

# Interactions between local climate and grazing determine the population dynamics of the small herb *Viola biflora*

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Received: 8 May 2009 / Accepted: 9 April 2010 / Published online: 28 April 2010  
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**Abstract** Plants of low stature may benefit from the presence of large herbivores through removal of tall competitive neighbours and increased light availability. Accordingly, removal of grazers has been predicted to disfavour small species. In addition to this indirect beneficial effect, the population dynamics of plants is strongly influenced by variation in external conditions such as temperature and precipitation. However, few studies have examined the interaction between large herbivores and inter-annual variation in climate for the population

dynamics of small plant species not preferred by herbivores. We studied three populations of the perennial herb *Viola biflora* exposed to different sheep densities (high, low and zero) for 6 years in a field experiment. Plants were also impacted by invertebrate and small vertebrate herbivores (rodents). Rates of growth were marginally higher at high sheep densities, and during warm summers both survival and growth were higher when sheep were present. Thus, while the height of tall herbs was positively related to July temperature, it was less so in the treatments with sheep, suggesting that sheep reduce the negative effects of interspecific competition for this small herb. Life table response experiment analyses revealed that the population growth rate ( $\lambda$ ) was slightly lower in the absence of sheep, but between-year variation in  $\lambda$  was larger than variation among sheep density treatments.  $\lambda$  was negatively related to July temperature, with an additional negative effect of vertebrate grazing frequency (sheep or rodent grazing). The evidence from this 6-year study suggests that the population dynamics of *Viola biflora* is determined by a complex interplay between climate and grazing by both large and small herbivores.

Communicated by Miguel Franco.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-010-1637-x) contains supplementary material, which is available to authorized users.

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**Keywords** Climate · Grazing effects · Avoidance ·  
Matrix models · Field experiment

## Introduction

Large herbivores affect plants directly and indirectly through selective foraging, trampling, urination and defecation, thereby modifying intra- and inter-specific interactions and altering resource availability for plants (Hobbs 1996; Augustine and McNaughton 1998). Correspondingly, exclusion of herbivores in habitats exposed to long-term

grazing results in a change of overall plant community composition and structure (Tansley and Adamson 1925; Moen and Oksanen 1998). Avoidance through low stature is one means of resisting grazing by large herbivores (Evju et al. 2009) and small species are indirectly favoured by the tendency of large grazers to remove tall neighbours and thereby to increase light availability and reduce competition intensity (Olofsson et al. 2002). Indeed, several studies show that small species increase in abundance with increasing grazing pressure (see review in Díaz et al. 2007), whereas cessation of grazing is found to reduce the abundance of small plants. Additionally, seedling recruitment is generally increased by disturbances creating gaps exposing the soil (Carson and Peterson 1990). Studies of effects of grazing on plant communities in general, and in alpine and arctic habitats in particular, are abundant (see reviews in Mulder 1999; Díaz et al. 2007). More scarce are studies of effects of grazing on plant population dynamics, in particular of small, non-preferred plants. Bullock et al. (1994) found that intensified summer grazing by sheep increased rates of seedling emergence whereas winter grazing increased survival rates of small- and medium-sized rosettes of the non-preferred species *Cirsium vulgare*. Continuous summer grazing by sheep was found to increase recruitment rates and growth of rosettes, but reduce seed production of *Gentianella campestris* (Lennartsson and Oostermeijer 2001), and for *Primula veris* grazing and clipping increased survival rates of seedlings and juveniles (Brys et al. 2004; Ehrlén et al. 2005).

Long-term monitoring of plant communities shows that the abundance of plants may fluctuate considerably between years (e.g. Økland and Eilertsen 1996). In alpine ecosystems, which are characterised by a very short growing season, variation in temperature and precipitation contribute strongly to fluctuations in plant growth (Callaghan et al. 1989), seed production (Chambers 1995) and seedling establishment (Forbis 2003). Arctic and alpine herbs and graminoids show rapid response to warmer growing seasons, in terms of increased growth (Arft et al. 1999; Brooker and van der Wal 2003), which may reduce light availability and thus disfavour low-stature species (Klanderud 2008).

Herbivores and climate likely interact to affect plant population dynamics. In an experimental study of plant community responses to warming in the Arctic, Post and Pedersen (2008) found that natural herbivory reduced biomass accumulation and prevented a change in species composition in favour of deciduous shrubs, which was observed in the warming treatment without herbivores. However, few studies of effects of vertebrate grazing on plant population dynamics have lasted long enough to incorporate temporal variability in vital rates. Unfavourable climatic conditions can exacerbate negative effects of

grazing on preferred plant species (Bastrenta et al. 1995). Rydgren et al. (2007) therefore suggest that under less favourable climatic conditions, population decline may occur at lower grazing severities. The relative importance of climate and grazing on the population dynamics of plants can only be disentangled by detailed experimental demographic studies that last for many years.

In this study, we set out to examine effects of sheep grazing and inter-annual variability in local climate on the vital rates and population dynamics of *Viola biflora*. *V. biflora* is a small perennial herb only sporadically grazed by sheep (Evju et al. 2006), assumed to be favoured by increasing grazing pressure due to reduced interference from other species (e.g. Eskelinen and Oksanen 2006). Three populations, located in areas with high sheep density, low sheep density and with no sheep, respectively, were monitored from 2002 up to and including 2007. Small mammalian and invertebrate herbivores have potentially large impacts on plant populations (e.g. Doak 1992; Rydgren et al. 2007), and the impact of rodents on plants in alpine systems may exceed the impact of large herbivores (Olofsson et al. 2004). We therefore included observational data on rodent and invertebrate grazing in our study to estimate the effect of variation in vertebrate and invertebrate grazing frequencies on *V. biflora* population growth rate ( $\lambda$ ).

We hypothesise that sheep grazing favours *V. biflora* through removal of tall neighbours and creation of gaps, thereby increasing rates of survival, growth, flowering and recruitment (seedling emergence). Conversely, we expect the increased abundance of tall competitive species following cessation of grazing to affect the population negatively through reduction of these rates. Since low-stature plants may be negatively affected by the presence of tall neighbours, we predict that in years with climatically favourable growing conditions, growth and survival of *V. biflora* would be more strongly reduced than in years in which growing conditions are less favourable. However, as grazing contributes to the removal of tall neighbours, we predict that plants would be less negatively affected by benign growing conditions in the high and low sheep density treatments than in the ungrazed control.

