| Factors | Seedlings | | | Juveniles | | |
|----------------|-----------|-------------------|---------|---------------------|------|---------|
| | df | F | p | df | F | p |
| Fertilizer (F) | 3 | 15.32 | <0.001* | 3 | 9.04 | <0.001* |
| Management (M) | 1 | 5.77 | 0.018* | 1 | 6.41 | 0.013* |
| F × M | 3 | 0.87 | 0.459 | 3 | 2.39 | 0.072 |
| Error | 120 | | | 120 | | |
| | | Vegetative adults | | Reproductive adults | | |
| Fertilizer (F) | 3 | 11.92 | <0.001* | 3 | 6.94 | <0.001* |
| Management (M) | 1 | 0.06 | 0.814 | 1 | 0.19 | 0.663 |
| F × M | 3 | 1.21 | 0.308 | 3 | 0.10 | 0.959 |
| Error | 120 | | | 120 | | |

* Significant p value.

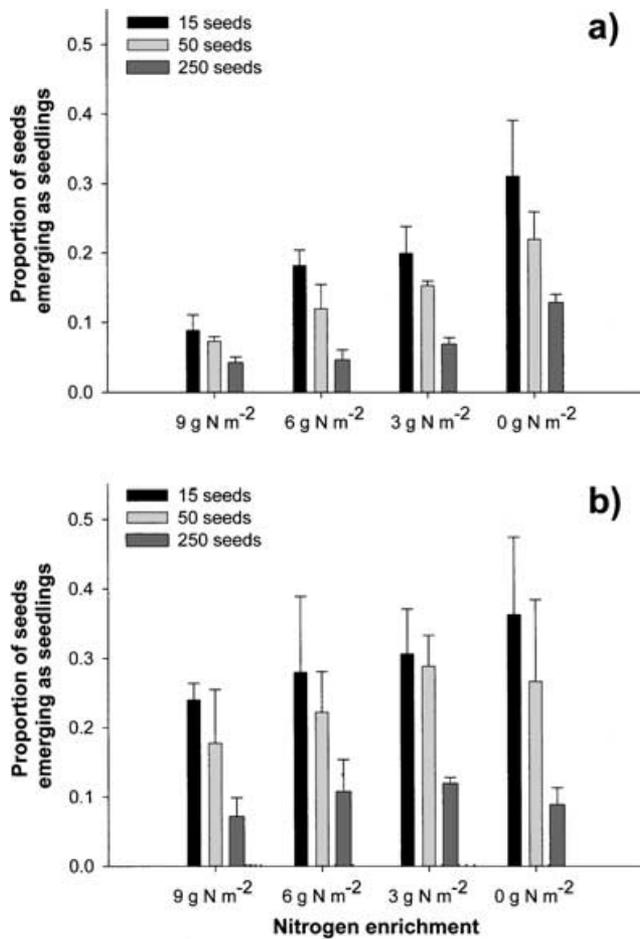


Figure 2. The proportion of *P. veris* seeds emerging as seedlings, calculated as the ratio between the number of seedlings/number of sown seeds \pm SE, in the spring (2003), after sowing (2002), for three different seed densities (15, 50, and 250 seeds) under four N levels (9, 6, 3, 0 g N/m²/year) and two management regimes: (a) mowing and (b) grazing.

4.06; $p = 0.012$; Figs. 2a, b). Whereas grazing resulted in significantly higher proportional recruitment rates than did mowing ($F_{1,48} = 9.28$; $p = 0.004$), proportional recruitment decreased significantly when the number of sowed seeds was increased ($F_{2,48} = 16.49$; $p < 0.001$). Although a smaller proportion of seeds emerged at high sowing densities, the total number of emerged seedlings was still higher compared with lower seed densities.

