

Dynamics of isolated *Saponaria bellidifolia* Sm. populations at northern range periphery

Anna-Mária Csörgő · Edit Molnár ·
Maria Begoña García

Received: 25 January 2010 / Accepted: 8 October 2010 / Published online: 17 November 2010
© The Society of Population Ecology and Springer 2010

Abstract Four populations of *Saponaria bellidifolia* situated at the species' northern range periphery (Apuseni Mountains, southeastern Carpathians) were monitored over a period of 5 years. They were chosen to represent different habitat types (rocky, fixed screes, open screes and grassy), disturbance regime (fire), and population sizes (categorized as large and small). The reproductive effort was quantified, and matrix models were used to describe the population dynamics and to assess population viability. *Saponaria bellidifolia* had very stable population dynamics in the harsh and stable abiotic conditions of the outcrops where populations occur. Habitat conditions exerted a notable influence on the species' population reproductive performance, growth rate, and vital rates, whereas population size and climate did not have a clear-cut effect on the dynamics of the species. *Saponaria bellidifolia* maintains viable populations in the southeastern Carpathians, at its northern range periphery.

Keywords Disturbance · Matrix population models · Peripheral populations · Population viability analysis · Vegetation succession

A.-M. Csörgő (✉)
Department of Horticulture, Sapientia Hungarian University
of Transylvania, Sighișoarei 1C,
540485 Târgu Mureș, Romania
e-mail: csorgo.anna.maria@gmail.com

E. Molnár
Hungarian Academy of Sciences, Institute of Ecology
and Botany, Vácrátót, Hungary

M. B. García
Pyrenean Institute of Ecology (CSIC), Zaragoza, Spain

Introduction

When situated at the northern, leading edge, species of the northern hemisphere may experience harsher ecological conditions than in the southern, central locations of their distribution area. Populations are often restricted to south-facing hillsides with warmer mesoclimate (Jonsson et al. 2008), wind-sheltered depressions (Payette and Delwaide 1994), limestone outcrops (Lammi et al. 1999) or alvar habitats known for their high heat-retaining capacity (Bengtsson 1993; Lönn and Prentice 2002). These “ecological islands”, separated by less suitable landscape matrix elements, usually contain isolated or small-sized populations.

The sensitivity of these kinds of populations to limiting environmental factors has been assessed by studies on the populations' genetic structure, population dynamics, and fitness (Gaston 2003; Crawford 2008). The interplay of these features can influence the viability of northern populations and hence conservation decisions (Lesica and Allendorf 1995), but results are not always unidirectional. For instance, Lammi et al. (1999) found viable peripheral populations on rock outcrops, in terms of germination rate, seed production and seedling mass, despite small population size and low isozyme variability. In contrast, Lönn and Prentice (2002) evidenced higher adult mortality and faster turnover of individuals within small-sized and genetically impoverished peripheral populations.

The persistence of northern peripheral populations can be better addressed by modelling their dynamics and the spatiotemporal variation in fitness components. Such studies on northern populations of woody and herbaceous perennials have found that their persistence depends mostly on the survival of mature individuals, and less on individual reproduction (Bengtsson 1993, 2000; Nantel and

Gagnon 1999). Remnant dynamics allow the populations to bridge periods of unfavourable environmental conditions (Eriksson 1996) and is common among long-lived perennials (Picó and Riba 2002; García 2003, 2008).

Some northern populations seem to be unable to expand due to different fire frequency (Despouts and Payette 1992), absence of suitable habitats (Meilleur et al. 1997), dispersal limitation, and failure to establish at suitable sites (Norton et al. 2005; Samis and Eckert 2007). Other limiting factors are related to disturbance and vegetation succession (Nantel and Gagnon 1999; Moretti et al. 2006, 2008), habitat size and degree of isolation (Lammi et al. 1999; Lönn and Prentice 2002), and management (Bengtsson 1993). Climate severity is also considered an important limiting environmental factor at range periphery (Sexton et al. 2009), and some studies have demonstrated that climatic constraints induced dramatic demographic changes within northern populations, e.g., reduced fecundity (Bengtsson 1993; Carey et al. 1995; Dorken and Eckert 2001; Jump and Woodward 2003), shift from reproductive to clonal propagation (Beatty et al. 2008), decline of population size (Bengtsson 2000; Hatcher et al. 2004), higher mortality and interannual variation of vital and growth rates (Bengtsson 1993; Nantel and Gagnon 1999), or increased demographic turnover (Lönn and Prentice 2002).

Here, we report the demography and population dynamics of *Saponaria bellidifolia* Sm. (Caryophyllaceae) at its northern limit of distribution. This sub-Mediterranean mountain plant has a pronounced disjunct distribution area in southern Europe, being more widespread in the Balkan Peninsula (Jalas and Suominen 1986). It reaches the northernmost margin of its distribution in the Apuseni Mountains of the southeastern Carpathians (Romania), where populations are considered postglacial colonisers (Csörgő et al. 2009a), and are restricted to eight limestone and dolomite outcrops with predominantly southern exposures. These marginal populations occur within an area of 13 km radius, and are separated by forests, valleys and pastures. *Saponaria bellidifolia* is listed as “Rare” in the red list of Romania (Oltean et al. 1994), “Lower Risk” in Italy (Conti et al. 1997), and “Vulnerable” in France (Olivier et al. 1995) and Spain (Bañares et al. 2003). The main threats considered are isolation from the main area of distribution and the small size of some populations.

We monitored four out of these eight northern peripheral populations over 5 years in order to: (1) assess the effect of habitat and population size on reproduction and demography, (2) estimate population trends and extinction risk of the species at the northern periphery, and (3) analyse the limiting effect of regional climate on demographic traits. Some hypotheses were drawn up and tested in our study: (1) given their marginal situation, the populations will show remnant dynamics; (2) the importance of recruitment

will be higher in populations on more disturbed and open habitats; (3) small populations will experience higher population vulnerability than large populations; and (4) regional climate will have a strong influence on populations’ dynamics.