## Materials and methods

### Study species

*Viola biflora* L. (Violaceae) is a perennial, short-statured (<15 cm), iteroparous herb confined to mountain forests and alpine areas (early melting snowbeds, short and tall herb meadows) on more or less base-rich soil in Eurasia and Western North America (Lid and Lid 2005). *V. biflora*

has a slender, creeping rhizome. No vegetative reproduction has been observed in the study area (M. Evju, unpublished data). Flowering takes place in early to mid-summer, and each plant normally produces one to a few yellow flowers that may develop to capsules, containing up to 12 seeds (M. Evju, unpublished data). To our knowledge, no detailed studies of seed bank longevity exist, but establishment from seed is common in alpine meadow and early snowbed habitats (Welling and Laine 2002). Seeds have been found only in the top layer of the soil (Molau and Larsson 2000), but densities of seeds in the soil are strongly dependent on habitat (Welling et al. 2004). In a seed-sowing experiment, Vandvik (2002) observed germination in the field both one and two seasons after sowing, suggesting a short-term persistent seed bank (cf. Thompson et al. 1997). Germination seems to benefit from cold stratification (Vandvik 2002).

### Experimental design

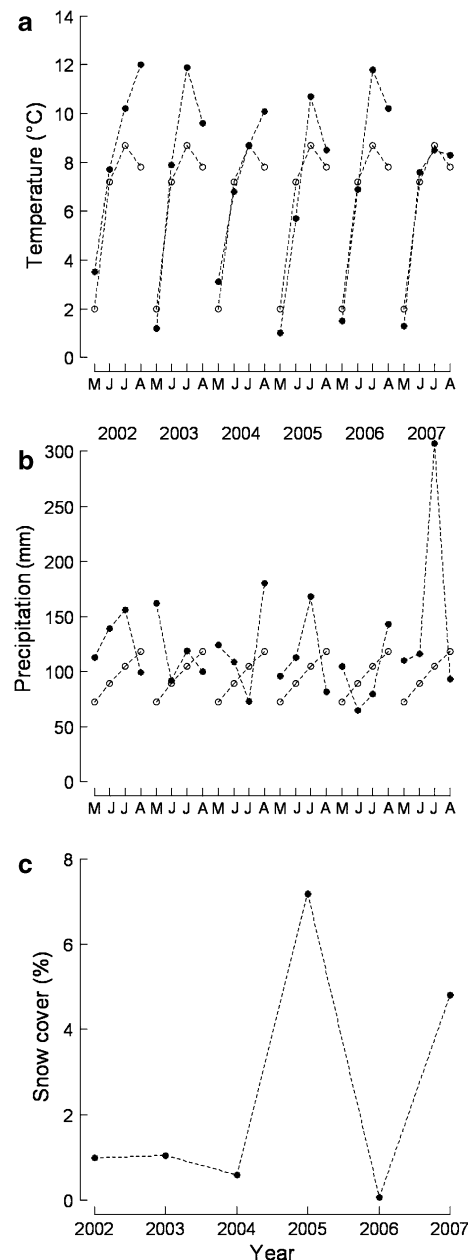
We studied the species in a landscape-scale experiment with three sheep densities (high, low and no sheep) in an alpine habitat, 1,050–1,300 m a.s.l. (see Austrheim et al. 2008 for details). The study area is located in Hol municipality, Buskerud county, south Norway (60°40′–60°45′N, 7°55′–8°00′E). Estimated mean annual temperature is  $-1.5^{\circ}\text{C}$ , with January temperature  $-10.8^{\circ}\text{C}$  and July temperature  $8.9^{\circ}\text{C}$ , and the mean annual precipitation is ca. 1,000 mm (Evju 2009). During the summer of 2001, we established a large enclosure covering 2.7 km<sup>2</sup> with a total of 17.3 km of standard sheep fencing (110 cm high) on a mainly south-facing hillside. The large enclosure was divided into nine parallel sub-enclosures running from low to high elevations, each covering on average 0.3 km<sup>2</sup>. Using a block-wise randomised design, three treatments were replicated 3 times; high sheep density (80 sheep km<sup>-2</sup>), low sheep density (25 sheep km<sup>-2</sup>) and no sheep. Grazing lasted from the end of June to the end of August or the beginning of September in all years, starting in 2002.

The vegetation mainly consists of a mosaic of low-stature dwarf-shrub heaths and grass-dominated meadows, with scattered birches (*Betula* spp.) in the low-lying areas (Mobæk et al. 2009). In 2001, we established 180 permanent plots (0.5 × 0.5 m) for vegetation sampling, 20 within each sub-enclosure, using a random, stratified design that ensured a balanced distribution of plots between altitudinal levels and an even representation of main vegetation types (Austrheim et al. 2008). These plots form the basis of this population study of *V. biflora*, which lasted from 2002 up to and including 2007. Mean monthly temperatures and precipitation data, interpolated from weather stations surrounding the study area, were provided by the Norwegian Meteorological Institute (see Tveito et al. 2005 for methods). During the

study period, summers were particularly warm in 2003 and 2006 (Fig. 1a), whereas precipitation (Fig. 1b) and duration of snow cover (Fig. 1c) were variable.

### Field sampling

All 180 plots were used except in the high sheep density treatment in which the species was so abundant that a



**Fig. 1** **a** Mean monthly temperature ( $^{\circ}\text{C}$ ) and **b** total monthly precipitation (mm) in May, June, July and August (M J J A) during the study period (*open symbols* show average temperature and precipitation in the reference period 1961–1990, *closed symbols* show observed values), and **c** snow cover, measured as the percentage of the study area covered by snow on 1 July each year

subset of four plots in each sub-enclosure was randomly selected at the start of the study (yielding a total of 12 plots in which the species was monitored). In the other treatments, the species was present in 12 (low sheep density) and 11 (no sheep) plots at the start of the study. In plots in which more than 20 *V. biflora* plants were present at the start of the study, only a part of the plot was used for monitoring. Two reduced plot sizes were used; 25 and 56.3% of the plot.

All plants present at the first census (2002) were non-destructively tagged. In order to estimate the size of all plants non-destructively, we counted the number of leaves and measured plant height and length of the largest leaf, and noted the number of capsules on reproductive plants. All measures were made in late July or early August every year, so that the census interval 2002–2003 includes the period from August 2002 to July 2003. At each census new plants were recorded and tagged. An additional census was performed in late June each year except 2006 to search for newly emerged seedlings. Signs of herbivore damage were recorded for each plant, making it possible to quantify grazing frequency in the census interval  $t$ . Grazing frequency could then be characterised as being due to either invertebrates or vertebrates, the latter including both sheep and rodents, as it was difficult to distinguish between physical signs of grazing by these animals in the treatments in which sheep were present.

