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Effects of management regimes and extreme climatic events on plant population viability in *Eryngium alpinum*

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ABSTRACT

Extreme climatic events like the 2003 summer heatwave and inappropriate land management can threaten the existence of rare plants. We studied the response of *Eryngium alpinum*, a vulnerable species, to this extreme climatic event and different agricultural practices. A demographic study was conducted in seven field sites between 2001 and 2010. Stage-specific vital rates were used to parameterize matrix population models and perform stochastic projections to calculate population growth rates and estimate extinction probabilities. Among management regimes, spring grazing and land abandonment decreased vital rates and population growth, while autumn grazing and late mowing had positive effects on population viability. The 2003 heatwave reduced fecundity rates and survival rates. Only spring grazed sites presented considerable extinction risk. Stochastic projections showed that an increased frequency of 2003-like events may exacerbate extinction risk, but extinction probability depends mainly on land management regimes. To better conserve *E. alpinum* populations, we recommend conversion of presently spring grazed and abandoned sites to late mowing or autumn grazing.

Keywords : Fecundity ; Grazing ; Land abandonment ; Matrix population models ; Mowing ; Survival

1. Introduction

Extreme climatic events can negatively affect plant population dynamics and increase extinction risk in threatened species (Marrero-Gomez et al., 2007; Maschinski et al., 2006). Increased temperature extremes and severe drought induce significant stress to plants, which can lead to increased mortality rates (McDowell et al., 2008; Saccone et al., 2009; Yordanov et al., 2000) and reduced photosynthetic rates and reproductive performances (Chaves, 1991; Epron and Dreyer, 1993; Schulze, 1986; Yordanov et al., 2000). Europe has undergone an extremely dry and hot summer in 2003 (Meehl and Tebaldi, 2004; Schàr et al., 2004; Zaitchik et al., 2006), which resulted in exceptional human mortality (Le Tertre et al., 2006), decreased ecosystem productivity (Ciais et al., 2005; Reichstein et al., 2007), loss in crop yield (van der Velde et al., 2010) and increased plant mortality (Saccone et al., 2009). Such reductions in plant survival may compromise the persistence of vulnerable plant populations and increase their risk of extinction. A temperature anomaly such as that registered in 2003 had never been observed in the last 140 years (Schär et al., 2004). The occurrence probability of such an extreme event can nonetheless increase with global climate change as a result of the greater between-year variability in meteorological conditions and an increase of mean temperatures (Meehl and Tebaldi, 2004; Schär et al., 2004).

Many Alpine plant species can be found in sites that were historically used as pastures for grazing by domestic animals or meadows harvested by farmers. Current management strategies in Alpine ecosystems still include seasonal mowing or grazing, but with varying frequency, intensity and timing, and absence of management is also common. These new management regimes can lead to changes in plant community structure (Jantunen et

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al., 2007; Stammel et al., 2003) and to an increase of extinction risk for the most vulnerable species (Brys et al., 2004; Jantunen et al., 2007; Lennartsson and Oostermeijer, 2001; Marage et al., 2008). Populations can exhibit different vital rates and population growth rates between sites subject to different management strategies and characterized by variable ecological conditions. Some management conditions might not allow rare and protected plant species to persist and are incompatible with their conservation.

The objective of this work was to study the population dynamics of *Eryngium alpinum*, a rare Alpine perennial plant threatened by changes in land use (Cherel and Lavagne, 1982; Gaudeul and Till-Bottraud, 2003, 2004, 2008; Gillot and Garraud, 1995), in relation to: (i) the effects of the 2003 heatwave and (ii) the effects of management regimes. Field data were collected between 2001 and 2010 in seven sites submitted to various management regimes and survival, flowering and fecundity rates were measured for plants of different life stages: seedlings, juveniles, vegetative adults and reproductive adults. Through statistical analysis of vital rates and demographic modeling, we were able to predict how a 2003-event will increase the extinction risk of populations and to identify the best management regimes for the conservation of this species.

2. Materials and methods

2.1. Species, study sites and management regimes

E. alpinum L. (Apiaceae) is a perennial, rare species. Its distribution area extends over the Alps (France, Italy, Switzerland, Austria, Croatia) between 1300-2500 m (Cherel and Lavagne, 1982). The species is present in open sunny but relatively humid habitats; restricted to hayfields and avalanche corridors. The species is protected by the Bern convention, the European Habitat Directive of Natura 2000 (Wyse-Jackson and Akeroyd, 1994), the French Red List of protected species and it is considered vulnerable by IUCN (Gillot and Garraud, 1995). The threats are mainly due to human activities such as cutting for commercial use (flower bouquets) and land use change (from late hay harvest to spring grazing, or abandonment leading to land closure by forest). Flowering occurs from mid July to mid August. Mature fruits (schizocarpous diachenes) fall near the mother plant at the end of August and seeds germinate in the spring.