Materials and methods

The species

Saponaria bellidifolia is a long-lived iteroparous chamaephyte, with a branching rhizome and taproots belowground, a rosette composed of 1 to about 60 vegetative shoots, and up to 30 flowering stems in the studied area (A.-M. Csörgő, unpublished data). Fragmentation of the rhizome can occur in senescent individuals, resulting in a limited clonal propagation. Inflorescences are capitata, develop in July and are composed of about 50 flowers on average. Flowers are hermaphroditic, self-compatible and protandrous. Hawkmoths, burnet moths, beetles and bees have been observed visiting flowers and are potential pollinators (A.-M. Csörgő, personal observation). Infructescences contain about 200 seeds on average, of which about half are sterile, following failure of fruit production and seed sterility (A.-M. Csörgő, unpublished data). Although seeds are not dispersed by any specific agent, secondary dispersal by herbivores (rabbits, deer) is possible. Seed germination is inhibited by light (Şuteu and Mocan 1998) and requires vernalisation, so that most seedlings appear in the following spring.

Study sites

Four outcrops were chosen to represent the variety of habitats, disturbance regime and population size of *S. bellidifolia* within the Apuseni Mountains (Table 1; Fig. 1). The Pinet (PIN) and Cheile Poşegii (POS) populations occur on larger outcrops, are larger in size, and have higher genetic variability than the Piatra Urdaşului (URD) and Dealul Vidolm (VID) populations (Table 1; Csörgő et al. 2009a). The four populations represent rather different situations of ecological succession on rock outcrops: open screes affected by fire disturbance and dominated by the pioneer chamaephyte *Teucrium montanum* (POS), fixed screes dominated by the small grass *Festuca pallens* (PIN), and grassy habitats dominated by the dwarf sedge *Carex humilis* (VID). The rock ledges of the URD stand are open in the upper part and are dominated by *Festuca pallens*, whereas in the lower part, they are more closed and are dominated by the tall tussocky grass *Helictotrichon decorum*. The abundance of individuals of *S. bellidifolia* is

Table 1 Summary of population and habitat characteristics for *S. bellidifolia* (Apuseni Mountains, southeastern Carpathians)

Locality acronym	PIN	POS	VID	URD
Latitude	46°28'54.76"	46°27'53.50"	46°27'07.57"	46°26'48.65"
Longitude	23°24'53.86"	23°24'12.81"	23°30'19.96"	23°31'41.61"
Years sampled	2004–2008	2005–2008	2004–2008	2004–2007
Population size	>5,000	>5,000	<1,000	<500
H_{exp}	0.089	0.062	0.042	0.022
Habitat type	Fixed screens	Open screens (fire-disturbed)	Grassy habitat	Rock ledges

H_{exp} = Nei (1978) heterozygosity (extracted from Csergő et al. 2009a)

PIN Pinet, POS Cheile Poșegii, URD Piatra Urdașului, VID Dealul Vidolm

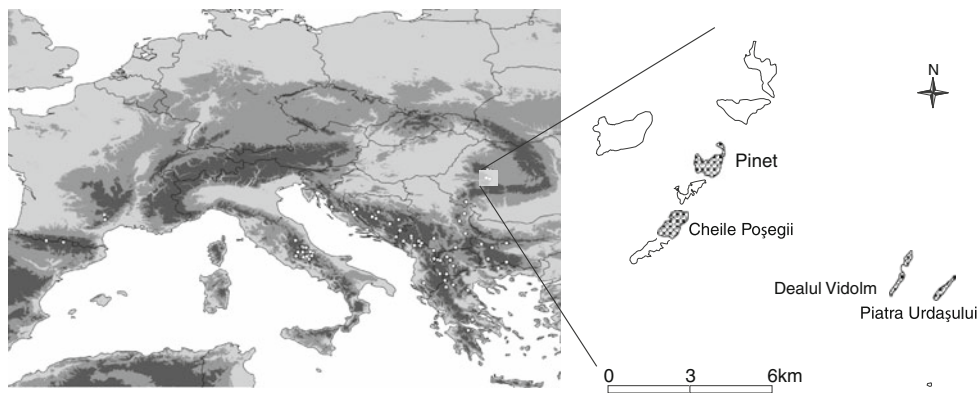


Fig. 1 Distribution of *S. bellidifolia* in Europe (data from the literature and herbaria collections), distribution of its northern populations in the Apuseni Mountains (southeastern Carpathians,

Romania) (polygons), and location of the four study stands (filled polygons). Locality acronyms used in the text: Pinet (PIN), Cheile Poșegii (POS), Piatra Urdașului (URD), Dealul Vidolm (VID)

positively related to habitat disturbance in the studied area (Csergő and Cristea 2008; Csergő et al. 2009b).

Demographic census

Because of the difficult access to the outcrops, only one permanent plot (approximately 5 m sides) was laid out in each site, containing 100 individuals in PIN and POS, 83 in VID and 30 in URD at the beginning of the study. All individuals sampled were genets. Stands were set up in relatively isolated habitat patches, in order to avoid seedling input from outside sources. Plants were marked with a numbered vinyl tag and censused once per year. The number of vegetative and flowering shoots, together with the larger axis and its perpendicular, small axis of the basal rosette were used to estimate plant developmental stage. The number and two perpendicular axes (the largest and the small one) of the inflorescences were also recorded. In each visit, we looked carefully for new seedlings in the permanent plots.

Reproductive success

In order to estimate seed production, we randomly collected 36–50 infructescences outside each permanent

census plot, and calculated seed output for each population through linear regression, using infructescence area (inferred from the ellipsis shape defined by the two axes) and the number of seeds.

To assess the reproductive success of *S. bellidifolia* in each habitat, we calculated the mean number of flowering stems and seeds per plant, using the linear regressions obtained above. Interannual and interpopulation differences were tested by Kruskal–Wallis H test based on rank transformation (data were not always normally distributed). Pairwise comparisons between years and populations were computed using the exact Mann–Whitney post hoc test based on a Monte Carlo simulation with 100,000 permutations, using sequential Bonferroni correction (Holm 1979), to avoid the problem of multiple comparisons.