#### The life cycle graph and matrix parameterisation

In 2002, aboveground parts of 200 plants were collected well outside of the plots, measured, dried to constant weight at 80°C and weighed. A multiple regression model was constructed from data on dry mass (DM; mg) plant height ( $H$ ; cm), number of leaves ( $L$ ), and length of the largest leaf (LL; cm). To reduce heteroscedasticity, the variables were  $\log_2$ -transformed to zero skewness by the procedure described by Økland et al. (2001). The regression model for estimation of *V. biflora* dry mass plants that was best in terms of fraction of variation explained ( $R^2 = 0.950$ ) was:

$$\begin{aligned} \log_2 \text{DM} = & 3.6012 \log_2(\text{LL} + 1.2985) + 0.7461 \log_2 L \\ & + 0.5810 \log_2 H \\ & - 0.2766 \log_2(\text{LL} + 1.2985) \log_2 H - 4.1996 \end{aligned}$$

An increase in size by one  $\log_2$  unit thus implied a doubling in DM. The size of non-seedling plants in the field was in the range 0.3–146 mg. A continuous decrease in mortality with size (logistic regression,  $G = 105.3$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n = 3,049$ ), and a continuous increase in the probability of setting fruit with size (logistic regression,  $G = 394.9$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n = 3,049$ ),

were observed. No plants were observed to set fruit if  $\log_2 \text{DM} < 2$ , and the proportion of plants setting fruit was markedly higher for plants with  $\log_2 \text{DM} > 4$  (Table 1). We defined life stage classes so that approximately the same number of plants was present in each class and at the same time each class represented a doubling of size compared to the next smaller class (Table 1). For each life stage class the conditional total life span, i.e. the average time to death for individuals that survive to the given stage, was calculated (Caswell 2001; Table 1).

To estimate seed production, 100 well-developed (reproducing) plants were collected in 2007, distributed evenly among sub-enclosures. The number of capsules and seeds on each plant was counted in the laboratory. The number of intact seeds per capsule was neither related to individual plant size nor to the number of capsules per individual, and did not vary significantly among the sheep density treatments (M. Evju, unpublished data). These data were thus pooled to give a species-specific mean of 4.59 seeds per capsule, which was considered as invariant between years.

In order to study the relative importance of seed rain and seed bank for seedling emergence, we set up a seed-addition experiment in 2005. Two permanent plots in each sub-enclosure were randomly selected, and seed sowing plots ( $0.50 \times 0.25$  m) were placed 2 m to the west of each of these. In mid-August 2005, twenty-five seeds were sown in one quarter of each plot, leaving the remaining three quarters as control. Floral parts of *V. biflora* plants in and adjacent (ca. 20 cm) to the plot were removed to reduce input from seed rain. Seedling emergence was recorded in late June 2006. A low and variable number of seedlings were recorded in the seed-addition plots (mean  $\pm$  SD in 2006:  $1.0 \pm 1.4$ ), and only a few seedlings were recorded in the control plots (mean  $\pm$  SD, adjusted for size difference between seed-addition plots and control plots:  $0.2 \pm 0.9$ ). To estimate the contribution from the seed bank to observed seedling emergence, we counted the number of seedlings emerging in the unsown control plots (adjusted for size differences), and calculated the proportion of seedlings that were likely to come from the seed bank in the seed-addition plots. This varied from 0 to 100% in the plots, with an average of 22%. In late June 2007, new seedlings were searched for. In the seed-addition plots,  $0.3 \pm 0.5$  (mean  $\pm$  SD) new seedlings were found, whereas in the control plots an average of  $0.1 \pm 0.3$  new seedlings were found. There was thus a negligible contribution from the seed bank to new seedlings after 2 years of no seed input, which confirms the assumption of a short-term persistent seed bank in this species. Our modelling was therefore based upon the assumption of a maximum life time of seeds in the seed bank of 1 year. Furthermore, we assumed that all seeds produced in year  $t - 1$  that did

**Table 1** Definition of life stage classes, with important demographic characteristics of these classes; average mortality (% of plants in that stage class at time  $t$  recorded as dead at  $t + 1$ ), fecundity (% of plants in that stage class setting seeds), conditional life span (average time to

death for individuals that enter that life stage) and the total number of plants recorded in that life stage class (pooled over populations and years)

Stage class	Definition	Mortality (%)	Fecundity (%)	Conditional life span (mean $\pm$ SD)	Total number
Seedling	<1 year old	48.6	0.0	3.8 $\pm$ 5.0	422
X-small	$\text{Log}_2\text{DM} < 1$	27.0	0.0	5.2 $\pm$ 5.6	653
Small	$1 \leq \text{Log}_2\text{DM} < 2$	19.2	0.0	6.1 $\pm$ 5.9	579
Medium	$2 \leq \text{Log}_2\text{DM} < 3$	14.8	1.7	6.6 $\pm$ 6.1	574
Large	$3 \leq \text{Log}_2\text{DM} < 4$	12.5	3.7	7.0 $\pm$ 6.2	630
X-large	$\text{Log}_2\text{DM} \geq 4$	8.5	23.1	7.5 $\pm$ 6.3	615
Dormant	Not observed	Not observed	0.0	6.3 $\pm$ 6.0	169

*X-small* Extra small, *X-large* extra large, *DM* dry mass

not establish as seedlings in year  $t$ , entered the seed bank and survived until year  $t + 1$ , when they either germinated or died. We constructed four scenarios within the range of observed contributions from the seed bank to newly emerged seedlings: 0, 25, 50 and 75% of new seedlings originating from the seed bank. We calculated the  $\lambda$  for all transition matrices for all seed bank scenarios, and  $\lambda$  varied only very little between the scenarios (Table S1). As seed-bank dynamics were not a main issue of this study, for further analysis of the population dynamics of *V. biflora* we chose the scenario that most closely accounted for the results of our seed-addition experiment; that 75% of the observed seedlings originate directly from seeds produced the previous year, that 25% originate from the seed bank, and that seeds may survive in the seed bank for 1 year. To estimate seed bank size the first year (2002), we assumed that in 2000, the number of seeds produced ( $s$ ) was the average of the observed number of seeds produced in the 2002–2006 period. Furthermore, we assumed that in 2001, the number of seedlings emerging ( $sd_{em}$ ) equalled the average number of seedlings emerging from 2003–2007. The seed bank size ( $s_{bank}$ ) was thereby estimated as:

$$s_{bank} = s - 0.75 \times sd_{em}$$

$s_{bank}$  was calculated separately for each population.

Because we observed seedlings emerging throughout the whole growing season and these appeared at census as new plants beyond the cotyledon stage, we defined as seedlings all new, extra-small plants. At the first census (2002), seedlings could not be distinguished from older plants. We therefore used the population-specific pooled transition probabilities (2003–2006) as an estimate for transitions from seedlings to other life stage classes in 2002.