Population growth rates varied among treatments and among years within each treatment (range = 1.208 – 0.700). With 0 or 3 g N/m²/year added, mowing resulted in higher population growth rates compared with grazing (mean = 1.123_{mowing} vs. 1.027_{grazing} and 0.986_{mowing} vs. 0.968_{grazing}, respectively). Irrespective of the management applied, however, N enrichment, even under the lowest level (3 g N/m²/year), resulted in population growth rates below 1. When N levels were 6 or 9

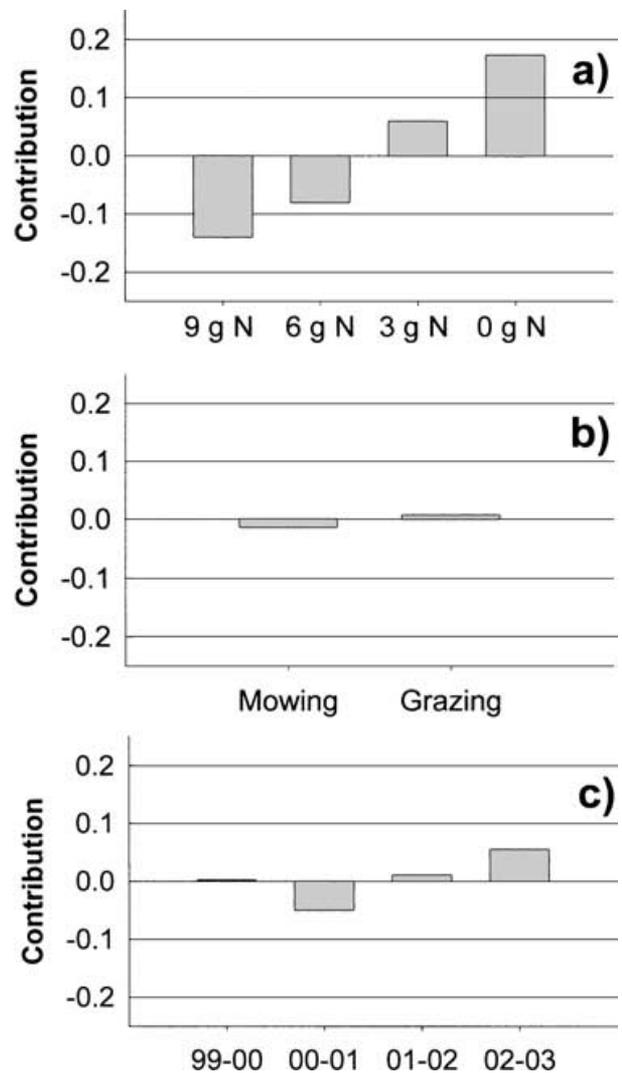


Figure 3. The main effects of (a) fertilizer (9, 6, 3, 0 g N/m²/year), (b) management (mowing and grazing), and (c) year (1999–2000, 2000–2001, 2001–2002, and 2002–2003) on the observed variation in population growth of *Primula veris* examined by life-table response experiment analysis.

g N/m²/year, mowing appeared to be more detrimental to population growth rate than grazing (mean = 0.8137_{mowing} vs. 0.8819_{grazing} and 0.7335_{mowing} vs. 0.8396_{grazing}, respectively). Finally, there was a significant and positive correlation between calculated population growth rates and the annual observed proportional population increase or decrease ($r_s = 0.783$; $n = 32$; $p < 0.001$).

Results of the LTRE showed that fertilizer treatment had the strongest effect on the variation of population growth rate compared with the main effects of management and year (Fig. 3). Addition of 9 g N/m²/year contributed most negatively to the variation among different N levels, and its negative effect was almost twice as large as that of the 6

Table 2. Interaction effects between fertilizer, management, and year on the observed variation in population growth rate in *Primula veris* examined with life-table response experiment.*

| Management | Fertilizer (g N/m ² /yr) | | | |
|-------------------------------------|-------------------------------------|-----------|-----------|-----------|
| | 9 | 6 | 3 | 0 |
| mowing | -0.192 | -0.093 | 0.078 | 0.241 |
| grazing | -0.089 | -0.062 | 0.038 | 0.107 |
| Year | | | | |
| Management | 1999–2000 | 2000–2001 | 2001–2002 | 2002–2003 |
| mowing | 0.017 | -0.036 | 0.015 | 0.068 |
| grazing | -0.050 | -0.056 | -0.006 | 0.047 |
| Fertilizer (g N/m ² /yr) | | | | |
| 9 | -0.143 | -0.091 | -0.141 | -0.194 |
| 6 | -0.084 | -0.031 | -0.081 | -0.135 |
| 3 | 0.057 | 0.109 | 0.058 | 0.005 |
| 0 | 0.170 | 0.226 | 0.171 | 0.119 |