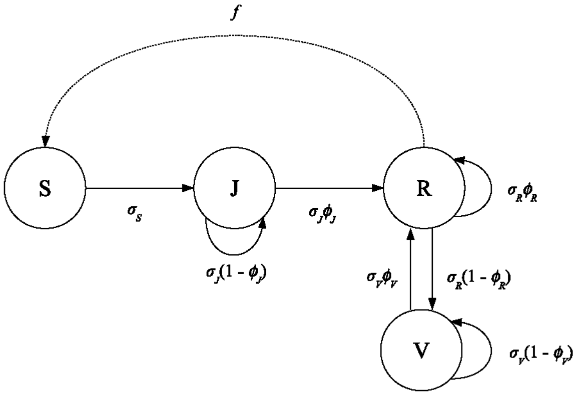
Two regions were studied: the Pralognan region (Pralognan la Vanoise, Savoie, France) is located in the "aire d'adhésion" of Vanoise National Park and the Fournel region (L'Argentière la Bessée, Hautes Alpes, France) is located in the "Vallon du Fournel-les Bans" Natura 2000 site and the "aire d'adhésion" of Ecrins National Park. The two regions are located approximately at the same elevation (1500 m) but in contrasting situations: Pralognan is in the Northern Alps on a steep East-facing slope while Fournel is in the Southern Alps on a mild North-facing slope. Respectively three (DES, BER and BOU in Fournel, located 1-5 km apart) and four (PRA, PRB, PRC and PRD in Pralognan, located less than 100 m apart) different sites were studied. Three permanent rectangular plots, located less than 5 m apart and measuring between 4 and 20 m^2, were set up for annual census in each site. In the two regions, the National Parks are testing various management practices to limit or even reverse the population decline observed due to agricultural abandonment (Table 1). These management practices are based on local traditional and present uses of mountain prairies.

Table 1 *Management regimes in the seven sites.*

Region	Site	Management regime
Fournel	DES	Autumn grazing: 1800 sheep (306 LU[a]; 7.1 ha, 43 LU/ha) for 1 week around the 10th of September and for 2 weeks between the 1st and the 15th of October
	BER	Late mowing (after the 15th of August)
	BOU	Spring grazing: 800 sheep (136 LU on 3.0 ha, 45 LU/ha) for 10 to 15 days between the 5th and the 15th of June
Pralognan	PRA	Abandoned
	PRB	Late mowing every other year
	PRC	Late mowing every year
	PRD	Spring + autumn grazing: 40 heifers and occasionally some cows (24 LU, 2.2 ha, 11 LU/ha) from the 1st of June to the 1st of July and from the 1st of September to the 10th of October

[a] Livestock unit (LU) coefficients were 0.17 for sheep and 0.6 for heifers (Conseil Fédéral Suisse, 1998).

Fig. 1. *Life-cycle of E. alpinum. S, seedlings; J, juveniles; V, vegetative adults; R, reproductive adults;* σ_i*, survival rate;* ϕ_i*, flowering rate; f, fecundity rate.*



2.2. Life cycle and data collection

The life cycle of *E. alpinum* was subdivided into four biological stages (Fig. 1). Seedlings (S) are small plants younger than one year. Juveniles (J) are older than one year and have not yet flowered in their life. Reproductive adults (R) are plants bearing one or more inflorescences. Vegetative adults (V) do not bear inflorescences but have already flowered in their life. Seedlings become juveniles in one year, while juveniles and adults can remain in the same stage for more than one year or make a transition to another stage.

For the first 2 years of survey (2001 and 2002), juveniles and vegetative adults were distinguished on the basis of morphological traits (number of basal leaves and length of the longest petiole). An individual was considered juvenile when it bore less than four leaves and when the longest petiole measured less than 20 mm, otherwise it was classified as a vegetative adult. These criteria had to be slightly modified for BOU, where spring grazing results in enhanced vegetative growth and plants have more leaves (juveniles identified as individuals bearing less than ten leaves with the longest petiole measuring less than 20 mm).