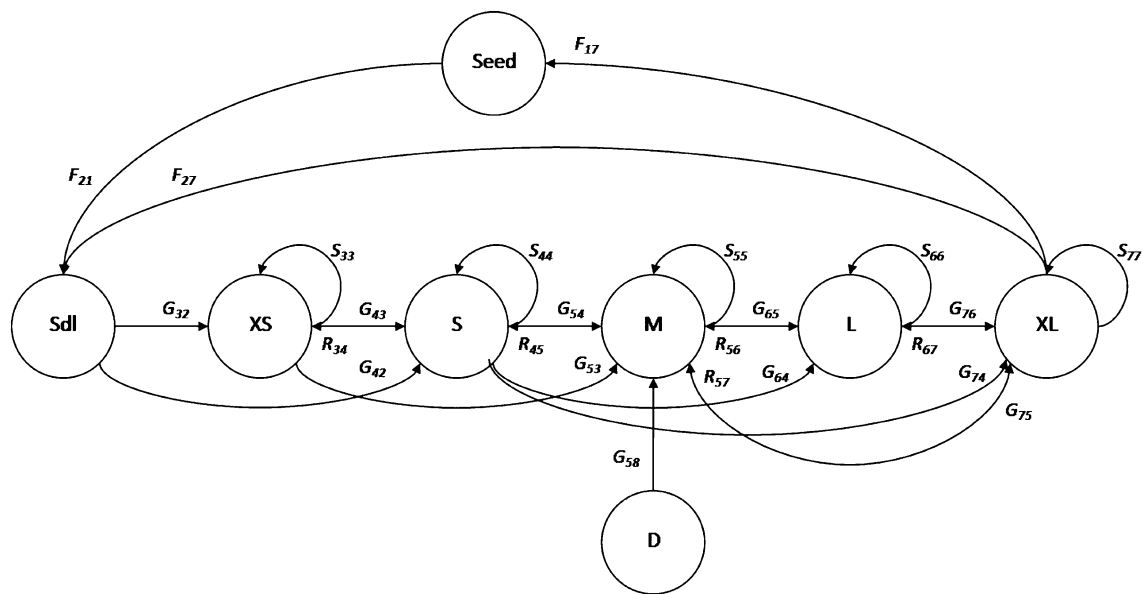
We observed prolonged dormancy, i.e. failure to produce above-ground parts for one or several growing seasons (Lesica and Steele 1994) in *V. biflora*. Of the plants recorded both the first and the last year of the study, 73% never went dormant, 20% went dormant for one growing season,

and 6% went dormant for two growing seasons. Only four plants (1%) were observed to be dormant for more than two growing seasons, and in order not to make population models exceedingly complex we excluded these observations from the dataset. The observed proportion of dormant plants varied between 4 and 12% among populations.

Mortality rates of dormant plants cannot be observed directly and have to be estimated. We based our estimation on the assumption that plants which entered dormancy had the same mortality rates as non-dormant plants, and accordingly set the weighted mean mortality rate for dormant plants equal to the life stage class-specific mortality rate  $\times$  the proportion of dormant plants from this life stage class, summed over all life stage classes. We assumed that transition rates from the dormant stage at time  $t$  to all other stages at time  $t + 1$  were affected equally by mortality in the dormant stage, and reduced transition rates by subtracting from observed transition rates the estimated mortality rate. As transitions to dormancy could not be observed in the last transition period (2006–2007), we used pooled data for 2002–2006 for each population to calculate the transitions from each life stage class to dormancy in this transition period. Correspondingly, we down-weighted estimated mortality rates in 2005–2006 by adding the population- and life stage-specific probability of a plant going into dormancy to remain dormant for two growing seasons.

From the classification into life stage classes we constructed a life cycle graph for *V. biflora* (Fig. 2). All transitions were defined as belonging to one of four life history components (cf. Silvertown et al. 1993): fecundity (recruitment of seeds to the seed pool, and recruitment of seedlings from current seed production and from the seed pool); growth (transition to a larger life stage class); stasis (survival in the same life stage class); and retrogression (transition to a smaller life stage class or to dormancy).

Demographic analyses require a minimum number of observations for each combination of factors, the response



**Fig. 2** Life cycle graph for *Viola biflora*, including the life stage classes seedling (*Sdl*), extra small (*XS*), small (*S*), medium (*M*), large (*L*), extra large (*XL*) and dormant (*D*). Matrix elements are subdivided into: fecundity (*F*), expressed as the mean number of seeds or seedlings produced per plant per stage, growth (*G*; transition to a

larger stage class), stasis (*S*; survival in the same stage class), and retrogression (*R*; the transition to a smaller stage class). In the life cycle graph, transitions with elasticity >0.01 are shown as *arrows* (based on the pooled matrix of the full dataset; see individual matrices in the Supplementary Material)

to which is to be studied. In order to provide reliable estimates of transition probabilities for between-year and between-treatment variation, we sacrificed finer-scale (within-treatment) spatial variability of vital rates and performed all matrix analyses on pooled data from sub-enclosures within each of the three treatments (high density, low density and no sheep).

#### Statistical analyses and transition matrix modelling

We investigated the effect of sheep density and between-year variation in local climate on vital rates (survival, growth and flowering) using generalised linear mixed-effect models (GLMMs). GLMMs were fitted to address how rates of growth, survival and flowering varied with sheep density treatment and weather conditions during the growing season (mean July temperature; Fig. 1), with a focus on the interaction between sheep density and July temperature. Mean July temperature was chosen as a proxy for overall favourableness of growth during the growing season, representing mid-summer conditions during a short alpine growing season (cf. Callaghan et al. 1989). To account for repeated measurements and spatial dependence in the design of the study, plant identity, plot and sub-enclosure were included as random factors. Plant size ( $\log_2 DM$ ) was used as a covariate, as survival and flowering probability were strongly size dependent (Table 1). To explore the hypothesis that increased presence of tall neighbouring plants would affect the *V. biflora* plants in the

no sheep treatment we also investigated the effect of sheep density and July temperature on plant height of seven tall, abundant herbs species recorded in the same plots between 2003 and 2007 (>10 cm; G. Austrheim and M. Evju, unpublished data). The effect of sheep density on seedling emergence rates was evaluated at the population level (mean for each population and year) using ANOVA. The effect of sheep density on the probability of being grazed by vertebrate or invertebrate herbivores, and the effect of grazing on vital rates, was analysed using GLMMs as described above. Models were compared using the  $\chi^2$ -test of deviance (Crawley 2003).

We constructed 15 population transition matrices (3 populations  $\times$  5 transition periods; Table S2) and calculated the projected  $\lambda$  and elasticity values for each matrix (Caswell 2001). We summed elasticity values for each life history component and used linear regression to analyse the functional dependency of  $\lambda$  on the life history component. One-way ANOVA was used to test for differences in summed elasticities between populations.

We constructed confidence intervals around  $\lambda$  by bootstrapping. For each population and transition period, plants were resampled with replacement to construct bootstrap samples. The bootstrap sample size equalled the observed population size, and 1,000 bootstrap replicates were constructed for each transition matrix (Caswell 2001). We used the percentile method (Caswell 2001) to construct 95% confidence intervals (CI) for each  $\lambda$ . For the 2002–2003 transition we estimated seedling number by calculating the

proportion of plants in the extra-small life stage class that was recorded as seedlings in 2003–2006 for that population. We constructed ten bootstrap datasets, in which the estimated number of seedlings was drawn randomly among plants in the extra-small life stage class, to allow for random variation in the fate of seedlings. For each of these ten bootstrapped datasets, 100 bootstrap replicates were constructed. For the last transition period (2006–2007), we estimated the number of plants in each life stage class expected to go dormant from data on the proportion of transitions to dormancy versus death pooled over 2002–2006, for each population separately. The seedling emergence rate from the seed bank was kept constant.

