

SEEDLING ESTABLISHMENT AND LIFE HISTORY TRADE-OFFS IN ALPINE PLANTS¹

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Seedling establishment is central to population maintenance for nonclonal plant species. Plants with low recruitment rates are expected to have high survival rates, and life history theory indicates there should be a single curve for the trade-off between recruitment and mortality that applies to most or all plant species. Alpine perennials are thought to have extraordinarily low recruitment rates because of the harsh environment, but the importance of recruitment in the life history of these plants is unknown. Two alpine cushion plant species, *Minuartia obtusiloba* and *Paronychia pulvinata*, were used to (1) determine the role of recruitment in population maintenance and (2) determine whether the fecundity/mortality trade-off for these alpine plants falls on or off of the curve for other perennial plant species. Using size-based population projection matrices, we determined that the life history of *Minuartia* and *Paronychia* emphasizes recruitment less than that of any other nonclonal species in a literature survey. Estimated maximum life spans of these two species are 200 and 324 yr, respectively, and a regression with other perennial species from the literature indicated that the relationship between fecundity and mortality in these alpine species is consistent with the predicted trade-off curve for perennial species from other environments.

Key words: demography; elasticity; life history; longevity; matrix model; perennial; seedling; trade-off.

Recruitment dynamics can be a key determinant of plant population growth and persistence, and these dynamics differ among species with different life history strategies (Franco and Silvertown, 1996). Organisms must allocate limited resources to competing functions in order to maximize lifetime reproductive value (Williams, 1966), an individual's lifetime contribution to population growth. The resulting trade-offs between life history functions include a positive correlation between fecundity and adult mortality (Charnov, 1991). This trade-off may be the result of two related phenomena: (1) limitations on reproduction due to physiological costs of survival and/or (2) the necessity to evolve high survival rates in environments where fecundity is low.

The extent to which the strength and form of trade-offs are shaped by environmental differences is a general question in population ecology (Rees, 1994; Pfister, 1998; Heppell et al., 2000). If physiological limitations determine these trade-offs, the relationship between reproductive success and survival may be strongly altered in different environments, potentially resulting in weak correlations and a pattern in which trade-offs in some environments lie off the expected curve. Alternatively, if life history correlations primarily result from the necessity to maintain population growth, or at least stability, then one would predict that the fecundity/survival correlation should lie on a single trade-off curve in all environments. Here we examine these two alternatives in the context of alpine plant recruitment and longevity.

Alpine tundra plant communities are dominated by long-

lived perennials (Billings and Mooney, 1968), a life history that is predicted to feature low fecundities and rates of offspring survival (Silvertown et al., 1993). Having high longevity is one strategy that allows persistence in an environment with high interannual climate variation (Morris and Doak, 1998). This strategy has likely evolved in alpine plant species because the climate is unfavorable for sexual reproduction in a high proportion of years (Bell and Bliss, 1980). Some studies have shown that tundra seedlings are abundant at times (Söy-rinki, 1938; Forbis, 2003) and that seedling survival rates fall within the range for perennial species of other habitats (Forbis, 2003) but the demographic importance of seedling establishment in tundra plant life histories is still largely undetermined. Therefore, it is not clear how important a role fecundity and seedling survival play in the persistence of alpine plant populations.

We examined two long-lived nonclonal alpine fellfield species, *Paronychia pulvinata* Gray, and *Minuartia obtusiloba* (Rydb.) House, to determine (1) the role of recruitment in alpine plant population dynamics and (2) whether the fecundity/mortality trade-off for these two alpine species follows the same relationship as that seen in perennial species from other ecosystems or whether the trade-off is particularly strong for these alpine plants. If the fecundity/mortality trade-off for our focal species deviates from this general trade-off curve, it would lend support to the theory that the alpine environment plays a unique role in shaping plant life histories.