In each permanent plot, plants were individually tagged and their presence/absence and biological stage were scored every year from 2001 to 2010, leading to a dataset including nine annual transitions, the first one being 2001-2002 and the last one being 2009-2010. Stage-specific annual survival rates σ_i were defined as the proportion of plants surviving from one census to the next one. Stage-specific flowering rates ϕ_i were defined as the proportion of surviving plants that make the transition to the reproductive adult stage. The annual fecundity rate *f* for year *t* was defined as the ratio of the number of seedlings emerging in year $t + 1$ over the number of reproductive adults in year t, assuming equilibrium between seed immigration and emigration among plots and no seed bank. Seed immigration and emigration rates between plots were likely equivalent because plots were located in areas of uniform density; moreover, fruits disperse by gravity over a few decimetres from their mother plant (Gaudeul and Till-Bottraud, 2004). As the number of seedlings was only recorded since 2003, seedling survival rate in the 2001-2002 and 2002-2003 transitions and fecundity rate in the 2001-2002 transition were not available. No reproductive adult was observed in BOU in 2008, so survival and flowering rates for the reproductive adult stage could not be estimated. Since census was performed in July, the effect of the 2003 heatwave were associated with both the 2002-2003 and the 2003-2004 transitions. For simplicity, we will refer to these transitions as "dry years" and to the other transitions as "normal years".

2.3. Spatiotemporal variation in vital rates

We tested for spatio-temporal variation in fecundity rates, survival rates and flowering rates of the different life stages. Fecundity rates were analyzed using a linear model with Gaussian errors, after log-transformation to achieve normality and homoscedasticity. Survival rates and flowering rates were analyzed using generalized linear models with binomial errors and a logit link; in case of overdispersion, models were fit through quasi-likelihood approaches (Williams, 1982; Faraway, 2006). Region, site within region, year and the interactions between region and year and between site and year were included in the models as fixed factors. The three permanent plots were considered as independent replicates of the same site-by-year cell. For each vital rate, the full model was tested. When the region effect was significant, subsequent analyses were performed separately for Fournel and Pralognan. When no region effect was detected, the model factors were reduced to site, year and their interaction in order to test directly differences between all sites. Orthogonal comparisons were used to test for significant differences between dry and normal years. Differences between sites were tested using Tukey's multiple comparison method. When the interaction between site and year was significant, orthogonal comparisons were performed separately for each site and Tukey's multiple comparisons were performed separately for each year. All statistical analyses were performed in R 2.10.1 (R Development Core Team, 2008) using the packages *multcomp* (Hothorn et al., 2008) and *dispmod* (Scrucca, 2009).

2.4. Deterministic analysis

The life-cycle of *E. alpinum* was described by a birth-pulse matrix model with pre-breeding census (Caswell, 2001). The elements of the **A** matrix, a_{ij}, gave the annual transition rates from stage j to stage i and were defined in terms of survival rates σ_j, flowering rates ϕ_j and fecundity rate f:

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & f \\ \sigma_S & \sigma_J(1-\phi_J) & 0 & 0 \\ 0 & 0 & \sigma_V(1-\phi_V) & \sigma_R(1-\phi_R) \\ 0 & \sigma_J\phi_J & \sigma_V\phi_V & \sigma_R\phi_R \end{pmatrix}$$

To increase the precision of matrix element estimates and avoid problems linked to small sample sizes and missing life stages, the observations from the three permanent plots were pooled together within each site. We defined a transition matrix for each site and each year from 2001 to 2009 (Table S1). Since seedling survival rates were not available for 2001 and 2002 and fecundity rates were not available for 2001 (see Section 2.2), their values were set equal to their averages over the other years. The 2008 transition matrix for BOU was not estimated because of lack of data on the reproductive adult stage.

The deterministic growth rate λ was estimated for each site and year as the dominant eigenvalue of the **A** matrix. The uncertainty in λ estimation was accounted for by bootstrapping individual state/fate pairs for each site and each year. Ninety-five percent confidence intervals (CIs) were derived by the percentile method using 2000 bootstrap replicates (Caswell, 2001). We derived the sensitivities and elasticities of λ to survival, flowering and fecundity rates from the sensitivities and elasticities to the matrix elements through the chain rule (Caswell, 2001; pp. 218-220 and 232). Sensitivities and elasticities were calculated in relation to the overall mean matrix and to the mean matrix of each site.

The differences in λ between sites and years were analyzed with a Life-Table Response Experiment (LTRE) (Caswell, 2001; Cooch et al., 2001 ; Lucas et al., 2008). This method allows for the estimation of the site effect $\alpha^{(l)}$, the year effect $\beta^{(m)}$ and the site-year interaction $(\alpha\beta)^{(l,m)}$ and the decomposition of these effects into the contributions of stage-specific survival, flowering and fecundity rates. In order to identify the vital rates contributing the most to the overall between-site and between-year differences in 1, we summed the contributions across sites and years for each vital rate. The overall contribution of a given vital rate to between-site differences was obtained by summing the absolute values of its contributions to between-site differences across sites. Similarly, the overall contribution to between-year differences was obtained by summing across years.