Developmental stage category and life cycle construction

Based on our field observations, individuals were separated into six stage categories: seedlings, juveniles, small and large vegetatives, small and large reproductives. The separation of seedling and juvenile stage was not easy, because small plants showed morphological similarity and

produced only one vegetative shoot. To exactly distinguish the seedling phase from the juvenile one, binomial logistic regressions were used to model their survival probability as a function of rosette size attributes (large and small diameter), for each year separately. To dissociate plants with more than one shoot into different classes, we modelled their flowering probability as a function of vegetative shoots number. As the climate seemed to influence the flowering stem production, we factored out its effect by choosing the year with the most favourable climate regime (2005), and analyzed all populations taken together. As an external validating measure of all final models, the receiver operating characteristic (ROC) curve and the associated area under the ROC-curve (AUC) were applied to both analyses.

For young individuals, the two rosette diameters (taken separately) gave significant predictions on seedlings survival probability ($P < 0.045$, $AUC > 0.668$ in all cases). Therefore, new seedlings and plants with one vegetative shoot and both axes below 3 cm were all considered seedlings, as they showed survival probabilities $< 75\%$ in all cases. Plants with one vegetative shoot and the large axis above 3 cm were considered juveniles, as they showed survival probabilities $> 75\%$ in all regressions. For larger vegetative plants, the number of vegetative shoots was a good predictor of flowering stem production [$\beta = 0.162$, $SE(\beta) = 0.036$, $Z = 4.541$, $P < 0.001$, $n = 298$]. Thus, smaller plants (< 5 vegetative shoots) had flowering stem production probability lower than 75% and developed one stem on average. For larger plants (> 5 vegetative shoots), flowering stem production probability was above 75% and developed four stems in average.

Subsequently, because of the small sample sizes, we grouped juveniles with small vegetatives and small reproductives with large reproductives, thereby resulting in four final stages: seedlings, small vegetatives, large vegetatives and reproductives.

Matrix analyses

A total of 14 annual (July to July) Lefkovich projection matrices (Lefkovich 1965) were set, after assembling transition probabilities of the life cycle graph (Fig. 2) and fecundities (defined as the mean number of seedlings in $t + 1$ per plant), following the standard procedure (Caswell 2001). The deterministic growth rate (λ), which characterizes the overall performance of the population in a given year, was calculated from each annual matrix, as well as from the average population matrix over years at each stand. We averaged annual transitions to reduce biases produced by the unequal number of individuals in each stage (Münzbergová and Ehlrlén 2005) and the low number of transitions in some cases. Differences between the

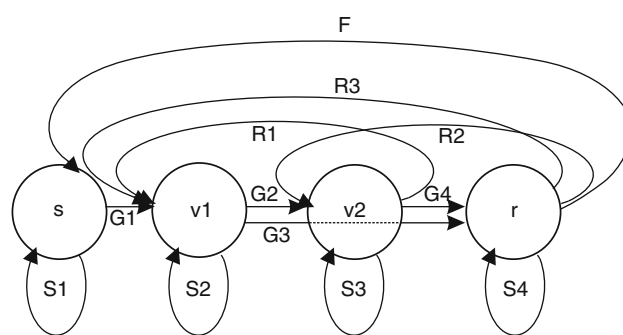


Fig. 2 Life cycle graph of *S. bellidifolia* populations. Nodes represent classes, arrows indicate probability of transitions between classes; *s* seedlings, *v*₁ small vegetatives, *v*₂ large vegetatives, *r* reproductives, *F* fecundity, *G* growth, *S* stasis, *R* retrogression

observed and predicted stable stage structure produced by the average matrix of each population were tested by contingency tables. Elasticity analyses (de Kroon et al. 1986) were also performed on average matrices to detect the contribution of different developmental stages to population growth rate. Elasticity matrices were divided into four regions: fecundity (seedling recruitment), stasis, retrogression (transitions to smaller categories), and growth (transitions to larger categories) (Silvertown and Franco 1993). The relationship between each matrix region and the respective lambda was assessed using Spearman's rank correlation, in order to detect which region impacts the changes in the population's growth rate. To depict the trade-offs of elasticities of different developmental stages, we also constructed a ternary plot of survival (stasis and retrogression together)—fecundity—growth for each population, following Silvertown et al. (1993).

The stochastic growth rate (λ_s), which characterizes the long-term performance of populations across the years, and an approximate 95% confidence interval (CI), was calculated by simulation of 50,000 population growth increments, with each yearly matrix having the same probability of occurrence. The arithmetic mean and variance of $\log(n_{t+1}/n_t)$ over all pairs of adjacent years was calculated by using the *Stoch_log_lam* routine, which uses all λ values from consecutive years (Morris and Doak 2002). The vulnerability of this species at the northern periphery in the next century was assessed by performing a population viability analysis (PVA). The probability of quasi-extinction (< 30 individuals) of each population was estimated by simulation, considering their actual size (number of plants: POS = 5,000; PIN = 5,000; VID = 1,000; URD = 500). The 'simex' routine of Morris and Doak (2002) was used, based on random selection of annual matrices (independently and identically distributed environmental conditions) and assuming no demographic stochasticity. Totals of 5,000 realizations of population growth were done for

each run, and 10 runs were used to simulate the quasi-extinction cumulative distribution function.

We also estimated the longevity of the plants in each population from the algorithm published by Cochran and Ellner (1992), as the maximum value of “conditional total life span” (see also Ehrlén and Lehtilä 2002). Given that different matrices were available for each population, we computed life span for each one from the average matrix over years. Matrix analyses were computed using PopTools (3.0.6 available from <http://www.cse.csiro.au/poptools>) and MATLAB (7.5 for Mac).

Demography and climate

We tested the relationship between the populations’ growth rate, the elasticity values of transitions, seed production, number of flowering stems and climate data, using multiple linear regressions, stepwise method. Habitat variables (habitat type, presence of disturbance) were also included in these models as “dummy” variables. The climate variables included in the models were total precipitation, and mean minimum and maximum temperature [grouped as follows: winter (December–February), autumn (September–October), spring (March–May), summer (June–July), but summer data were not used in modelling flowering stem production]. The final dataset comprised 18 rows, resulting from combining 4–5 years (2004–2008) and four populations (see Table 1). Data were obtained from Băișoara meteorological station, situated 1.5 km away from the nearest and 14.5 km from the furthest stand.