To address these questions, we used static data on population size distributions for *Minuartia* and *Paronychia* in combination with detailed demographic data on recruitment and seedling survival probabilities to estimate size-based population projection matrices and elasticity values. Elasticities are a useful tool for determining which demographic rates are most important for the growth or persistence of a population, because the elasticity (e_{ij}) of a matrix element a_{ij} (where a_{ij} is the probability of a transition from stage j to stage i over one time step) is a measure of the relative contribution of that element to λ , the annual population growth rate (de Kroon et

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al., 1986). Using seedling establishment elasticities allowed us to determine the importance of recruitment in maintaining alpine plant populations. Using these elasticities in combination with longevity calculations also allowed us to test the alternative hypotheses that alpine plants lie on or off of the expected fecundity/mortality trade-off curve.

MATERIALS AND METHODS

Study site and species—This study was carried out at three alpine fellfield sites located on two separate knolls (3550–3620 m above sea level) on Niwot Ridge in the Front Range of Colorado, USA. The fellfield plant community is located on exposed ridgetops with low soil moisture and a higher percentage of bare rock than of plants. The dominant species in these communities are four forbs with cushion growth form; *Silene acaulis*, *Minuartia obtusiloba*, *Trifolium nanum*, and *Paronychia pulvinata* (Komárková, 1979).

Both species studied here, *Paronychia pulvinata* and *Minuartia obtusiloba*, are in the Caryophyllaceae and both are caespitose, perennial herbs with branched, woody caudices. In both species, each branch terminates in an apical meristem surrounded by a rosette of leaves. Therefore, cushions are made up of many rosettes. Both species lack mechanisms for vegetative reproduction and rely entirely on sexual reproduction for population maintenance. Because both are cushion-forming, their size can be accurately measured as a two-dimensional area (Morris and Doak, 1998).

Seedling censuses and measurements of population structure—Germination and seedling survival were measured in a single 1-m² plot at each of the three sites. Germination and survival were censused at 2–3 wk intervals from snowmelt through snowfall. New cohorts were marked in each of three years (1998 through 2000), and survival was censused for four years (1998 through 2001).

In 2001, by searching expanding areas until 100 individuals were located (range of search = 1.5–7.6 m² per site), we measured the size of these 100 individuals of each species at each of the three sites. Seedlings were not included because seedling survival is lower than adult survival and contributes to the low probability of detecting seedlings in a one-time census. Instead, seedling data were based on the repeated censuses described above. To minimize measurement error for small plants, we counted rosette number for plants with 20 or fewer rosettes and then converted these counts to sizes using species-specific mean rosette sizes. One-rosette plants were distinguished from seedlings by the absence of cotyledons, which both species retain through their first growing season. For larger plants, an outline was drawn and digitized. Percentage of dead area for each cushion was subtracted from the total area.

Estimation of population matrices and elasticity values—To determine whether size distributions differed significantly between plots or species, we used two-sample Kolmogorov-Smirnov (K-S) tests (Sokal and Rohlf, 1995). Because there were not significant differences between most plots (K-S, *P* < 0.05 for five of 15 possible species–plot combinations), further analyses do not consider plots separately.

Construction of a demographic matrix model requires estimates of age- or size-dependent fecundity, survival, growth, and shrinkage probabilities for all life stages. To estimate fecundity, we assumed a linear relationship between plant size and seed production, estimating the number of new seedlings produced per square centimeter of adult plant by dividing average seedling density by average area covered by adult plants for each species (Table 1). This is an untested assumption. However, fecundity values were extremely low and did not make a large contribution to λ so this assumption is unlikely to affect our model significantly. We used the repeated seedling survey data, in combination with Kendall’s (1998) method to account for sampling variation, to estimate mean seedling and one-rosette survival rates.

Because the primary objective of our study was to determine the effects of seedling stages on overall population dynamics, field measurements focused on seedlings, for which we directly estimated survival over four seasons (Forbis, 2003). In contrast, we used maximum likelihood fitting to infer the

TABLE 1. Definitions of size classes, numbers of individuals per size class, and estimated vital rates underlying the matrix elements represented in Table 3 along with reproductive values (RV) and stable stage distribution (SSD). Size classes refer to the area of each cushion.