2.5. Stochastic projections

We used stochastic projections to study the effect of increased heatwave occurrence probabilities on population dynamics. The stochastic growth rate $a = \log\lambda_s$ was calculated under different heatwave occurrence probabilities p using a numerical approach (Caswell, 2001). On the basis of climatic projections (Schär et al., 2004), we considered values of heatwave occurrence probability p comprised between 0 (no heatwave) and 0.2 (one heatwave every 5 years). Extinction probabilities for each heatwave occurrence probability values were estimated using an individual-based simulation that took into account environmental and demographic stochasticity (Supplementary material). The calculation of eigenvalues, the LTRE and the stochastic projections were carried out in Matlab (The Mathworks, 2001).

3. Results

3.1. Spatiotemporal variation in vital rates

The effect of region was significant for seedling survival rate, juvenile survival rate, juvenile flowering rates and vegetative adult flowering rates (Table 2). For these vital rates, the statistical analysis of year and site effects was carried out separately in each region. With few exceptions, both year and site effects were significant, as well as the interaction between them, for all vital rates (Table 2).

Survival rates and fecundity rates were negatively affected by the heatwave. Reductions were particularly large for juvenile survival rates (Fig. 2) and fecundity rates. Conversely, flowering rates exhibited a marked year-to-year variation that could not be attributed to the heatwave (Fig. S1).

Differences between sites were often significant but their direction was not consistent across years (significant site * year interactions; Fig. S1). Between-site differences were most evident for fecundity rates, reproductive adult flowering rates and vegetative adult survival rates (Fig. 3). The differences in fecundity rates were particularly marked: DES (autumn grazing) and PRC (mowing) exhibited very large values, BOU (spring grazing) had the smallest rates, while the other sites exhibited intermediate values. As for reproductive adult flowering rates, BOU (spring grazing) and PRD (spring + autumn grazing) exhibited the smallest values, while DES (autumn grazing), BER (mowing) and PRB (mowing) exhibited the highest values. Between-site differences in vegetative adult survival rates were less marked than differences in fecundity rates or reproductive adult flowering rates, but BOU (spring grazing) and PRD (spring + autumn grazing) still exhibited the smallest values.

3.2. Deterministic analysis

The deterministic growth rate λ was comprised between 0.73 (95% CI: 0.63-0.82) in PRD in 2003 and 1.40 (95% CI: 1.27-1.53) in DES in 2004 (Fig. S2). DES showed larger λ than the other sites, except in 2003. Over years, BOU (1 = 0.92, mean over years), PRA (1 = 0.98) and PRD (1 = 0.94) exhibited decreasing dynamics, DES showed increasing dynamics (1 = 1.21) and the other sites showed stable dynamics (1 = 1.00 in BER, PRB and PRC). The average population growth rate in dry years (1 = 0.90, mean over all sites in 2002 and 2003) was smaller than in normal years (1 = 1.04).

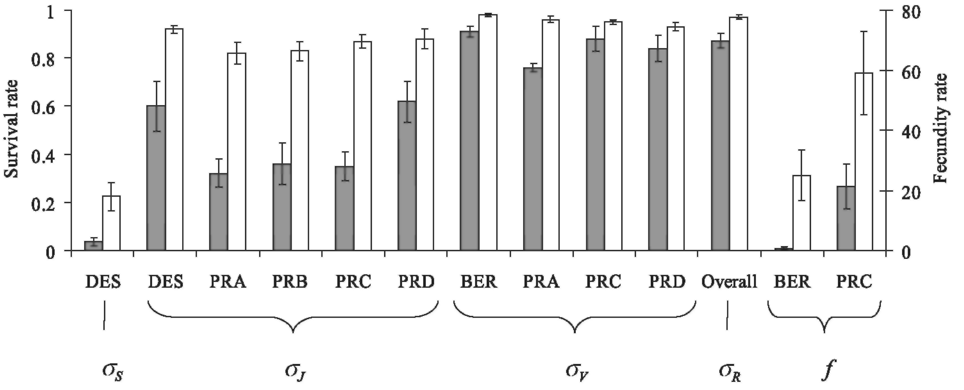
On the overall mean matrix, the largest sensitivity of λ was associated with seedling survival rate σ_S and the smallest one with fecundity *f* (Table S2). This pattern was observed also in each site, except for DES (largest sensitivity associated with juvenile flowering rate ϕ_J) and for BOU (largest sensitivity associated with vegetative adult survival rate σ_V). On the overall mean matrix, as well as in each site, the largest elasticities were associated with juvenile, vegetative and reproductive adult survival rates (Table S2). The elasticities to σ_S and *f* were smaller than the elasticities to the other survival rates. The smallest elasticities were associated with flowering rates.