Statistical analyses were performed using SPSS statistical software.

Results

Reproductive success

The mean number of flowering stems (results not shown) varied significantly among populations (Kruskal–Wallis test, $H_c = 16.5$, $P < 0.01$) and years (Kruskal–Wallis test, $H_c = 63.99$, $P < 0.001$). Stem number averaged over years was the lowest in the grassy VID population (mean \pm SD: 2.6 ± 2.2) compared with the other populations (PIN = 3.55 ± 3.12 , POS = 3.57 ± 3.53 , URD = 3.21 ± 2.79), but differed significantly only in 2006 and only from the two large populations (PIN and POS) ($P < 0.001$ in both cases). Flowering stem production changed significantly in some years in all stands (Kruskal–Wallis test, $H_c > 17.8$, $P < 0.01$), except the small URD, where no yearly pairwise differences could be revealed. Most pairwise comparisons showed a significant decrease of flowering stem number in 2007 in all populations.

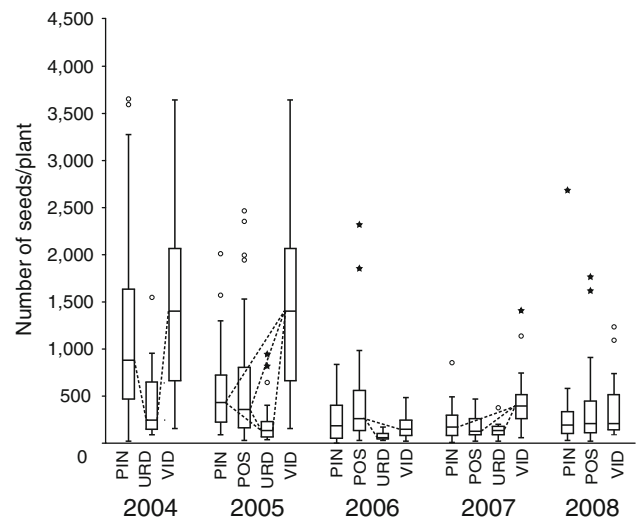


Fig. 3 Number of seeds produced per plant (mean \pm SD) across 2004–2008 within the four stands of *S. bellidifolia* from southeastern Carpathians. Mean number of observations (\pm SD) across years: PIN 40 ± 7.3 ; POS 55 ± 10.9 ; URD 22 ± 5.2 ; VID 27.6 ± 3.5 . Dotted lines represent significant pairwise differences at 0.05 level revealed by the Bonferroni corrected Mann–Whitney test, circles and stars represent outliers. Significant temporal variation within each stand: PIN all pairwise comparisons except 2006–2007–2008; POS 2005–2007, 2006–2007; URD 2004–2006, 2005–2006; VID all pairwise comparisons except 2005–2007, 2006–2008, 2007–2008

Seed production also varied significantly among populations (Kruskal–Wallis test, $H_c = 82.58$, $P < 0.001$) and years (Kruskal–Wallis test, $H_c = 128.9$, $P < 0.001$) (Fig. 3). The yearly variation was mainly due to the significantly higher production during the first 2 years of study in all stands (2004 and 2005). The differences between habitats were significant in all years except 2008 and were mainly explained by the significantly lower seed production in the rocky URD in all years, higher production within the grassy habitat of VID in 2005 and 2007 and the open screens of POS in 2006.

Matrix analyses

The deterministic growth rates of *S. bellidifolia* populations ranged between 0.974 and 1.041 (Table 2). The stochastic growth rates (Table 2) were also close to equilibrium, and showed that only the population of the grassy habitat (VID) had a growth rate lower than one (0.973).

The elasticity analysis showed that the population growth rate was mostly sensitive to the stasis of reproductive plants (Table 2; Fig. 4). All *S. bellidifolia* populations occupied the “Survival” corner of the ternary plot, as elasticity was highest for stasis/survival, and smallest for fecundity. However, fecundity contributed more to the growth rate of populations on open screens (POS) and in the rocky habitat (URD). On the fixed screens of PIN, the stasis

Table 2 Deterministic (λ) and stochastic populations' growth rate (λ_s) with 95% confidence intervals (CI), average projection matrices across time, and elasticity matrices for *S. bellidifolia* at four populations located in the southeastern Carpathians (s seedlings, v_1 small vegetatives, v_2 large vegetatives, r reproductives)

	λ	λ_s	CI	Demographic matrix				Elasticity matrix					
				s	v_1	v_2	r	s	v_1	v_2	r		
PIN	1.002	1.002	[1.0018–1.0024]										
s				0.14	0	0	0.06	0	0	0	0	0	0.01
v_1				0.28	0.83	0.06	0.01	0.01	0.12	0.01	0.01	0.01	0.00
v_2				0	0.12	0.51	0.22	0	0.02	0.14	0.12	0.12	0.12
r				0	0.01	0.43	0.78	0	0	0.13	0.44	0.44	0.44
Mortality				0.59	0.03	0	0						
POS	1.034	1.033	[1.0320–1.0343]										
s				0.55	0	0	0.46	0.04	0	0	0	0	0.04
v_1				0.12	0.77	0.14	0.12	0.04	0.26	0.01	0.01	0.01	0.04
v_2				0	0.03	0.1	0.18	0	0.01	0.01	0.01	0.08	0.08
r				0	0.16	0.76	0.7	0	0.07	0.08	0.32	0.32	0.32
Mortality				0.33	0.03	0	0						
URD	1.041	1.039	[1.0369–1.0408]										
s				0.16	0	0	0.49	0.01	0	0	0	0	0.04
v_1				0.17	0.59	0.03	0.03	0.04	0.07	0.01	0.01	0.01	0.01
v_2				0	0.1	0.56	0.32	0	0.01	0.18	0.14	0.14	0.14
r				0	0.27	0.41	0.65	0	0.04	0.15	0.31	0.31	0.31
Mortality				0.51	0.03	0	0						
VID	0.974	0.973	[0.9727–0.9734]										
s				0.21	0	0	0.02	0	0	0	0	0	0
v_1				0.13	0.61	0.06	0.17	0	0.13	0.01	0.01	0.01	0.07
v_2				0	0.03	0.38	0.27	0	0.01	0.10	0.15	0.15	0.15
r				0	0.23	0.56	0.58	0	0.07	0.15	0.31	0.31	0.31
Mortality				0.56	0.12	0	0						
Mean matrix	1.011												
s				0.25	0	0	0.23	0.01	0	0	0	0	0.02
v_1				0.18	0.70	0.07	0.08	0.02	0.15	0.01	0.01	0.01	0.03
v_2				0	0.07	0.40	0.25	0	0.02	0.09	0.12	0.12	0.12
r				0	0.16	0.54	0.67	0	0.05	0.13	0.35	0.35	0.35