* Positive and negative values indicate the observed effect is higher or lower, respectively, than would be expected from an additive model.

g N/m²/year treatment (Fig. 3a). Low or no annual N input positively contributed to the variation of λ . The effect of 0 g N/m²/year was on average three times greater than that of the 3 g N/m²/year. Grazing affected the variation of λ in a small and positive way. Mowing, on the other hand, resulted in a slightly stronger but negative effect on the variation of λ (Fig. 3b). The main year effects showed that the year 2002–2003 had the largest positive effect on the variation in λ , whereas 2000–2001 had a similar but negative effect on λ (Fig. 3c). Interaction effects between fertilizer treatments and management revealed that with 6 and 9 g N/m²/year, the population growth rate of *P. veris* decreased faster when the vegetation was mown than was predicted by the additive model (Table 2). Under the 0 and 3 g N/m²/year, on the other hand, both management regimes showed positive interaction effects in which the effect of mowing was on average twice as large compared with grazing.

The matrix entries that contributed most to the variation of λ due to fertilizer effects were growth of vegetative adults (G_{43}), fecundity (F_{14}), and seedling establishment (G_{21}) (Table 3), and they were all negatively affected by increasing N levels. Growth and survival of vegetative adults (G_{43} and S_{33}) and seedling establishment (G_{21}) appeared to be the most influential stage transitions contributing to the variation of λ due to management effects (Table 3). Mowing positively affected growth of vegetative individuals and resulted in a negative effect on stasis of vegetative adults and seedling establishment, whereas the opposite was found under grazing (Table 3). Interaction effects between N enrichment and management revealed that under the highest N additions (9 and 6 g N/m²/year), growth of vegetative adults and seedlings was more negatively affected by mowing than by grazing. In contrast, mowing

in combination with 3 and 0 g N/m²/year addition resulted in a larger and more positive interaction effect of these vital rates than grazing did. Interaction effects on fecundity were negative under all N levels regardless of the management applied. (The contribution of each vital rate to the management by fertilizer and management by year interaction effect on the observed variation in population growth rate is available from R.B.). Finally, the most influential vital rates to the variation of λ due to year effects were growth and survival of vegetative adults (G_{43} and S_{33}), followed by the vital rate in which flowering individuals remained flowering (S_{44}) (Table 3).

In stochastic simulations over a 200-year period *P. veris* populations declined most rapidly in size under the highest N levels (Fig. 4). When 9 and 6 g N/m² were applied annually, mowing resulted in higher extinction risks (mean time to extinction = 13.7 ± 0.9 and 20.9 ± 1.3 years, respectively) compared with populations that were grazed (mean time to extinction = 24.4 ± 1.3 and 28.0 ± 1.5 years, respectively). In addition, even populations with an initial size of 10,000 individuals had a relatively short mean time to extinction, 27.0 ± 1.3 years under mowing and 49.1 ± 1.8 under grazing, if subjected to the highest N levels. Mowing of a population containing 100 individuals in combination with the 3 g N treatment resulted in a mean extinction time that exceeded 200 years. When the vegetation was, however, grazed under the same N level, mean time to extinction was 100.7 ± 8.7 years. If no extra fertilizer is added to the vegetation, *P. veris* increased in population size irrespective of the management regime applied.