Table 2 *Spatiotemporal variation in vital rates.*

Vital rate		Effect					
		Region[a]	Site	Year	Site * year	Heatwave[b]	R^2
Fecundity rate	*f*	Overall	$P < 0.001$	$P < 0.001$	$P < 0.001$	BER PRC	0.57
Seedling survival rate	σ_S	Fournel	$P < 0.001$	$P < 0.001$	$P < 0.001$[c]	DES	0.81
		Pralognan	n.s.	n.s.	$P = 0.027$	No	0.54
Juvenile survival rate	σ_J	Fournel	$P = 0.23$	$P < 0.001$	$P < 0.001$	DES	0.76
		Pralognan	$P = 0.01$	$P < 0.001$	$P = 0.011$	PRA, PRB, PRC, PRD	0.88
Vegetative adult survival rate	σ_V	Overall	$P < 0.001$	$P < 0.001$	$P < 0.001$	BER PRA, PRC, PRD	0.64
Reproductive adult survival rate	σ_R	Overall	n.s.	$P < 0.001$	n.s.	all sites	
Juvenile flowering rate	ϕ_J	Fournel	n.s.	$P < 0.001$	$P < 0.05$	No	0.70
		Pralognan	$P < 0.001$	$P < 0.001$	n.s.	No	0.48
Vegetative adult flowering rate	ϕ_V	Fournel	$P < 0.001$	$P < 0.001$	$P < 0.001$	No	0.81
		Pralognan	$P = 0.007$	$P < 0.001$	$P = 0.005$	No	0.59
Reproductive adult flowering rate	ϕ_R	Overall	$P < 0.001$	$P < 0.001$	$P < 0.001$	No	0.76

[a] When the region effect was significant, the analysis was performed separately for Fournel and Pralognan.
[b] Sites where a significant difference between dry and normal year was observed (orthogonal comparison).
[c] The site * year interaction for seedling survival rates was no more significant when the model was refitted through quasi-likelihood.

Fig. 2. *Mean vital rates in dry years (grey bars) compared to mean values over normal years (white bars). Lines represent ±1 standard error. Only vital rates that were significantly reduced in dry vs. normal years are shown.*



In the LTRE, DES showed a large positive effect ($\hat{\alpha}^{(DES)}$= 0.26; Table S3; Fig. S3), while BOU showed a large negative effect ($\hat{\alpha}^{(BOU)}$= -0.17); BER showed a small positive effect ($\hat{\alpha}^{(BER)}$= 0.001); all the other sites showed negative effects. The vital rates contributing the most to differences between sites were fecundity rate f (sum of absolute values of contributions: 0.53) and seedling survival rate σ_S (0.43). Fecundity rates made large contributions in DES (positive), BOU (negative) and, to a lesser extent in PRA, PRB, PRD (negative) and PRC (positive). DES was also the site exhibiting the largest fecundity rate (Fig. 3). Seedling survival rates made moderately large contributions in DES, BOU (positive) and BER, PRB, PRC and PRD (negative).

The years 2001, 2002, 2003 and 2009 exhibited negative effects (Fig. S3), while the other years showed positive effects. The effect of 2003 was very large and negative ($\hat{\beta}^{2003)}$ = -0.20) and the effect of 2006 was very large and positive ($\hat{\beta}^{(2006)}$ = 0.15). The large negative effect showed by 2003 was due to negative contributions of all vital rates : in particular, there were large negative contributions of juvenile and vegetative adult survival rates and juvenile flowering rates. Across all years, the vital rates contributing the most to the differences in λ were juvenile survival rate (0.47), seedling survival rate (0.35), juvenile flowering rate (0.30) and fecundity rate (0.25).