Size Class	Size range (cm ²)	<i>Minuartia obtusiloba</i>					<i>Paronychia pulvinata</i>								
		N	F	s	g	h	RV	SSD	N	F	s	g	h	RV	SSD
seedling		23.0 ^a	0	0.9980	1.0000	0	1.0000	0.0748	11.3 ^a	0	0.9345	1	0	1.0000	0.0351
1-rosette		8	0	0.9068	1.0000	0	1.0020	0.0747	10	0	0.6131	0.9960	0	1.0701	0.0331
3	Up to 2.8	76	0	0.8131	0.0187	0.2125	1.1050	0.3350	70	0	0.9456	0.0300	0.001	1.7481	0.2411
4	2.8–5.6	64	0.0314	0.9901	0.0165	0	13.8880	0.1946	32	0.0070	0.9901	0.0275	0	5.0252	0.1844
5	5.6–19.6	100	0.0711	0.9901	0.0127	0	20.3849	0.1416	87	0.0159	0.9901	0.0229	0	6.5961	0.1541
6	19.6–44.2	33	0.2311	0.9901	0.0044	0	30.7365	0.1250	55	0.0517	0.9901	0.0108	0	8.7808	0.1690
7	44.2–78.5	14	0.4443	0.9901	0.0010	0	47.6593	0.0493	29	0.0994	0.9901	0.0040	0	12.0699	0.1311
8	78.5–122.7	2	0.7288	0.9901	0.0002	0	74.4316	0.0050	14	0.1630	0.9901	0.0010	0	17.2089	0.0473
9	122.7–176.7	2	1.0843	0.9901	0	0	109.6776	0.0001	3	0.2425	0.9901	0	0	24.5052	0.0049

Notes: F, fecundity; s, survivorship probability; g, growth probability; h, shrinkage probability. ^a Numbers of seedlings are the product of the average density of seedlings seen in seedling surveys (no./m²) and the total area surveyed for larger plant sizes.

growth, shrinkage, and survival probabilities of larger size classes. The basic approach used to make these estimates is to match the predicted size distribution of a population matrix with the observed population size distributions seen in the field. To merge our data on seedling numbers with the observed population size structure of larger plants, we used area-adjusted estimates of seedling numbers with all data on adult sizes to generate a single size distribution (Table 1). The growth, shrinkage, and survival rates that, when included in a matrix model, yield the best prediction of the observed size distribution of plants are judged as the best estimates of these rates. Because we have only a single population size distribution, we estimate only a single deterministic matrix model for each species.

To construct a matrix model and estimate these vital rates, we first divided the populations into nine size classes following Morris and Doak's (1998) classification for Alaskan populations of another alpine cushion plant in the Caryophyllaceae, *Silene acaulis*. Rather than estimate separate rates for each class, we fit size-dependent functions for the probabilities of survival (s) and of growth (g) and shrinkage (h) to adjacent size classes as logistic functions (Doak and Morris, 1999):

$$p = \exp(b_{0|p} + b_{1|p} \times \text{midsize}) / 1 + \exp(b_{0|p} + b_{1|p} \times \text{midsize}) \quad (1)$$

where p is a probability and midsize is the mean size of each class. We used these formulae to model survival and shrinkage for classes 3–9 and growth for classes 3–8, with growth of class 2 (one-rosette), which had a much higher growth rate than other adult stages, fit separately. Thus, we needed to estimate seven parameters (separate b_0 and b_1 for survival, growth, and shrinkage functions, plus survival for class 2).

To quantify how well a model constructed using particular parameter values predicted the observed size distribution, we calculated the likelihood of seeing the observed distribution, given the predicted stable stage distribution from the model, using the formula for multinomial probabilities (see Doak and Morris, 1999, and Monson et al., 2000, for details of this calculation). For each species, we searched for the parameter values that yielded the best (maximum likelihood) prediction of observed population size distribution. In making these fits, we initially constrained parameter combinations to those predicting λ between 0.99 and 1.01, but found that model fits did not differ when these constraints were removed, indicating that observed λ values did not differ from one. We show results only for the described logistic function; a wide range of other model forms, including quadratic effects of size in logistic and linear equations, were all less supported by the data (Akaike Information Criterion results not shown). Elasticity matrices were calculated from the resulting population matrices using Matlab code from Morris and Doak (2002, pp. 223, 335; "eigenall" and "vitalsens").