of reproductive plants had by far the largest elasticity value (Table 2). In the disturbed POS and the average matrix, elasticity values of the small vegetative stage were also outstanding. Growth usually had larger elasticity values than retrogression in all populations and all years, except the grassy VID, where the two values were similar. The largest retrogression values were registered in VID, whereas the largest growth values in the two small populations URD and VID. Population growth rate significantly correlated with the elasticity of fecundity ($n = 14$, $R = 0.477$, $P < 0.05$, Spearman's rank correlation).

The observed and expected stage structure of populations differed significantly in three populations: PIN ($\chi^2 = 20.41$, $P < 0.001$), POS ($\chi^2 = 46.13$, $P < 0.001$) and URD ($\chi^2 = 8.83$, $P = 0.03$) but it did not differ in the

grassy habitat of VID ($\chi^2 = 5.89$, $P = 0.12$) (Fig. 5). On the fixed screes of PIN, a much lower frequency of seedlings and a higher frequency of large vegetatives are expected. On the open screes of POS, the number of seedlings and of small vegetatives is expected to grow, whereas the number of reproductives is expected to fall. In the rocky habitat of URD, all developmental stages are expected to fall, except seedlings and large vegetatives, which are going to be more frequent.

According to the survival vital rates recorded over the study period, mature individuals die at ages between 43 (VID) and 474 (URD) years. Under the current situation of population size and structure, the quasi-extinction probability projected over the next century was 0% for POS, PIN and URD, and 4.3% for VID. In the latter case, the

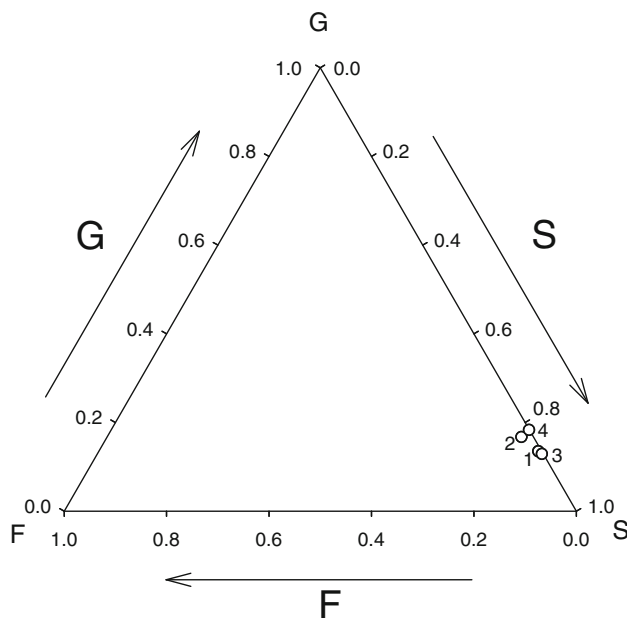


Fig. 4 The position of the four *S. bellidifolia* populations in the fecundity (F), growth (G), survival (S) triangle. Locality numbers: 1 PIN, 2 POS, 3 URD, 4 VID

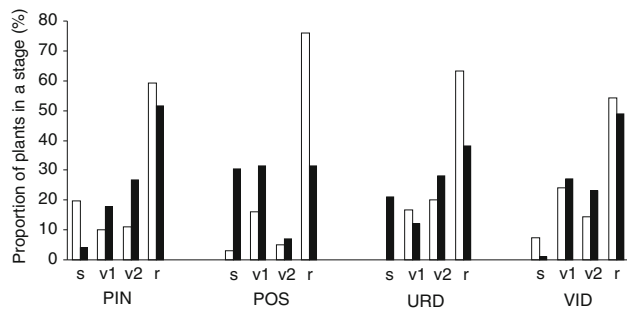


Fig. 5 Observed proportion of developmental stages (white bars) and the corresponding projected stage structure (black bars) for each *S. bellidifolia* population in the study area (southeastern Carpathians); s seedlings, v₁ small vegetatives, v₂ large vegetatives, r reproductives

probability of total extinction ($n = 1$ individual left) would be null. Thus, stochastic simulations indicated that there is no risk of extinction for any population studied.

Spatiotemporal variation of vital traits

Most of the seedlings remained in the same developmental category over the study period, only very few became large vegetatives, and none of them reached adulthood. Habitat type influenced differentially the fate of different categories. More than 50% of seedlings survived within the open habitat POS, exceeding two- to fourfold other populations (Table 2). Growth from seedlings to small vegetatives was

the highest on the fixed screes of PIN (28%), exceeding by twofold other populations. The proportion of small vegetatives that flowered varied largely between sites and years. It was the lowest in the same PIN in all years (0–4%), and the highest in the other populations in different years (Table 2). A much higher proportion of large vegetatives flowered each year, but this depended largely on the year: 80% of them flowered in 2005 and only half in 2007. Stasis of the large vegetatives was very low in the open POS as compared to other populations. Recruitment was extremely low in the more closed habitats (2–6%), while it was much higher in the open ones (up to 49%). Regardless of the habitat conditions, mortality affected mainly seedlings (33–59%). No large vegetative or reproductive individual died across the whole study period, whereas 12% of small vegetatives died in the grassy VID ($n = 92, 144, 60$ and 83 plants in PIN, POS, URD and VID, respectively, at the end of the study).