3.3. Stochastic projections

In absence of heatwaves (p = 0), DES (autumn grazing) showed a large positive growth rate (a = 0.146; 95% Confidence Intervals: 0.138, 0.154), BOU (spring grazing) exhibited a pronounced decline (a = -0.062; 95% CI: -0.067, -0.057) and PRD (autumn + spring grazing) a modest decline (a = -0.015; 95% CI: -0.021, -0.009); the other sites had small positive growth rates (Fig. S4). When heatwave occurrence probability p = 0.20, the stochastic growth rate was significantly smaller than 0 in all sites except for PRB (a = -0.006; 95% CI: -0.012, 0.000), BER (a = 0.000; 95% CI: -0.010, 0.011) and DES (a = 0.062; 95% CI: 0.054, 0.070). For intermediate heatwave occurrence probability ($0 < p < 0.20$), increasing p lead to smaller a. The reduction in a was most pronounced in DES, but the relative ranking of sites did not change much: DES showed always the largest a, BOU the smallest and PRD the second smallest, for all values of heatwave occurrence p.

Extinction probabilities were larger than zero only in BOU (spring grazing), PRA (abandonment) and PRD (spring + autumn grazing) (Fig. 4), BOU having always the highest probabilities of extinction and being the only site in which extinction probability was nonzero even in absence of heatwaves (p = 0). Increasing heatwave occurrence probability lead to higher extinction probabilities. The increase in extinction probability was very small for PRA and PRD and large for BOU (from 0.03 when p = 0 to 0.63 when p = 0.20).

Fig. 3. *Fecundity rates, reproductive adult flowering rates and vegetative adult survival rates in the seven sites averaged over all years. Lines represent ±1 standard error.*

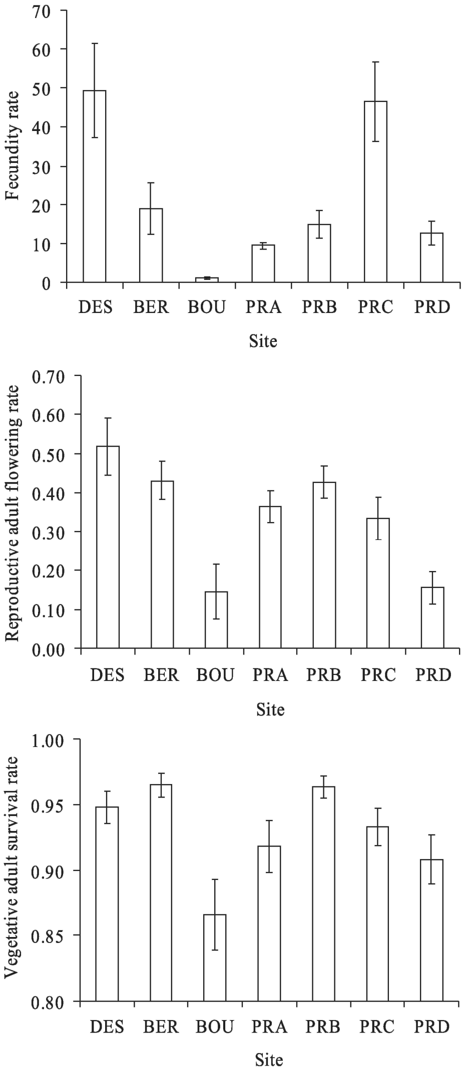
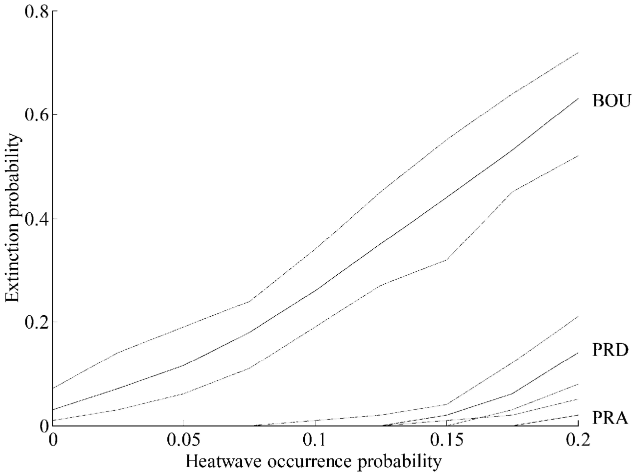


Fig. 4. *Effect of heatwave occurrence probability on extinction probability. Solid lines represent means and dotted lines represent the 2.5 and 97.5 percentiles of extinction probability evaluated over 100 replicate simulations.*