We used a two-way life table response experiment (LTRE) with sheep density treatment and year as fixed effects to quantify the contribution of different matrix elements to the differences in  $\lambda$  between populations and years (Horvitz et al. 1997; Caswell 2001). To investigate if some life history components contributed consistently to the variation in  $\lambda$  between years, we calculated Pearson's correlation coefficients between LTRE contributions to the year effect and deviations of  $\lambda$  from  $\lambda$  of the overall mean matrix. To investigate the causes of interaction effects, we calculated Pearson's correlation coefficients between the LTRE treatment-by-year interaction effect with variables for which population-specific data were available: invertebrate grazing frequency and vertebrate grazing frequency in the census interval  $t$ .

We used linear mixed-effect models to address how the  $\lambda$  varied with sheep density, mean July temperature and invertebrate and vertebrate grazing frequency in the census interval  $t$ . Year was used as a random factor to account for three observations of  $\lambda$  each year. Models were evaluated using Akaike's information criterion.

All statistical analyses were performed with R version 2.10.0 (R Development Core Team 2009), packages popbio (Stubben et al. 2008) and lme4 (Bates and Maechler 2009).

## Results

### Effects of sheep and between-year variability on vital rates

Including only sheep density treatment as a predictor variable, no effect was found on survival or flowering of *V. biflora* plants, but growth was marginally higher in the high density than in the no sheep treatment (GLMM;  $t = 2.33$ ,  $df = 6$ ,  $P = 0.059$ ). Mean July temperature was negatively correlated with survival and growth of *V. biflora* (Table 2). There was a significant interaction between July temperature and sheep density treatment for survival, i.e. survival was higher in the treatments with sheep than in the no

sheep treatment during warm summers (Table 2). Growth was higher in the high density treatment than in the no sheep treatment during warm summers (which we here characterise as marginally significant at  $P < 0.10$ ; Table 2). No effect of July temperature or sheep density treatment was found on the probability of flowering (Table 2). The height of the seven tall herbs was positively related to mean July temperature, but a negative interaction between July temperature and grazing treatment was observed, i.e. plant height was significantly lower in the high density than in the no sheep treatment in warm summers, and marginally lower in the low density compared to no sheep (Table 3).

Effects of sheep density treatment on seedling emergence from the seed bank or seed rain, and on seedling survival were not significant at  $\alpha = 0.05$  (Table 4), although between-year differences in seedling emergence from both seed bank and seed rain were marginally significant ( $P = 0.082$  and  $P = 0.061$  for seed bank and seed rain emergence, respectively). Because the data consisted of only one observation for each combination of treatment and year, the interaction could not be tested for significance.

Signs of invertebrate as well as vertebrate herbivores were visible mainly on leaves. The probability of being grazed by a vertebrate herbivore was higher in the high sheep density treatment than in the no sheep treatment [Fig. 3a; odds ratio (OR) =  $e^{1.077} = 2.94$ , 95% CI = 1.41–6.11,  $P = 0.016$ ], while no difference was found between the low density and the no sheep treatments (OR =  $e^{0.032} = 1.03$ , 95% CI = 0.48–2.24,  $P = 0.967$ ). Vertebrate grazing probability varied significantly between years (comparing models with plant size and grazing, and plant size, grazing and year:  $\chi^2 = 35.37$ ,  $df = 5$ ,  $P < 0.001$ ). Neither survival ( $\chi^2 = 0.15$ ,  $df = 1$ ,  $P = 0.700$ ), growth ( $\chi^2 = 1.18$ ,  $df = 1$ ,  $P = 0.277$ ) nor probability of flowering the following year ( $\chi^2 = 0.65$ ,  $df = 1$ ,  $P = 0.420$ ) decreased with increased vertebrate grazing.

The probability of being grazed by invertebrate herbivores was highest in the no-sheep treatment, but the difference was only marginally significant (Fig. 3b; high density vs. no sheep, OR =  $e^{-0.924} = 0.40$ , 95% CI = 0.24–0.66,  $P = 0.072$ ; low density vs. no sheep, OR =  $e^{-0.810} = 0.44$ , 95% CI = 0.27–0.73,  $P = 0.099$ ). Plants that were grazed by invertebrate herbivores in year  $t$  had a lower probability of producing flowers in  $t + 1$  ( $\chi^2 = 7.26$ ,  $df = 1$ ,  $P = 0.007$ ), but invertebrate herbivory did not affect survival ( $\chi^2 = 0.28$ ,  $df = 1$ ,  $P = 0.595$ ) nor growth ( $\chi^2 = 0.13$ ,  $df = 1$ ,  $P = 0.714$ ).

### $\lambda$ , elasticities and life table response experiments

The  $\lambda$  varied significantly among years ( $R^2 = 0.584$ ,  $F_{4,10} = 3.51$ ,  $P = 0.049$ ) but not among sheep density

**Table 2** Generalised linear mixed-effect model (GLMM) of survival [response binomial; alive = 1, dead = 0, no. of observations = 3,332, no. of plant identities (IDs) = 1,204], growth (response continuous; no. of observations = 2,542, no. of plant IDs = 838) and flowering (response binomial; flowering = 1, non-flowering = 0, no. of observations = 3,332, no. of plant IDs = 1,204) over 5 years

Fixed effects	Estimate	SE	<i>z</i>	<i>P</i>
<b>Survival</b>				
Intercept	6.208	1.132	5.484	<0.001
Plant size <sup>a</sup>	0.406	0.033	12.179	<0.001
July temperature <sup>b</sup>	-0.512	0.101	-5.062	<0.001
Density <sup>c</sup> (high vs. no)	-4.195	1.351	-3.104	0.002
Density (low vs. no)	-3.246	1.378	-2.355	0.019
July temperature × density (high vs. no)	0.385	0.122	3.166	0.002
July temperature × density (low vs. no)	0.310	0.124	2.505	0.012
<b>Growth</b>				
Intercept	2.370	0.433	5.48	<0.001
Plant size	0.672	0.014	49.71	<0.001
July temperature	-0.155	0.040	-3.87	<0.001
Density (high vs. no)	-0.665	0.541	-1.19	0.278
Density (low vs. no)	0.653	0.534	1.22	0.267
July temperature × density (high vs. no)	0.083	0.050	1.67	0.095
July temperature × density (low vs. no)	-0.044	0.049	-0.89	0.375
<b>Flowering</b>				
Intercept	-11.262	2.351	-4.791	<0.001
Plant size	1.483	0.101	14.738	<0.001
July temperature	0.209	0.208	1.005	0.315
Density (high vs. no)	3.853	2.658	1.450	0.174
Density (low vs. no)	3.228	2.732	1.182	0.237
July temperature × density (high vs. no)	-0.301	0.242	-1.246	0.213
July temperature × density (low vs. no)	-0.277	0.247	-1.121	0.262

Non-significant parameter estimates of random factors (plant ID, plot and sub-enclosure) are not shown