Comparison with other species—To compare our focal species with other perennials, we searched the literature for demographic studies of perennial forbs that included a seedling stage and either presented elasticities or allowed for their calculation. For each species, we summed elasticity values that contribute to reproduction (fecundities and germination; $e_{\text{fecundity}}$). The sum of $e_{\text{fecundity}}$ and the elasticity of seedling survival ($e_{\text{sd|surv}}$) provided seedling establishment elasticity ($e_{\text{sd|est}}$). We used this elasticity value to answer the two general questions presented in this paper: what is the relative importance of recruitment in alpine plant populations; and do these two alpine species follow the general fecundity/survival trade-off pattern set by other species?

We chose to use seedling establishment elasticity rather than using raw demographic values because the selective forces that create the trade-offs of interest are better represented by elasticities than by separate demographic rates. Most of the commonly accepted correlations between pairs of traits are only one of many ways to "solve" the same ecological problem, while life history theory rests on the concept of fitness as the product of processes occurring across all life history stages (Charnov, 1997). The strength to which fitness is correlated with, or influenced by, any particular demographic rate is properly measured by its elasticity rather than raw demographic values, because elasticities account for effects across the entire life cycle. Additionally, the $e_{\text{sd|est}}$ parameter incorporates several traits that contribute to recruitment—reproductive effort, reproductive output, seed bank, germination, and seedling survival. Viewing these reproductive traits as part of an integrated life history

rather than in isolation allows us to look at the overall contribution of recruitment to population persistence in these species.

To estimate individual longevity, we used a starting vector consisting of one seedling and zero adults and multiplying this vector by each species' matrix with all fecundities set to zero (Caswell, 2001). Matrices were iteratively multiplied by the resulting population vectors until the summed probability of survival for all age classes reached 0.01, providing a consistent measure of maximum longevity.

To date, the most comprehensive efforts to determine whether proposed life history trade-offs exist in plants have tested for negative correlations between elasticities (Silvertown et al., 1993; Franco and Silvertown, 1996). However, Shea et al. (1994) pointed out that elasticities sum to one by definition; therefore, this system assumes trade-offs by default. Analyses of simulated data sets have shown that even attempts to deal with intercorrelations by using randomization tests find spurious negative correlations between most elements of the elasticity matrices (Shea et al., 1994). Therefore, to ask whether the relationship between seedling establishment elasticity and longevity in *Minuartia* and *Paronychia* differs from the relationship seen in other herbaceous perennials, we performed a linear regression of $e_{\text{sd|est}}$ on raw longevities for our focal species in combination with the species from the literature (both variables were first log-transformed).

RESULTS

Size distributions and demographic patterns—*Minuartia* had a higher proportion of small (<0.5 cm²) individuals than did *Paronychia* (K-S; $P < 0.05$, $D_{\text{max}} = 0.180$, $D_{0.05} = 0.111$). The fitted models for both species had high survival probabilities and low growth and shrinkage probabilities (Tables 1, 2). For *Minuartia*, survival rates were greater than 0.900 for all classes except class 3, and even the rates that were directly observed for seedlings and one-rosette plants exceeded 0.900. While *Paronychia* also had very high survival probabilities, small plants of *Paronychia* had lower survival probabilities than small plants of *Minuartia*. For both species, the probability of growth was low for classes 3–8, ranging from 0.0002 to 0.0300. The estimated probabilities of shrinkage were essentially zero for most classes for both species. Fecundities, which were calculated from seedling recruitment data, were extremely low for both species as well. Only for *Minuartia*'s largest size class did individuals on average produce one or more seedlings within a single year ($F < 1$).

Relative reproductive value (an individual's lifetime contribution to population growth, scaled to the contribution of newborns) increased with increasing size, particularly for *Minuartia*, in which class 9 had a relative reproductive value of 109.6776 (Table 1). The increase was less marked for *Paronychia*, in which the reproductive value of the largest size class was only 24.5052 times that of class 1 (Table 1).