Relationship with climate variables

Almost none of models fitting climatic variables to population growth rate, elasticity values or seed production yielded significant results. For flowering stem production, the best predictors were the mean minimum temperature in spring and the grassy habitats, both having negative effect on *S. bellidifolia* (average number of flowering stems = $4.481 - 0.803$ spring minimum temperature $- 0.919$ grassy habitat; $R^2 = 0.664, P < 0.01$). In the univariate model, spring minimum temperature was also significant ($R^2 = 0.532, P < 0.01$).

Discussion

Our study revealed some important features that portray the performance and viability of *S. bellidifolia* populations at the northern limit of the species’ distribution. They showed high survival rates of reproductive individuals, high elasticity values for stasis transitions, high seedling mortality, and a population growth rate correlated with elasticity of fecundity, all these being collective attributes of species with similar life-history (Silvertown et al. 1993). The revealed dynamics indicated that populations are stable, similar to other long-lived perennials that subsist in the harsh but constant abiotic conditions of the rocky habitats (Picó and Riba 2002; García 2003, 2008).

Reproductive performance

As in other small peripheral populations confined to rocky cliffs (Lammi et al. 1999), habitat peculiarities influenced the overall reproductive fitness of *S. bellidifolia*. Plants of

the grassy habitat (supposedly on deeper and richer soil) produced the largest mean number of seeds per adult plant, while plants in the rocky habitat (probably the poorest soil with less humidity) produced the lowest. Harsher conditions on rock ledges might constrain the development of this rhizomatous plant and lower seed production, whereas litter accumulation, shading, etc. that negatively affect the young stages in grassy habitats are probably less important for larger plants, which can survive for a long time within the “persistence niche” (Bond and Midgley 2001). Yet, some negative influence manifested on the number of flowering stems within the grassy habitat, but it was rarely significant and might accentuate only at later stages of vegetation succession (e.g., under bush or tree cover).

Habitat and population dynamics

Among-population differences in the studied parameters of *S. bellidifolia* seem to be associated with habitat peculiarities like vegetation succession and fire disturbance. Recruitment was higher in the open habitats (rocks and fire-disturbed screes) and extremely low in closed grasslands (fixed screes and grassy habitat), suggesting a strong association between seedling establishment and existence of suitable spaces to regeneration. The importance of regeneration niche has already been suggested for *S. bellidifolia* (Csörgő et al. 2009b) and it is common among species with low competitive abilities (Kalliovirta et al. 2006; Moretti et al. 2008). Screes are the most important habitats to *S. bellidifolia* regeneration at the localities studied because of intermediate natural disturbance (Csörgő et al. 2009b). Sometimes fire represents another source of disturbance in these habitats. Fires on rock outcrops have previously been reported to make possible the persistence of other populations at range periphery by slowing down the succession and formation of empty microsites, favourable to seedling establishment (Nantel and Gagnon 1999; Moretti et al. 2008). In three out of the eight known peripheral populations of *S. bellidifolia* within the mountain range studied, outcrop fires are quite frequent and occur both accidentally and deliberately initiated by people living nearby. Contrary to other situations, in the studied population where fire is a recurrent environmental factor (POS), young vegetative plants have a higher elasticity, suggesting a more dynamic demographic system. Thus, fire seems to be an important factor that favours the persistence of *S. bellidifolia* at regional level in the Apuseni Mts. In contrast, lower population growth rates of the grassy VID population, occurring in a late successional habitat, indicate a slow decline and higher vulnerability of *S. bellidifolia* populations on this kind of habitat. The negative effects of the increased woody vegetation cover on population trends have been recently highlighted for the

vulnerable French populations of *Saponaria bellidifolia* (Fonderflick et al. 2010). The same negative effects of vegetation succession manifested on other rare species like the rupicolous endemic *Silene douglasii* var. *oraria* (Kephart and Paladino 1997) and *Gypsophila fastigiata* on alvar habitats at the species’ northern range periphery (Bengtsson 2000).

Two habitats provided some particular benefits for the populations. On the one hand, the fire-disturbed open screes were advantageous to flowering of large reproductive individuals and to seedling survival. On the other hand, in the fixed screes, the growth of seedlings was more advanced, but the flowering of small vegetative plants was delayed. Such habitat-related differences contrast with what was observed in *Fumana procumbens* populations at their northern range edge, where the fate of different stages was more similar among sites, despite important differences in habitat quality (Bengtsson 1993). Nevertheless, it is possible that part of the temporal and spatial variability registered here is attributed to other sources than environmental variation. Descriptive studies of wild populations, like the present one, do not always allow a suitable methodological design, and hold some limitations, like the relatively low number of plants taken into study and the lack of repetitions for population size and habitat type. Yet, studies on the ecology of this species (Csörgő and Cristea 2008; Csörgő et al. 2009b; Fonderflick et al. 2010), agree or support the present results.

Projected population structure and future persistence

Our analyses indicate that *S. bellidifolia* is a very long-lived plant, compared to other perennials (Ehrlén and Lehtilä 2002). It grows very slowly, and under the current environmental conditions, it establishes very old populations. The predicted stage structure of different stands may serve to explore the degree of similarity between past and present vital rates. The grassy VID is currently experiencing a declining phase, and no changes are foreseen until a hypothetical new disturbance occurs. The fixed screes of PIN stand are predicted to have a shortness of recruitment, probably as vegetation cover advances, and both vegetative and generative stages will prevail. In the fire-disturbed and currently established POS stand, young stages are growing dynamically and higher recruitment is also expected.