<sup>a</sup> Plant size ( $\log_2$ DM) is used as a covariate

<sup>b</sup> Mean July temperature is fitted as a continuous variable

<sup>c</sup> Sheep density is fitted as a factor variable (no, low, high) with 'no sheep' as the reference level

**Table 3** GLMMs of plant height (cm, log-transformed) of seven tall plants (>10 cm; G. Austrheim and M. Evju, unpublished data) in the permanent plots in 2003–2007 as a function of sheep density treatment and mean July temperature

Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	1.762	0.158	11.164	<0.001
July temperature	0.0424	0.00730	5.809	<0.001
Density (high vs. no)	-0.0424	0.220	-0.193	0.854
Density (low vs. no)	0.00409	0.222	0.0184	0.986
July temperature × density (high vs. no)	-0.0331	0.0102	-3.247	0.001
July temperature × density (low vs. no)	-0.0169	0.0101	-1.679	0.093

Non-significant parameter estimates of random factors (plot and sub-enclosure) are not shown ( $n = 9,542$ )

treatments ( $R^2 = 0.025$ ,  $F_{2,12} = 0.156$ ,  $P = 0.857$ ). In ten of the 15 cases, the 95% CI of  $\lambda$  did not include 1.0 (Fig. 4);  $\lambda$  was significantly lower than unity in all populations in 2002–2003, 2003–2004 and 2006–2007, and in the high sheep density treatment in 2005–2006. Populations with  $\lambda > 1$  were characterised by low elasticities for

retrogression and, partly, by high elasticities for fecundity (Fig. 5). The summed elasticities for the life history components showed very little difference among populations (results not shown).

Sheep density treatment effects (Fig. 6a) on the  $\lambda$  were smaller (mean of absolute values of LTRE treatment



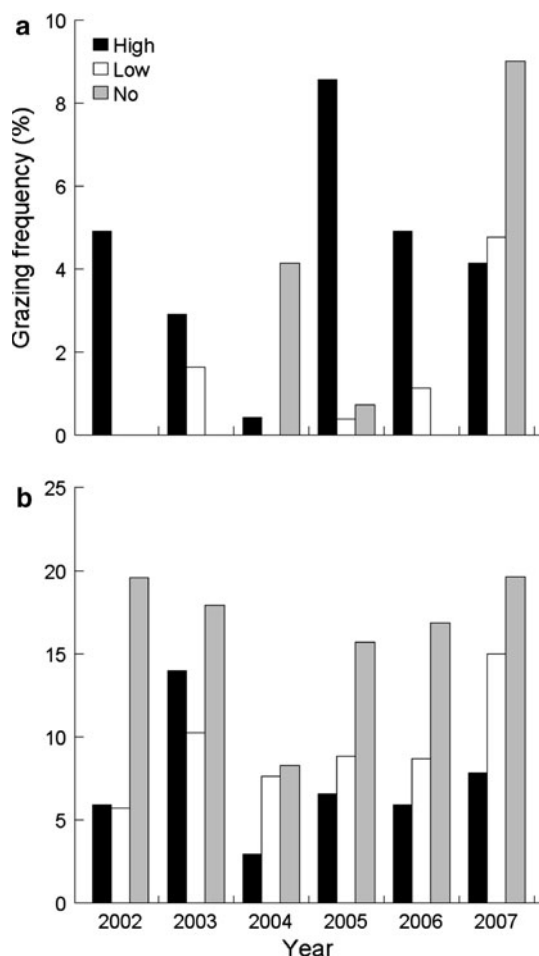
**Table 4** Seedling emergence from seed bank and seed rain, and seedling survival, averaged for each sheep density treatment and each year

	Treatment			<i>F</i>	<i>df</i>	<i>P</i>
	High density	Low density	No sheep			
Seed bank emergence	0.258	0.395	0.391	0.153	2, 9	0.860
Seed rain emergence	0.362	0.426	0.480	0.182	2, 12	0.836
Seedling survival	0.525	0.587	0.520	0.286	2, 9	0.758

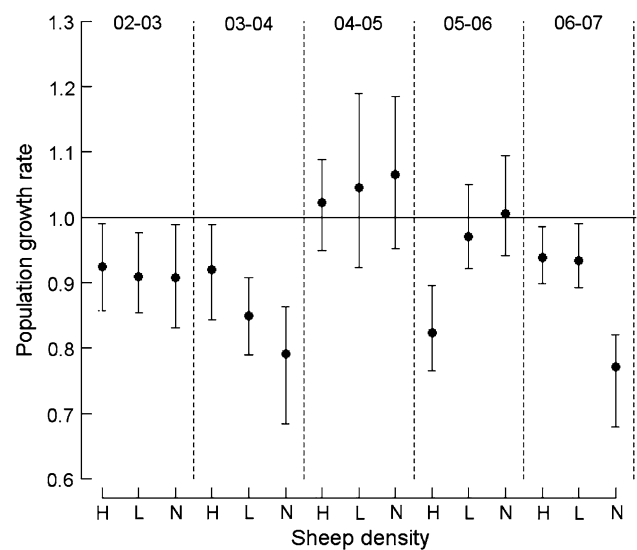
	Year					<i>F</i>	<i>df</i>	<i>P</i>
	2002–2003	2003–2004	2004–2005	2005–2006	2006–2007			
Seed bank emergence	NA	0.122	0.492	0.702	0.076	3.236	3, 8	0.082
Seed rain emergence	0.469	0.447	0.778	0.199	0.220	3.223	4,10	0.061
Seedling survival	NA	0.457	0.659	0.568	0.492	1.655	3, 8	0.253

*F* values, *df* and *P* values refer to ANOVA tests of significant differences in means between treatments and years



**Fig. 3** Proportion of plants in each population and year being grazed by **a** vertebrate herbivores (sheep and rodents) and **b** invertebrate herbivores. Note that the scales of the y-axes differ

effect  $\pm$  SD:  $0.014 \pm 0.008$ ,  $n = 3$ ) than year effects (Fig. 6b; mean year effect  $\pm$  SD:  $0.055 \pm 0.044$ ,  $n = 5$ ). Grazing-by-year effects were of intermediate size (Fig. 6c; mean interaction effect  $\pm$  SD:  $0.042 \pm 0.036$ ,  $n = 15$ ).