Elasticity values, longevities, and comparisons—Elasticity matrices for the two species were similar (Table 2). Both had the highest elasticity values (e) for stasis (survival without growth) of intermediate classes. For *Minuartia*, elasticity of stasis of individuals in stages 4–7 ranged from 0.1839 to 0.2993. For *Paronychia*, elasticity of stasis of individuals in stages 4–8 ranged from 0.1244 through 0.2430. Conversely, both species had low elasticity values for fecundities, most growth elements, and survival of individuals in the largest size class. *Minuartia* had the lowest elasticity values for the fecundity of individuals in classes 3, 4, 8, and 9 and for growth out of class 8. *Paronychia* had its lowest elasticity values for fecundities in classes 3, 4, and 9 and growth out of class 8 (Table 3).

TABLE 2. Population projection matrices for (A) *Minuartia obtusiloba* and (B) *Paronychia pulvinata*. Elements representing stasis, growth, and shrinkage are composites of underlying vital rates as follows: $S(1 - g - h)$, $S \times g$ and $S \times h$, respectively, where S represents survival, g represents growth, and h represents shrinkage.

Size class	Seedling	One-ros	3	4	5	6	7	8	9
A									
Seedling	0	0	0.0122	0.0314	0.0711	0.2311	0.4444	0.7288	1.0843
one-ros	0.9980	0	0	0	0	0	0	0	0
3	0	0.9068	0.7979	0	0	0	0	0	0
4	0	0	0.0152	0.9738	0	0	0	0	0
5	0	0	0	0.0163	0.9775	0	0	0	0
6	0	0	0	0	0.0126	0.9858	0	0	0
7	0	0	0	0	0	0.0043	0.9891	0	0
8	0	0	0	0	0	0	0.0010	0.9899	0
9	0	0	0	0	0	0	0	0.0002	0.9901
B									
Seedling	0	0	0.0027	0.0070	0.0159	0.0517	0.0994	0.1630	0.2425
one-ros	0.9345	0.0025	0.0010	0	0	0	0	0	0
3	0	0.6106	0.9162	0	0	0	0	0	0
4	0	0	0.0284	0.9629	0	0	0	0	0
5	0	0	0	0.0272	0.9675	0	0	0	0
6	0	0	0	0	0.0226	0.9794	0	0	0
7	0	0	0	0	0	0.0107	0.9862	0	0
8	0	0	0	0	0	0	0.0039	0.9891	0
9	0	0	0	0	0	0	0	0.0010	0.9901

Note: One-ros, one-rosette plant, the stage immediately following the seedling stage.

Values of e_{sdlest} for *Minuartia* and *Paronychia* were in fact near the bottom of the range of e_{sdlest} for perennial forb species (Table 4). Indeed, the only species with an e_{sdlest} lower than that of our two focal species was *Potentilla anserina*, a stoloniferous cinquefoil.

The high survival rates of these species confer extremely long life spans to both. At least 1% of seedlings are predicted to live 324 yr for *Paronychia* and 200 yr for *Minuartia* (Figs. 1, 2). This longevity means that, in spite of the extremely low elasticities for recruitment for *Minuartia* and *Paronychia*, the relationship between e_{sdlest} and longevity for these alpine species is consistent with the relationship for all species from

Table 3. In a linear regression, longevity was a highly significant predictor of e_{sdlest} ($F_{1,21} = 11.34$, $P = 0.0031$; Fig. 3), and none of the observations were outliers.

DISCUSSION

Demography of cushion plants—*Minuartia* and *Paronychia* are in the same family and share the cushion growth form. Our data indicate that they also share a broadly similar life history. With a lower total fecundity and a longer life span, *Paronychia* resides closer to the “slow” end of the fast–slow life history continuum (sensu Harvey et al., 1989). That said,

TABLE 3. Elasticity values for (A) *Minuartia obtusiloba* and (B) *Paronychia pulvinata*. Values shown in boldface type were summed to calculate total elasticities for seedling establishment for Table 4.