Discussion

Our results demonstrate that population growth of *P. veris* is affected strongly by N enrichment and management because of underlying differences in demographic transition rates. Growth of vegetative individuals into the flowering stage appeared to be the life-stage transition that contributed most to the observed variance in population growth rate (λ) under different levels of N addition and management. The latter is in accordance with earlier findings of García and Ehrlén (2002) and Brys et al. (2004a), who observed that damage of above-ground tissue (leaves and flower stalks) during the growing season reduced plant size and future reproductive performance of *P. veris* individuals. This explains, at least partly, the lower population growth rates under grazing when 3 and 0 g N/m²/year was applied in comparison with population growth rates under mowing. A strong and negative interaction effect between the highest N applications and mowing, on the other hand, indicated that under high nutrient conditions mowing affected flowering probabilities of *P. veris* more negatively than grazing.

Table 3. The contributions of each vital rate to the fertilizer effect (9, 6, 3, 0 g N/m²/year), the management effect (mowing and grazing), and the year effect (1999–2000, 2000–2001, 2001–2002, and 2002–2003) on the observed variation in population growth rate of *P. veris* examined with a life-table response experiment.

| Entry* | Fertilizer (g N/m ² /year) | | | | Management | | Year | | | |
|-----------------|---------------------------------------|--------|--------|--------|------------|--------|--------|--------|--------|--------|
| | 0 | 3 | 6 | 9 | grazing | mowing | 99–00 | 00–01 | 01–02 | 02–03 |
| F ₁₄ | 0.048 | -0.005 | -0.011 | -0.028 | 0.010 | 0.008 | 0.037 | -0.017 | -0.010 | -0.008 |
| G ₂₁ | 0.025 | 0.012 | -0.015 | -0.013 | 0.012 | -0.015 | 0.009 | -0.012 | 0.014 | -0.009 |
| S ₂₂ | 0.001 | 0.001 | 0.002 | -0.003 | 0.000 | 0.000 | -0.003 | 0.002 | -0.001 | 0.001 |
| G ₃₂ | 0.007 | 0.006 | -0.012 | 0.002 | 0.004 | -0.004 | -0.001 | -0.001 | -0.002 | 0.005 |
| S ₃₃ | 0.006 | 0.013 | 0.006 | -0.027 | 0.029 | -0.027 | -0.044 | 0.056 | 0.035 | -0.031 |
| S ₃₄ | 0.010 | -0.012 | 0.006 | -0.005 | -0.002 | 0.002 | -0.004 | 0.020 | 0.006 | -0.032 |
| G ₄₂ | 0.005 | 0.002 | -0.001 | -0.002 | 0.001 | -0.001 | -0.002 | 0.001 | 0.004 | -0.004 |
| G ₄₃ | 0.067 | 0.015 | -0.035 | -0.055 | -0.032 | 0.029 | 0.037 | -0.063 | -0.056 | 0.062 |
| S ₄₄ | 0.004 | 0.029 | -0.021 | -0.009 | 0.006 | -0.006 | -0.028 | -0.035 | 0.013 | 0.071 |

*Matrix entries are subdivided into fecundity (F, number of seedlings per reproductive adult), growth (G, transition to higher stages), and survival (S, remaining at the same or retrogression to a lower stage).

Flowering probabilities of this species are strongly reduced under light limitation (Whale 1984), so the latter result can be explained by much stronger reductions in light penetration under high-nutrient conditions when the vegetation was mown compared with the grazed vegetation (Jacquemyn et al. 2003*a*). In other words, the negative effect of increased competition and the resulting limitation in light penetration under mowing exceeded the negative effect of grazing pressure on the performance of flowering individuals when the vegetation was subjected to high levels of N enrichment. Regardless of the management regime applied, N addition resulted in reduced flowering probabilities and higher mortality and retrogression rates of the flowering stage, which further decreased the number of flowering individuals each year. Together with reduced flowering probabilities, increasing N input also

reduced seed production rates at plant level, further affecting overall seed shed in a negative way.