4. Discussion

4.1. Impact of the 2003 heatwave on vital rates and population growth

Survival rates of *E. alpinum* were reduced by the heatwave of 2003 in all sites. This extreme climatic event was associated with rainfall deficit and extreme summer heat that impaired plant productivity in Europe through heat stress and drought stress (Ciais et al., 2005; Reichstein et al., 2007). At a smaller scale, the summer of 2003 lead to reduced survival rates in tree populations located in the same geographical area as the *E. alpinum* populations studied here (Saccone et al., 2009). Drought can cause direct plant death through hydraulic failure, or reduce photosynthetic rates following stomatal closure, leading to a cascade of downstream effects that reduce plant fitness and increase mortality, especially for individuals with small roots as seedlings or juveniles (McDowell et al., 2008). In agreement with this prediction, we observed the largest reductions in survival rates for juvenile plants, while adults were much less affected by the 2003 heatwave (Fig. 2). Overall, the reduction in survival rates observed during the 2003 heatwave lead to smaller λs in 2002 and 2003. As shown by the LTRE, the negative impact on λ could be ascribed mainly to a reduction in survival rates rather than to a change in the pattern of flowering or fecundity. In fact, fecundity rates were reduced only in two sites out of seven and did not contribute much to the difference in λ between 2003 and the other transitions. Flowering rates exhibited strong between-year variation, but the comparison between normal and dry years did not uncover any significant differences.

The effects of increasing heatwave occurrence on future population dynamics were small if compared to between-site differences. Even when the frequency of heatwave occurrence was maximal ($p = 0.2$, one heatwave every 5 years on average), only two sites, PRC and PRA, changed from positive to negative a. Extinction risk increased with heatwave occurrence rate, but only three sites out of seven (BOU, PRD, PRA) showed nonzero extinction probabilities at high occurrence and only BOU showed a considerable extinction risk.

On the basis of demographic data collected over the last decade, the estimated generation time of *E. alpinum* plants can be as high as 65 years (Andrello, 2010). This long generation time implies that the species has a very long life-span, which can buffer the effects of extreme environmental variation on population dynamics (Morris et al., 2008). This result is reassuring for the persistence of *E. alpinum* populations, but it cannot be taken as evidence that the species will not be affected at all by climate change. The dramatic increase in the frequency of heatwaves and other extreme events is only one consequence of global climate change (Meehl and Tebaldi, 2004; Schär et al., 2004). A global increase of temperature will lead to an increase of ecosystem productivity in the Alps (Theurillat and Guisan, 2001), accelerating forest regeneration following land abandonment and thus loss of habitat for alpine and subalpine herbaceous species as *E. alpinum* (Dirnbock et al., 2003; Engler et al., 2011). Climate warming will also lead to modifications in species interaction, community dynamics and productivity, and ecosystem processes (Araujo and Luoto, 2007; Easterling et al., 2000; Hagvar and Klanderud, 2009; Klanderud, 2010). Some drought-tolerant grasses as *Festuca paniculata* (growing at high density in the DES site) may benefit from an increasingly drier and hotter climate and outcompete *E. alpinum* (Sandra Lavorel, Laboratoire d'Ecologie Alpine, unpublished manuscript). The projections that we used may therefore not be representative of the population dynamics under climate change, because they only take into account the effects of increased heatwave frequency and disregard potential modifications of vital rates due to other processes.

4.2. Effects of local conditions and management regimes

Overall, populations of *E. alpinum* were stable, except in the DES site, where population size was increasing, and in the BOU and PRD sites, which exhibited a pronounced (BOU) or modest (PRD) decline. Negative effects of grazing on plant survival are documented (Huhta et al. 2001) and were evident in *E. alpinum* because adult survival rates were reduced in BOU (spring grazed) (Fig. 3). In addition to affecting survival, grazing can have direct effects on fecundity: grazing can reduce fecundity rates by lowering seed set (Brys et al., 2004; Lennartsson and Oostermeijer, 2001), but can also increase fecundity by creating favorable conditions for seedling establishment, through the prevention of litter accumulation and the creation of gaps (Lennartsson and Oostermeijer, 2001). However, fecundity rates in BOU were the smallest of all sites and were the parameters contributing the most to the reduction in λ. This reduction in fecundity was at least partly driven by a decrease in seed set (data not shown), but it is possible that seed germination and seedling establishment were also affected. To a lesser extent, the negative effects of grazing were also confirmed by the reduced fecundity in PRD (spring grazed) compared to those in PRB and PRC (both mowed).