Size class	Seedling	One-ros	3	4	5	6	7	8	9
A									
Seedling	0	0	0.0003	0.0005	0.0008	0.0023	0.0017	0.0003	0.0000
one-ros	0.0059	0	0	0	0	0	0	0	0
3	0	0.0059	0.0233	0	0	0	0	0	0
4	0	0	0.0056	0.2075	0	0	0	0	0
5	0	0	0	0.0051	0.2216	0	0	0	0
6	0	0	0	0	0.0043	0.2993	0	0	0
7	0	0	0	0	0	0.0020	0.1839	0	0
8	0	0	0	0	0	0	0.0003	0.0285	0
9	0	0	0	0	0	0	0	0.0000	0.0008
B									
Seedling	0	0	0.0001	0.0002	0.0004	0.0014	0.0020	0.0012	0.0002
one-ros	0.0054	0	0	0	0	0	0	0	0
3	0	0.0055	0.0600	0	0	0	0	0	0
4	0	0	0.0053	0.1387	0	0	0	0	0
5	0	0	0	0.0051	0.1531	0	0	0	0
6	0	0	0	0	0.0048	0.2264	0	0	0
7	0	0	0	0	0	0.0034	0.2430	0	0
8	0	0	0	0	0	0	0.0014	0.1244	0
9	0	0	0	0	0	0	0	0.0002	0.0179

Note: One-ros, one-rosette plant, the stage immediately following the seedling stage.

TABLE 4. Elasticity values for fecundity, seedling survival, and overall seedling establishment for perennial plants. Species are ordered by descending values of seedling establishment total elasticity, which is the sum of fecundity and seedling survival elasticities ($e_{sdlest} = e_{fecundity} + e_{sdlsurv}$). Species in bold represent data from this study.

Species	Vegetative	Habitat	$e_{fecundity}$	$e_{sdlsurv}$	e_{sdlest}	Longevity	Reference
<i>Pinguicula villosa</i>	no	wet tundra	0.127	0.140	0.267	14	Svensson et al., 1993 ^a
<i>Panax quinquefolium</i>	no	temperate forest	0.155	0.072	0.227	25	Charron and Gagnon, 1991
<i>Cynoglossum virginianum</i>	no	temperate forest	0.142	0.065	0.207	28	Cipollini et al., 1993
<i>Espeletia timotensis</i>	no	paramo	0.080	0.110	0.190	10	Silva et al., 2000
<i>Achnatherum calamagrostis</i>	tillers	badlands	0.076	0.078	0.154	20	Guárdia et al., 2000
<i>Lomatium bradshawii</i>	no	prairie	0.073	0.072	0.145	4	Kaye et al., 2001
<i>Arisaema serratum</i>	no	temperate forest	0.068	0.068	0.136	7	Kinoshita, 1987
<i>Calathea ovandensis</i>	rhizomes	tropical forest	0.105	0.029	0.134	2	Horvitz and Schemske, 1995
<i>Pinguicula vulgaris</i>	no	wet tundra	0.051	0.069	0.120	29	Svensson et al., 1993 ^a
<i>Gentiana pneumonathe</i>	no	meadow	0.048	0.048	0.096	14	Oostermeijer et al., 1996
<i>Espeletia spicata</i>	no	paramo	0.020	0.070	0.090	2	Silva et al., 2000
<i>Pinguicula alpina</i>	no	wet tundra	0.031	0.058	0.089	106	Svensson et al., 1993 ^a
<i>Oxalis acetosella</i>	rhizomes	temperate forest	0.042	0.038	0.080	122	Berg, 2002
<i>Lathyrus vernus</i>	no	temperate forest	0.027	0.020	0.047	188	Ehrlén, 2000
<i>Geum rivale</i>	no	meadow	0.015	0.015	0.030	18	Kiviniemi, 2002
<i>Agrimonia eupatoria</i>	no	meadow	0.022	0.022	0.025	119	Kiviniemi, 2002
<i>Leptanthes caritensis</i>	no	tropical forest	0.002	0.018	0.020	207	Tremblay, 1997
<i>Silene acaulis</i>	no	alpine tundra	0.008	0.008	0.016	310	Morris and Doak, 1998
<i>Minuartia obtusiloba</i>	no	alpine tundra	0.006	0.006	0.012	200	this paper
<i>Paronychia pulvinata</i>	no	alpine tundra	0.006	0.005	0.011	324	this paper
<i>Potentilla anserina</i>	stolons	meadow	0.004	0.004	0.008	21	Eriksson, 1988

^a Longevity estimates for the three species of *Pinguicula* were taken from Ehrlén and Lehtilä (2002) because transition matrices for those species were not published in Svensson et al. (1993).

these species are very similar to one another when compared with other perennials—their e_{sdlest} values are within 0.001 of one another, and their life spans are well beyond the range of most other plant species surveyed.