Stochastic population growth rates indicated that the species persistence is assured in the long term in the studied area. No quasi-extinction risk resulted in three out of the four populations monitored, including the smallest one, and the risk was below 5% when *S. bellidifolia* grew under conditions of high vegetation cover. Therefore, even habitats dominated by strong competitors of the rupicolous grasslands, like *Carex humilis* (Wikberg and Mucina

2002), are likely to preserve populations of *S. bellidifolia*, in contrast to pine trees in the simulations of Fonderflick et al. (2010).

Effect of climate and population size

Except for flowering stem production, we did not find a clear relationship between the yearly variations in *S. bellidifolia* growth, demographic parameters and annual changes in local climate. By contrast, other rupicolous species censused over a similar period (4–7 years) showed a stronger dependence on the temporal variability of climate conditions. For instance, fruit production of the Iberian paleoendemic *Ramonda myconi* was positively correlated with the precipitation in June–July (Riba et al. 2002), and growth rate of populations decreased with minimum temperatures in June and increased with the precipitation from May to June (Picó and Riba 2002). Harsh winters affected survival and reproduction of the northern peripheral *Fumana procumbens*, and in the same species, low temperatures in early summer had a negative effect on flowering intensity and seed production (Bengtsson 1993).

According to the available data, only the flowering stem production was influenced by the regional climate in *S. bellidifolia*, but not in the expected way, because low spring temperatures boosted inflorescence production. Vernalisation is essential to the flowering of many plant species (Henderson et al. 2003), and is probably also important to *S. bellidifolia*, which is adapted to the mountain climate. Still, it is possible that the lower spring temperatures experienced by the target species within the northernmost habitats promote a higher number of flowering stems, comparatively to more southern localities, but this hypothesis needs further testing.

Although we cannot draw definitive conclusions on the effect of population size on growth rates, because we had only two small and two large populations, and because of the mixed effect with habitat peculiarities (see discussion above), it seems that the smallest population of the rocky habitat performed at least as well as the two large populations of screes from a demographic point of view (not in terms of seed production). This is not an unusual result: small populations of *Scorzonera hispanica* in a fragmented landscape of Cehia (Münzbergová 2006), the rupicolous endemic *Petrocoptis pseudoviscosa* (García 2008) or the peripheral *Cypripedium calceolus* populations (García et al. 2010) also had growth rates not significantly different from unity or not declining, and good chances to persist in the long run. Similarly, the dynamics of *Silene regia* populations in American prairies were primarily affected by management and only secondarily by size, isolation and genetic diversity (Menges and Dolan 1998).

Conclusions

In summary, the studied populations of *S. bellidifolia* seem stable, viable, and influenced rather by the habitat type and disturbance than by population size and local climate. Our results suggest a negative impact of vegetation succession on the dynamics of this rare rupicolous species. Preserving the habitats, and keeping some perturbation to avoid strong competition of grasses and sedges, seem the best management for the species' conservation. Management actions would be directed to provide opportunities for the recruitment enhancement and seedling establishment. In fact, it is highly probable that local people have involuntarily contributed to a certain extent to the species' persistence in the studied localities by setting fire to the outcrops. *Saponaria bellidifolia* shows remnant dynamics in these rocky habitats, being able to survive for long periods of time under unfavourable conditions, and also finding new opportunities to establish viable populations after disturbances. It may be considered a successful species of the studied rocky grasslands within the northern peripheral localities in the Carpathians.

Acknowledgments We thank Szilárd Nemes from University of Gothenburg, Sweden and Konrád Lájér from Eötvös József College, Hungary, for help with statistical analyses, Zoltán Pál from Babeş-Bolyai University, Romania, for help with climate data, and Attila Borhidi from University of Pécs, Hungary, for his support during the study. K. Lehtillä kindly wrote the Excel macro to calculate life span. We also thank the anonymous reviewers for their comments and suggestions. This paper is a part of the first author's PhD thesis and was partially financed by Domus Hungarica Scientiarum et Artium, Hungary, and also by the Spanish Ministry of Science (project CGL2006-08507 to MBG).

References

- Bañares A, Blanca G, Güemes J, Moreno JC, Ortiz S (eds) (2003) Atlas y libro rojo de la flora vascular amenazada de España. Táxones prioritarios, Dirección General de Conservación de la Naturaleza, Madrid (in Spanish)
- Beatty GE, McEvoy PM, Sweeney O, Provan J (2008) Range-edge effects promote clonal growth in peripheral populations of the one-sided wintergreen *Orthilia secunda*. *Divers Distrib* 14:546–555
- Bengtsson K (1993) *Fumana procumbens* on Öland—population dynamics of a disjunct species at the northern limit of its range. *J Ecol* 81:745–758
- Bengtsson K (2000) Long-term demographic variation in range-margin populations of *Gypsophila fastigiata*. *Folia Geobot* 35:143–160
- Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol* 16:45–51
- Carey PD, Watkinson AR, Gerard FFO (1995) The determinants of the distribution and abundance of the winter annual grass *Vulpia ciliata* ssp. *ambigua*. *J Ecol* 83:177–187
- Caswell HR (2001) Matrix population models. Construction, analysis, and interpretation. Sinauer, Sunderland