Reductions in seed output may result in reduced recruitment rates, a process that in some cases is the primary mechanism driving plant populations to local extinctions (e.g., Jules & Rathcke 1999; Benítez-Malvido & Martínez-Ramoz 2003). Our results from the sowing experiment, however, revealed that recruitment in *P. veris* is determined by seed production and by the occurrence of suitable germination conditions. Moreover, proportional seedling emergence decreased significantly with increasing N addition, indicating a limitation of suitable gaps for germination. This agrees with results on the perennial herb *Succisa pratensis* (Vergeer et al. 2003), in which total emergence declined under increased N enrichment. Thus, N enrichment, increasing light competition with

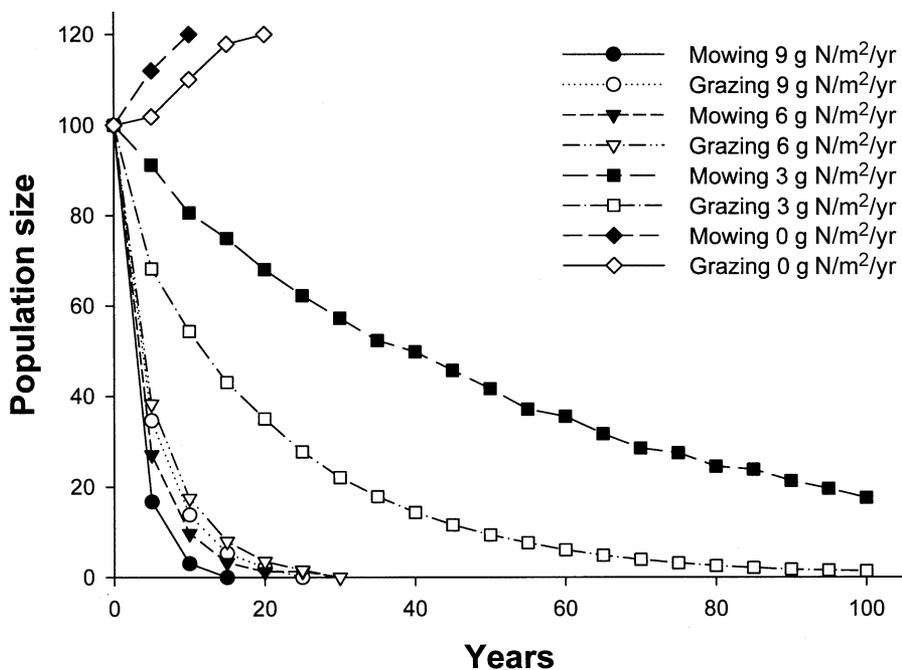


Figure 4. Stochastic simulations of development for populations of 100 *Primula veris* individuals distributed among stages according to the initial stable-stage distribution.

the surrounding vegetation, and fewer reproducing individuals with reduced seed set are responsible for the strong decline in recruitment success of *P. veris*.

Although grazing resulted in better germination conditions than mowing, recruitment rates under increasing N enrichment were too low to counterbalance increased mortality of established individuals. Consequently, the highest level of nitrogen addition (9 g N/m²/year) resulted in a mean annual population decline of 18.2% and 15.5% under mowing and grazing, respectively. The strong and negative impact of N enrichment on early phases of the life cycle in *P. veris* was further reflected in skewed population structures with an excess of old adults, which may jeopardize long-term population viability. Such “regressive” population structures were also found in small and remnant populations of *P. veris* in a strongly deteriorated agricultural landscape in the western part of Belgium (Brys et al. 2003). Lienert and Fischer (2003) observed in fragmented populations of the related *P. farinosa* that edge effects reduced the proportion of juvenile plants at the more deteriorated edges of habitat patches. Similar regressive structures were also reported in fragmented populations of the rare *P. vulgaris* (Jacquemyn et al. 2003b), *Gentiana pneumonanthe* (Oostermeijer et al. 1994), and the common *Trillium ovatum* (Jules 1998).