The emphasis on stasis in our models suggests that if we were to measure growth and survival of adults over four years we would see little change in populations of *Minuartia* and *Paronychia* on Niwot Ridge. Therefore, the use of size distributions to indirectly estimate vital rates is a reasonable approach in this case. The incorporation of adult size distributions and four years of seedling establishment data into a single model might also serve to buffer high expected interannual variability in alpine seedling recruitment due to high interannual variability in seed output (Arft et al., 1999), viability (Chambers, 1989), and survival (Forbis, 2003).

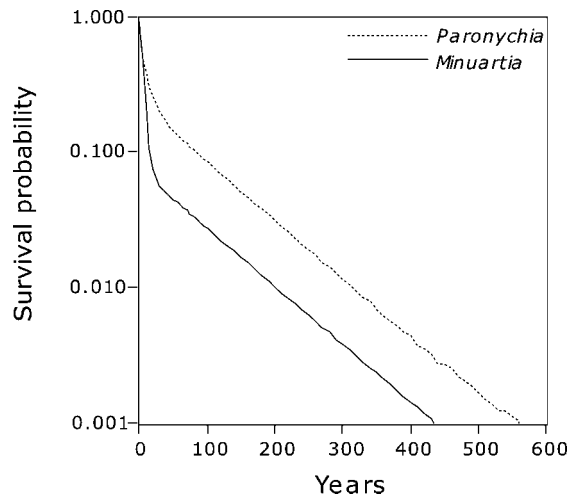


Fig. 1. The survivorship functions for newly germinated plants predicted by vital rates shown in Table 3 (see Table 2 for matrices).

Importance of recruitment—As expected, values of e_{sdlest} were lower for *Minuartia* and *Paronychia* than for virtually all other species from our literature survey. For at least these two alpine species, reproduction and the seedling stage contribute only a small part of the annual population change, which seems counterintuitive given the fact that these two species rely entirely on seedling establishment for recruitment. However, the e_{sdlest} values make sense in the context of reproductive value. The probability that a seedling will survive the many decades required to reach sexual maturity is low, whereas the probability that an established adult will contribute to future generations is high (Table 3).

Our results for e_{sdlest} are similar to those for Alaskan *Silene acaulis* (Morris and Doak, 1998; Table 4), but due to the wide variation in life histories among alpine plants, our results on e_{sdlest} in these two species are not directly transferable to other

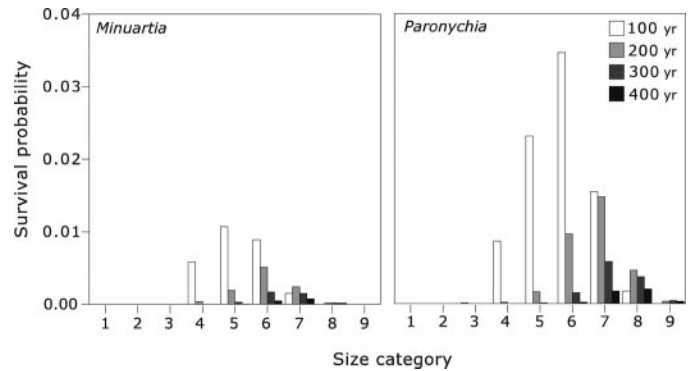


Fig. 2. Distributions of the probabilities of being alive and in each size class for individuals of four ages. Size class definitions are listed in Table 1. Probabilities were calculated by iteratively multiplying a population vector consisting of one seedling and zero adults by population projection matrices (with fecundities set to 0) for each species to simulate survival across 100, 200, 300, and 400 yr.