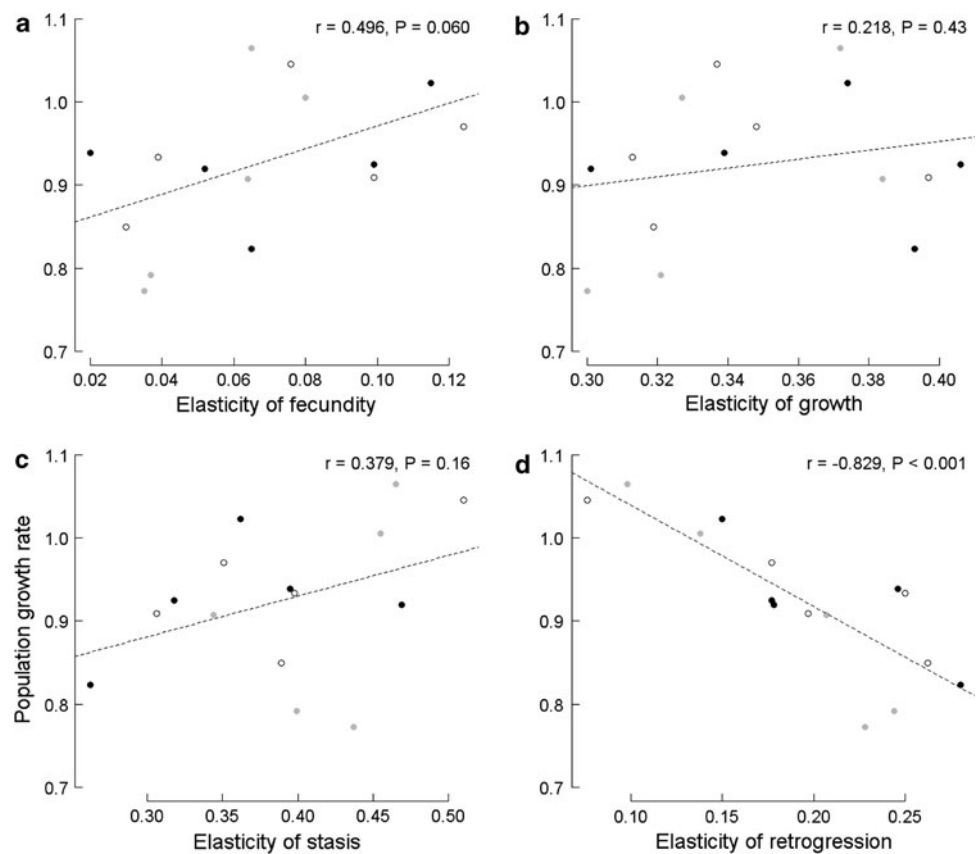


**Fig. 4** Projected population growth rates ( $\lambda$ ) of *V. biflora* in each population and year. Error bars are bootstrapped 95% confidence intervals based on 1,000 bootstrap replicates. H High sheep density, L low sheep density, N no sheep, 02–03 2002–2003, 03–04 2003–2004, 04–05 2004–2005, 05–06 2005–2006, 06–07 2006–2007

There was a small negative effect on  $\lambda$  of the no sheep treatment, a small positive effect of the low sheep density treatment, and a very small negative effect of the high sheep density treatment (Fig. 6a). Growth was less and stasis more important in the no sheep treatment. Differences in the contribution of fecundity among grazing treatments were negligible.

The effect of year on variation in  $\lambda$  was positive in two transition periods, 2004–2005 and 2005–2006, and negative in the three others (Fig. 6b). There was a tendency for contributions from growth to be positively ( $r = 0.862$ ,  $P = 0.060$ ,  $n = 5$ ) and contributions from retrogression to be negatively ( $r = -0.853$ ,  $P = 0.066$ ,  $n = 5$ ) related with the total LTRE year effect, i.e. growth tended to be

**Fig. 5** Correlations between  $\lambda$  and summed elasticities for **a** fecundity, **b** growth, **c** stasis and **d** retrogression. For description of life history compartments, see Fig. 2. *Black circles* represent high sheep density, *open circles* represent low sheep density, *grey circles* represent no sheep



higher and retrogression lower than average in years in which  $\lambda$  was higher than average. Stasis followed the same pattern as growth, though its pattern was less pronounced ( $r = 0.834$ ,  $P = 0.079$ ,  $n = 5$ ). Contributions from fecundity were in the same size range as those from stasis and retrogression; however, fecundity was higher than average both in years with  $\lambda$  above (2005–2006) and below (2002–2003) average.

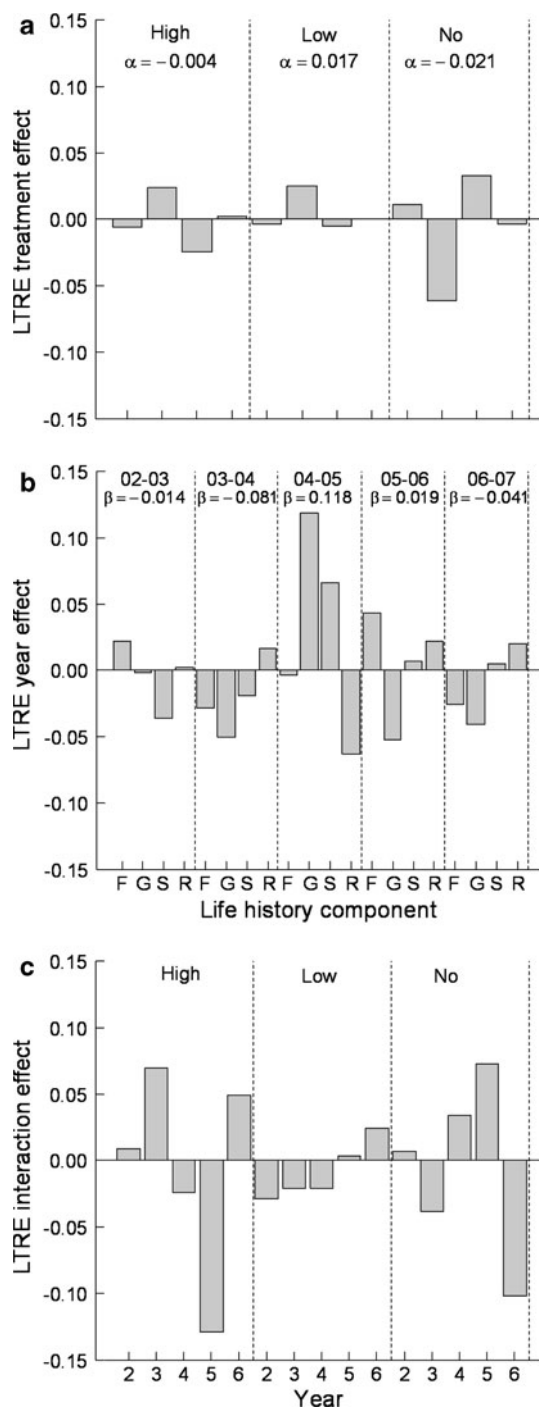
The treatment-by-year interaction effects (Fig. 6c) are estimates of the deviations in observed  $\lambda$  from an additive model of main effects (treatment and year). Their magnitude thus indicated that treatment and year did not influence  $\lambda$  independently. There was a negative correlation between treatment-by-year interaction effect and vertebrate grazing frequency in the census interval  $t$  ( $r = -0.544$ ,  $P = 0.036$ ,  $n = 15$ ), i.e. the interaction effect was negative in populations and years in which grazing frequency was high, and vice versa.

#### Causes of variation in $\lambda$

The AIC values of two alternative models for variation in  $\lambda$  were of the same magnitude (Table 5). Model 2, which had the lowest AIC, expressed  $\lambda$  as negatively related to mean July temperature, with an additional negative effect of vertebrate grazing.