In long-lived perennial plants, the vegetative adult stage is often the most stable stage that may function as a bridge to overcome unfavorable periods and ensure long-term population persistence (Horvitz & Schemske 1995; Eriksson 1996; Bruna 2003; García 2003). In *P. veris* we also found high survival rates of vegetative adults characterized by low variation in transition probabilities and associated high elasticity values (Brys et al. 2004a). When plants were subjected to high N levels, however, mortality rates were significantly elevated for this stage also, undermining the population viability. Even though *P. veris* is a long-lived perennial, with a conditional life-span of 52.3 years (Ehrlén & Lehtilä 2002), our experimental results suggest a strongly reduced population viability and long-term persistence if it is subjected to increased nutrient levels. Moreover, long-term projections based on our 5 years of demographic data reveal that populations that are subjected to N enrichment of 9 or 6 g N/m²/year might go extinct within 50 years. Because strong population reductions may affect other processes too, such as reductions in reproductive success (see Brys et al. 2003; 2004b), the calculated extinction times may be even shorter.

This high extinction threat, driven by deterministic changes in the life-cycle of *P. veris*, shows that the time lag in the response of perennial plants to habitat deterioration may be < 50 years, even for large populations of several thousands of individuals. Historical data on the related *P. vulgaris* and *P. farinosa* indeed revealed that local populations declined sharply some time after changing land-use practices or eutrophication, whereas populations not subjected to these changes survived or

even increased (Endels et al. 2002; Lindborg & Ehrlén 2002). Consequently, proposed time delays to extinction in perennial species following habitat decrease, as suggested by Tilman et al. (1994), Eriksson and Ehrlén (2001), and Hanski and Ovaskainen (2002), may thus be shortened considerably if habitat quality changes over a short period of time. Our results demonstrate that population extinction due to habitat deterioration is an ongoing process, which affects not only rare and short-lived plant species but also long-lived, common perennials.

Implications for Conservation

Habitat deterioration due to nutrient enrichment may drastically affect population dynamics of *P. veris* over a very short period of time. Because most of the fragmented *P. veris* habitats are very small (Kéry et al. 2000; Brys et al. 2003), they are highly vulnerable to edge effects. Consequently, the ongoing fragmentation combined with nutrient influx from the surrounding landscape may thus increasingly threaten many remaining populations of this once locally abundant species. To avoid their future extinction, habitat quality needs to be improved by adequate management (Holsinger 2000). Therefore, the first essential component of any conservation strategy is habitat preservation. Nowadays, however, many of the remaining habitat patches harboring *P. veris* populations in Belgium are not protected (Brys et al. 2003). To maintain habitat quality, excessive nutrient input from nearby agricultural fields should be avoided or at least minimized and sufficiently wide nutrient-free buffer zones around habitat fragments must be established (Endels et al. 2002; Jacquemyn et al. 2003b).

Preservation of habitats in most situations, however, will not be enough to conserve *P. veris* populations in the long run. Moreover, if a habitat patch is subjected to substantial nutrient enrichment, (re)establishment of an intensive grazing regime, after seed release, appears to be the best management strategy to counterbalance the negative effects of increased productivity. Under nutrient-poor site conditions, on the other hand, mowing after seed dispersal seems to be the best option to promote flowering and seed production and gain higher population growth rates (Brys et al. 2004a). Similar to other grassland herbs (e.g., Klinkhamer & de Jong 1988; Oostermeijer et al. 1998), germination and further establishment of new individuals are positively influenced by a low and open vegetation cover. Again under nutrient-rich conditions with a high standing crop, intensive grazing after seed dispersal until autumn may provide the best opportunities for this perennial herb to withstand increased competition levels and maintain recruitment. In case of low nutrient availability and a relatively open vegetation, mowing may provide sufficient germination possibilities by increasing light penetration. Finally, one

must pay attention to the fact that most remaining habitat fragments harboring *P. veris* individuals also function as refuges for several other vulnerable species. Therefore, management efforts should consider the critical phases of their life cycles as well. For example, Oostermeijer et al. (2002) reported that the late-flowering *Gentianopsis ciliata* and *Gentianella germanica* almost went extinct in the Netherlands because of early mowing of their remaining sites. Therefore, we recommend spatial or temporal rotation or both of management regimes and intensities, depending on the local species composition and requirements.

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