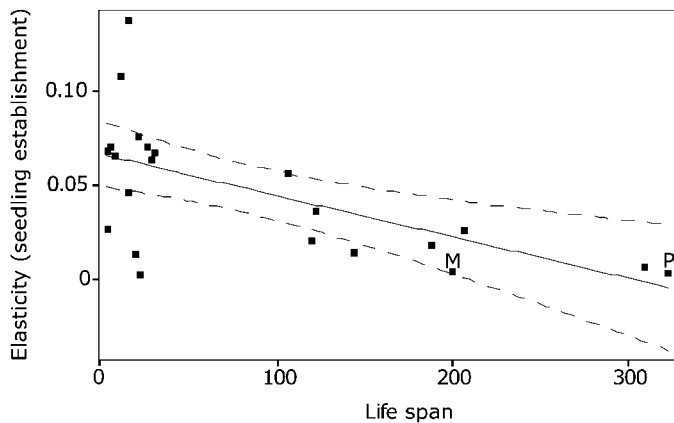


Fig. 3. Regression of elasticity values for seedling establishment on life spans for species from Table 4. Dashed lines indicate 95% confidence limits. Data shown are untransformed values; analyses were conducted on log-transformed values. M = *Minuartia*, P = *Paronychia*. Data for other species are from the literature.

high-elevation species. In the above-treeline grass-shrub paramos of the Andes, *Espeletia timotensis* and *E. spicata* (Silva et al., 2000) have higher e_{sdlest} (Table 4) and λ values (1.24 and 1.13, respectively) than *Minuartia* ($\lambda = 1$) and *Paronychia* ($\lambda = 1$). Both the greater importance of young life stages and rapid population growth rates show that these paramo species have a faster life history than do our alpine cushions.

Fecundity/mortality trade-off—Using e_{sdlest} and longevity, we asked whether the extremity of the alpine environment causes the fecundity/mortality trade-off for alpine plants to fall on or off of the trade-off curve set by other perennial plant species. Our regression results showed that the relationship between seedling establishment and longevity for *Minuartia* and *Paronychia* is consistent with relationships seen for all other species in Table 4 (Fig. 3). These two alpine species are not outliers with regard to the fecundity/mortality trade-off. Therefore, seedling establishment patterns for these two species are concordant with what would be predicted for any extremely long-lived species, and the alpine environment itself is not disproportionately affecting survival dynamics.

It is worth mentioning that while most species from this data set fit well along this curve, there are a few species with short life spans whose seedling establishment elasticities fall outside the confidence intervals (although they were not outliers). Of the three species that fall below the lower confidence limit, two (*Calathea ovandensis* and *Potentilla anserina*) reproduce asexually. The occurrence of clonal reproduction might be another important predictor of the fecundity/longevity trade-off, and it might be more appropriate to develop separate trade-off curves for clonal and nonclonal species. Another reproductive life history trait, the formation of long-lived seed banks, was not considered here. Due to its potential to strongly influence population longevity, it doubtless plays a role. While seed dormancy does correlate with other life history traits, these relationships are generally quite weak (Rees, 1993; Doak et al., 2002).

Our data indicate that these two cushion pink species live for centuries in the alpine fellfields of Niwot Ridge. Comparison with other studies indicates that *Minuartia* and *Paronychia* are among the longest-lived forbs whose longevity has

been estimated. Ehrlén and Lehtilä (2002) estimated longevities of 71 perennial plant species; their highest estimate for any herbaceous species was *Silene acaulis* at 337.16 yr. Our estimates of up to 324 yr for *Paronychia* and 200 yr for *Minuartia* place them among the longest-lived herbaceous plants known.

The life history strategy seen in *Minuartia* and *Paronychia* is likely the product of a history of selection in an environment with wide, random interannual climate variation and the inability to reach reproductive sizes quickly. In environments where juvenile mortality can be high, a long life with repeated episodes of reproduction is predicted (Charnov and Shaffer, 1973).

Previous results (Forbis, 2003) have shown that many alpine plant species have per capita recruitment rates and seedling survival rates similar to those of perennial plants from other environments. This study has shown that the importance of seedling establishment to population maintenance in two particularly long-lived alpine species is lower than in other perennial species. However, when longevity is taken into account, these two alpine species do not differ from other perennials in their seedling survival probabilities. This result indicates that while the alpine environment can strongly shape life history, it does not appear to alter the shape or strength of general life history trade-offs.

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