- Cochran ME, Ellner S (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecol Monogr* 62:345–364
- Conti F, Manzi A, Pedrotti F (1997) Liste rosse regionali delle piante d'Italia. Università degli Studi di Camerino - WWF Italia, Camerino
- Crawford RMM (2008) Plants at the margin. Ecological limits and climatic change. Cambridge University Press, Cambridge
- Csergő A-M, Cristea V (2008) Chorology and phytosociological context of *Saponaria bellidifolia* Sm. within the Apuseni Mts. (Southeastern Carpathians, Romania). *Contrib Bot* 43:25–38
- Csergő A-M, Schönswetter P, Mara Gy, Deák T, Boşcaiu N, Höhn M (2009a) Genetic structure of peripheral, island-like populations: a case study of *Saponaria bellidifolia* Sm. (Caryophyllaceae) from Southeastern Carpathians. *Plant Syst Evol* 278:33–41
- Csergő A-M, Nemes Sz, Gafta D, Demeter L, Jakab S (2009b) Two-scale modelling of *Saponaria bellidifolia* Sm. (Caryophyllaceae) abundance on limestone outcrops from its northern range periphery (Southeastern Carpathians). *Plant Ecol* 203:229–242
- de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431
- Despons M, Payette S (1992) Recent dynamics of jack pine at its northern distribution limit in northern Quebec. *Can J Bot* 70:1157–1167
- Dorken ME, Eckert CG (2001) Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *J Ecol* 89:339–350
- Ehrlén J, Lehtilä K (2002) How perennial are perennial plants? *Oikos* 98:308–322
- Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. *Oikos* 77:248–258
- Fonderflick J, Lepart J, Caplat P, Debussche M, Marty P (2010) Managing agricultural change for biodiversity conservation in a Mediterranean upland. *Biol Conserv* 143:737–746
- García MB (2003) Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conserv Biol* 17:1672–1680
- García MB (2008) Life history and population size variability in a relict plant. Different routes towards long-term persistence. *Divers Distrib* 14:106–113
- García MB, Goñi D, Guzmán D (2010) Living at the edge: local versus positional factors in the long-term population dynamics of an endangered orchid. *Conserv Biol* 25:1219–1229
- Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford
- Hatcher PE, Wilkinson MJ, Albani MC, Hebborn CA (2004) Conserving marginal populations of the food plant (*Impatiens noli-tangere*) of an endangered moth (*Eustroma reticulatum*) in a changing climate. *Biol Conserv* 116:305–317
- Henderson IR, Shindo C, Dean C (2003) The need for winter in the switch to flowering. *Annu Rev Genet* 37:371–392
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Jalas J, Suominen J (1986) Atlas Florae Europaeae. Distribution of vascular plants in Europe 7—Caryophyllaceae (Silenoideae). The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki
- Jonsson M, Bertilsson M, Ehrlén J, Lönn M (2008) Genetic divergence of climatically marginal populations of *Vicia pisiformis* on the Scandinavian Peninsula. *Hereditas* 145:1–8
- Jump AS, Woodward FI (2003) Seed production and population density decline approaching the range-edge of *Cirsium* species. *New Phytol* 160:349–358
- Kalliovirta M, Rytteri T, Heikkinen RK (2006) Population structure of a threatened plant, *Pulsatilla patens*, in boreal forests: modelling relationships to overgrowth and site closure. *Biodivers Conserv* 15:3095–3108
- Kephart SR, Paladino C (1997) Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). *Am J Bot* 84:179–189
- Lammi A, Siikamäki P, Mustajärvi K (1999) Genetic diversity, population size and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. *Conserv Biol* 13:1069–1078
- Lefkovich LP (1965) The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18
- Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? *Conserv Biol* 9:753–760
- Lönn M, Prentice HC (2002) Gene diversity and demographic turnover in central and peripheral populations of the perennial herb *Gypsophila fastigiata*. *Oikos* 99:489–498
- Meilleur A, Brisson J, Bouchard A (1997) Ecological analyses of the northernmost population of pitch pine (*Pinus rigida*). *Can J For Res* 27:1342–1350
- Menges ES, Dolan RW (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *J Ecol* 86:63–78
- Moretti M, Conedera M, Moresi R, Guisan A (2006) Modelling the influence of change in fire regime on the local distribution of a Mediterranean pyrophytic plant species (*Cistus salvifolius*) at its northern range limit. *J Biogeogr* 33:1492–1502
- Moretti M, Staehli C, Gillet F (2008) Determinants for the conservation of a vulnerable fire-dependent species at its marginal range. *Plant Ecol* 199:89–98
- Morris W, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland
- Münzbergová Z (2006) Effect of population size on the prospect of species survival. *Folia Geobot* 41:137–150
- Münzbergová Z, Ehrlén J (2005) How best to collect demographic data for PVA models. *J Appl Ecol* 42:1115–1120
- Nantel P, Gagnon D (1999) Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*. *J Ecol* 87:748–760
- Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583–590
- Norton LR, Firbank LG, Scott A, Watkinson AR (2005) Characterising spatial and temporal variation in the finite rate of population increase across the northern range boundary of the annual grass *Vulpia fasciculata*. *Oecologia* 144:407–415
- Olivier L, Galland J-P, Maurin H (1995) Livre rouge de la flore menacée de France. Tome 1—espèces prioritaires, Muséum National d'Histoire Naturelle, Institut d'Ecologie et de Gestion de la Biodiversité, Paris (in French)
- Oltean M, Negrean G, Popescu A, Roman N, Dihoru G, Sanda V, Mihăilescu S (1994) Lista roşie a plantelor superioare din România. Studii Sinteze Documentaţii Ecol 1:1–52 (in Romanian)
- Payette S, Delwaide A (1994) Growth of black spruce at its northern range limit in Arctic Quebec, Canada. *Arct Alp Res* 26:174–179
- Picó FX, Riba M (2002) Regional-scale demography of *Ramonda myconi*: remnant population dynamics in a preglacial relict species. *Plant Ecol* 161:1–13
- Riba M, Picó FX, Mayol M (2002) Effects of regional climate and small-scale habitat quality on performance in the relict species *Ramonda myconi*. *J Veg Sci* 13:259–268
- Samis KE, Eckert CG (2007) Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology* 88:1747–1758

- Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. *Annu Rev Ecol Evol Syst* 40:415–436
- Silvertown J, Franco M (1993) Plant demography and habitat: a comparative approach. *Plant Species Biol* 8:67–73
- Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol* 81:465–476
- Șuteu A, Mocan S (1998) Aspecte privind procesul de regenerare și multiplicare “in vitro” a speciei *Saponaria bellidifolia* Sm. In: Cachiță-Cosma D, Ardelean A, Crăciun C (eds) Culturi “in vitro” la cormofite. Lucrările reunite ale celui de-al VII-lea și VIII-lea Simpozion Național de Culturi de țesuturi și celule vegetale, Arad 1997, Buziaș 1998, pp 174–189 (in Romanian)
- Wikberg S, Mucina L (2002) Spatial variation in vegetation and abiotic factors related to the occurrence of a ring-forming sedge. *J Veg Sci* 13:677–684