In contrast, facilitation of seedling establishment and the gap effect may emerge more easily if grazing takes place in autumn, when seeds are mature and the possibility for plant damage is reduced. This might explain the large vital rates and population growth rates in DES (autumn grazed): the difference in λ between DES and the other sites were driven mainly by seedling survival rates and fecundity rates (LTRE; Fig. S3). However, the observed high recruitment might also be due to factors other than autumn grazing. DES is located in an avalanche debris cone that favors soil water retention and thus creates favorable conditions for plant growth and seedling establishment. The site is part of a protected area (Natura 2000) and is subject to regular shrub and tree cutting, which prevent forest regeneration. As a consequence, the vegetation is sparse, *E. alpinum* is the dominant species and exhibits a positive population growth rate.

The effects of grazing can also be seen on plant morphology, as plants usually reduce their flowering rates, allocate more resources to vegetative growth and show higher foliage productivity (Brys et al., 2004; Huhta et al., 2001; Turner et al., 1993). In agreement with these published observations, flowering rates were lower in BOU (spring grazed) than in the other sites and vegetative growth was greatly enhanced (the mean number of basal leaves per vegetative adult was 56 compared to 8 in the other sites).

PRD was subject to both spring and autumn grazing, but its vital rates, population growth rates and extinction probability resembled more those of BOU (spring grazed) than those of DES (autumn grazing). Therefore, it seems that the driving factor behind the negative effects of grazing is its timing and not its intensity (density of livestock units). Sites grazed in spring (BOU and PRD) exhibited similar reduction in vital rates and population growth rates even if they were affected by different grazing intensity, while sites experiencing comparable grazing intensities but at different times (BOU and DES) presented very different population dynamics. Spring grazing disturbs plants during active vegetative growth and before flowering, while autumn grazing can only have positive indirect effect, since vegetative growth and seed production are completed. As discussed above, such an indirect facilitation of plant recruitment by autumn grazing may act on seedling establishment.

The populations growing in the other sites (BER, PRA, PRB and PRC) were stable or slightly declining. These populations were left unmanaged or subject to various regimes of mowing (Table 1). Absence of management can lead to limited germination possibilities due to the disappearance of suitable microsites for recruitment (Brys et al., 2004) and invasion by more competitive species such as grasses and eventually shrubs and trees (Cherel and Lavagne, 1982). The negative effects of land abandonment were evident in PRA (unmanaged), which had nonzero extinction probabilities and smaller vegetative adult survival rates and fecundity rates than the other sites (Fig. 3 and 4). In addition, trees and shrubs were observed on the site in the last years of survey and are likely to invade the prairie if no cutting is performed. Therefore, even if the effects of land abandonment are less severe than those of spring grazing, total absence of management is not recommended for the conservation of *E. alpinum*.

Mowing can have positive consequences for persistence of weakly competitive species, as seed germination, seedling establishment and fecundity are favored by litter removal and harvest of more competitive plants (Brys et al., 2004; Huhta et al., 2001; Kahmen and Poschlod, 2008; Lennartsson and Oostermeijer, 2001). However, the three mowed sites (BER, PRB and PRC) did not show consistent responses in fecundity: large values were observed in PRC but not in BER or PRB. The other vital rates were similar across mowed sites and lead to larger population grow rates than in spring grazed sites (BOU and PRD) and the abandoned site (PRA), but were comparable to the autumn grazed site (DES). Applying different mowing frequencies did not lead to large differences in population dynamics: even if a reduction in mowing frequency was associated with higher vegetative adult survival and flowering rates in PRB (mowed every other year) than in PRC (mowed every year), the latter site exhibited much higher fecundity, resulting in similar stochastic growth rates for the two sites (Fig. S4). The observed differences in vital rates between sites may also be ascribed to local conditions not depending on management regimes. For instance, BER exhibited extremely low seedling survival rates, a feature that was not observed in PRB or PRC, and that can be explained by the dry conditions and dense vegetation cover of this site.

While the effects of climate change on the persistence of *E. alpinum* are still difficult to predict, a reassuring result of the present work was that an extreme 2003-like event per se will not translate into considerable extinction risk thanks to the long life span of the species. Conservation efforts should be concentrated on land use change, as this aspect was the main driving factor behind population growth rate variation. We have collected substantial evidence that spring grazing is certainly to be discouraged, because it reduced vital rates and considerably increased extinction risk. Land abandonment turned out to be a suboptimal practice too, even if the effects of absence of management on demography might emerge more slowly. It seems that late mowing and late grazing are the best management regimes for the conservation of *E. alpinum* populations. Following the results of the present work, the "Vallon du Fournel-les Bans" Natura 2000 site has decided to negotiate changes in land use with the private owner of the BOU site.

Similarly, the Vanoise National Park should conduct an assessment of agricultural agreements between local farmers and the community of Pralognan, in order to reverse the population decline observed in PRD.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.12.012.

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