#### Discussion

This study examined the interaction between inter-annual climatic variation and sheep on the population dynamics of a low-stature herb not preferred by sheep. Identification of demographic processes and life history stages that are affected by specific environmental factors allows for evaluation of predictions of long-term population trends (Carlsson and Callaghan 1994). The prediction that small, competitively inferior species are favoured by grazing is partly supported by our results. We did find a small positive effect of high sheep densities on growth of *V. biflora* plants, and the LTRE analyses showed a negative effect of the no sheep treatment on the  $\lambda$  of this plant as well as higher contributions from growth to  $\lambda$  when sheep were present. The observed effects were nevertheless small. Plant responses to cessation of grazing in terms of abundance change are often slow in alpine habitats (Olofsson 2006) and exclusion of herbivores does not necessarily reinforce plant competition on short time scales (Eskelinen 2008). A previous study (Evju et al. 2009) indeed showed that the response to cessation of grazing was smaller than the response to increased grazing pressure, indicating that slow rates of succession after cessation of grazing in the no sheep treatment is a likely explanation for the observed demographic patterns.



**Fig. 6** **a** Life table response experiment (LTRÉ) treatment effects, **b** LTRÉ year effects and **c** LTRÉ treatment-by-year interaction effects on variation in  $\lambda$ . Only the last digit of the year is shown. Main effects are decomposed into contributions from life history components. For abbreviations, see Fig. 2

Between-year climatic variation affects populations of small plants considerably (e.g. Svensson et al. 1993; Økland 1997). We found the relative importance of inter-annual variability on  $\lambda$  to be much larger than that of the sheep density treatment, explaining 58 vs. 2.5% of the

**Table 5** Parameter estimates and Akaike information criterion (AIC) values of alternative models explaining variation in  $\lambda$  as a function of mean July temperature and observed grazing frequency

Model	Variable	Estimate	SE	df	t	P	AIC
1	July temperature	-0.0527	0.0138	3	-3.811	0.032	-34.41
2	July temperature	-0.0496	0.0187	3	-2.651	0.077	-34.50
3	Grazing	-0.0124	0.0052	9	-2.391	0.041	

Non-significant parameter estimates of year, fitted as a random factor, are not shown

variation in  $\lambda$ . Correspondingly, observed LTRÉ year effects were on average 4 times larger than LTRÉ grazing effects. Our results show that the  $\lambda$  was lowest in warm summers, and that both survival and growth rates of *V. biflora* plants were negatively correlated with mean July temperature. Growth of deciduous shrubs in alpine tundra is positively related to mean annual temperature (Olofsson et al. 2009), and negative effects of interspecific interactions on competitively inferior species may be amplified by elevated temperatures (Dunnett and Grime 1999). Thus, grazing may be expected to be particularly beneficial in years with favourable conditions for growth. Our findings support this; during warm summers, rates of survival of *V. biflora* were higher in the presence of sheep, and rates of growth tended to be higher at high sheep density compared to no sheep. Furthermore, the observation of significantly lower height of tall, competitive herbs in the high and marginally lower height in the low sheep density compared to the no sheep treatment during warm summers strongly suggests that sheep affect *V. biflora* positively through alleviating interspecific competition. Recent studies show that shrub expansion on alpine and arctic tundra in response to increased temperatures may be delayed or even prevented by the presence of large herbivores (Post and Pedersen 2008; Olofsson et al. 2009). In a climate change scenario, grazing by large herbivores may thus be important for maintenance of populations of small alpine plants.

Our results revealed considerable variation in observed vertebrate grazing frequency on *V. biflora* plants. Vertebrate grazing was negatively correlated with the  $\lambda$  of *V. biflora*, although no effects of grazing were found on rates of growth, survival or flowering. In the treatments with sheep, the relative contribution of sheep versus rodents to the observed grazing marks could not be separated. It is thus not possible to clarify whether sheep graze *V. biflora* at rates sufficiently high to affect  $\lambda$ . Observed grazing in the no sheep treatment in 2 years (2004 and 2007) does, however, show that the species is affected by rodents. This also accords with the observation in other alpine areas that the abundance of *V. biflora* increases strongly in snowbed habitats protected from rodents (Moen

and Oksanen 1998). Our results thus suggest that long-term effects of sheep grazing on *V. biflora* may depend on a complex set of factors that include the future population dynamics of rodents as well as the long-term effects of sheep on rodent densities (see also Rydgren et al. 2007). In the short term, rodent  $\lambda$  was higher in the low sheep density than in both the high density and no sheep treatments (Steen et al. 2005).

Invertebrate grazing frequency was consistently highest in the no sheep treatment, suggesting that invertebrates have an effect that is compensatory to that of sheep (cf. Ritchie and Olff 1999). Nevertheless, invertebrate grazing did not reduce rates of growth and survival, and invertebrate grazing frequency did not contribute to explaining variation in  $\lambda$ s. This is in accordance with previous observations that leaf grazing by insects has much smaller effects on plant performance than vertebrate grazing (Piqueras 1999).

On the time-scale addressed in our study, no effects of sheep density treatments were found on seedling recruitment or seedling survival. This may indicate that gap creation by sheep is low relative to the disturbance created by other biotic factors such as rodent activity (Austrheim et al. 2008). Furthermore, we found no effect of sheep on flowering rates. Plant reproduction is, however, frequently regulated by a threshold plant size necessary for flowering (Lacey 1986), and this is also suggested by our results. Thus, if cessation of grazing reduces growth and lowers the size of individual plants, reduced seed production would be the expected result (Knight 2004). This would contribute to reduced population growth (Hunt 2001) if recruitment is seed and not safe-site limited (Andersen 1989). However, a long lifespan of individual plants tends to increase population persistence (Eriksson 1996), also under sub-optimal environmental conditions. Despite the relatively long duration of our study, time-delayed population-level grazing effects cannot be totally accounted for here because the life expectancies of almost all stages of *V. biflora* plants exceed its duration.

## Conclusion

This 6-year study of population dynamics of the low-stature herb *V. biflora* reveals small, but negative effects of cessation of grazing on vital rates and population dynamics. These effects are amplified in warm summers when grazing contributes to a reduction in the height of neighbouring tall plants. High rodent grazing in enclosures with no sheep indicates a grazing impact in years with high rodent densities. In the longer term, the population dynamics of *V. biflora* will likely be determined by a complex interplay between weather conditions, sheep, rodent and invertebrate grazing populations.

**Acknowledgments** This study was funded by the Research Council of Norway (project 153601/432 and 134361/720). We are grateful to Synnøve Lindgren for help with field work in 2003, to Dagrun Vikhamar Schuler at the Norwegian Meteorological Institute for providing interpolated climate data, and to Miguel Franco and two anonymous referees for valuable comments that have greatly improved the manuscript. The sheep grazing experiment complies with the laws of Norway.

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