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Increasing Population Density and Seed Production with Altitude in Eritrichium nanum (Boraginaceae)—an Arctic Alpine ObligatorySeeder

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Abstract
At 17 sites in the European Alps (2170–3310 m), the population density and seed production of the high alpine cushion plant Eritrichium nanum were investigated. Recruitment in this non-clonal species relies exclusively on seeds. The population density rose significantly with increasing altitude. A mean number of 368 seeds per m² was observed. Whereas the quantity of the generative rosettes (metamers) was relatively constant, the annual seed production strongly varied and was found vulnerable, particularly in 1996, when it was suppressed by unfavorable weather conditions. In 1997 seed production again reached the usual level, when about the same amounts of seeds were recorded as in previous years, indicating the strong resistance of elevated E. nanum populations against the severe climate at high altitudes. With rising population density, E. nanum produces distinctly higher seed numbers. This increasing amount of seeds seems essential for the persistence of its uppermost populations. Our results indicate that it is caused by the rising number of rosettes/surface and not a higher reproduction by single rosettes. Compared to other alpine species, the seed weight of E. nanum (average 0.76 mg) is high. Most of its neighboring species are clonal, producing much lighter seeds. The strategy of producing heavy seeds favors successful recruitment and appears to be decisive for an obligatory seeder such as E. nanum.

Introduction
Since the classic textbook about pollination of alpine forbs by Müller (1881), it has been assumed that dense carpets of flowers are a characteristic feature at high altitudes. Some few countings by Steiger (1913) at different altitudes in the Swiss Alps seemed to confirm this opinion. Günthart (1926) suggested increasing flower density in alpine meadows to be a fact. Besides several alpine plants (species of the Silenoideae and Alsinioideae, and of the genera Saxifraga, Androsace, etc.), he named also two arctic dwarf shrubs: Cassiope tetragona and Diapensia lapponica. Later, countings of flowers or individuals per surface (population density) hardly took place, whereas altitudinal trends of clonal reproduction and autogamy were more often investigated. According to Hartmann (1955) and Stöcklin (1992), alpine grasslands and scree vegetation of the European Alps are characterized by 80% to 90% as clonal. These findings seem to indicate that clonal propagation is an effective strategy of plants living under the ecological stress of alpine habitats, in any case less risky than sexual propagation with flowering, pollination, and seed development, which waste too much energy in environments where the supply of nutrients is low. However, Söyirinki (1938) has pointed out in his basic study of the Scandinavian alpine flora, that only the dominant species in terms of their biomass strongly rely on vegetative propagation (grasses, sedges, and dwarf shrubs) but not the majority in terms of species number. Furthermore, Söyirinki (1938) found among plants inhabiting hostile places such as snowbeds the following obligatory seeders: Sibbaldia procumbens L., Veronica alpina L., Gnaphalium supinum L. This is in line with the observations of Grukel and Bliss (1985), Marchand and Reach (1980), and Billings (1974), who suggested that clonal propagation is less abundant in alpine than in arctic environments. After Stöcklin (1992), it appears that there is an abundance peak of clonal plants in the lower alpine belt (heaths of dwarf shrubs and meadows) and a reduction in frequency of vegetative multiplication at higher elevations in the upper alpine belt (alpine grasslands) and in the subnival zone (open scree; Kikvidze, 1993; Kikvidze and Nakhtutsrishvili, 1998; Nakhtutsrishvili, 1998) and finally in the nival zone (isolated individuals above the line of permanent snow; Gottfried et al., 1998). In fact, sexual propagation seems to be quite common among species occurring in the nival zone. In contrast to the opinion of Bliss (1971), some of these high alpine species are obligatory seeders such as Eritrichium nanum (L.) Schrader ex Gaudin (Zoller et al., 2002).

According to various textbooks, autogamy increases with higher latitude in the Arctic and at higher altitude in the mountains of the temperate zone. This is probably true for butterfly-pollinated flowers such as Dianthus, Primula, etc. (e.g., Erhardt and Jäggi, 1995). However, in some recent studies it was shown that there are different species which are heterogamous (e.g., Saxifraga oppositifolia L.; Gugerli, 1998, 2000) and in other cases simultaneously non-clonal (e.g., E. nanum; Zoller et al., 2001, 2002). Investigations about visitation rates to flowers of E. nanum and about its breeding system revealed that this species is fly-pollinated and mainly heterogamous. For an obligatory non-clonal plant such as E. nanum, the production of many large seeds seems to be indispensable for successful reproduction. There are several studies about seed weight in relation to environmental conditions (e.g., Baker, 1972; Urbanska and Schütz, 1986; Schütz and Stöcklin, 2001), but we could not find reliable information about the number of seeds produced by alpine forbs, especially by cushion plants. Furthermore, we know practically nothing about population densities and their relation to the seed production of high-alpine plants. Körner (1999) summarizes several case studies of clonal alpine plants in relation to their seed production. On the other hand, nothing is known about population density and seed production in obligatory seeders and about possible altitudinal trends. Therefore, the present study deals with the population density of E. nanum (cm²/m², % per plot) with its seed production/m² and its seed weight. These three dependent traits were investigated (1) in different populations, (2) at different altitudes, and (3) during several years (seed number).
Material and Methods

*Eritrichium nanum* is a pioneer of screes and rocks in the Arctic and in the high mountains of the temperate zone growing in open hostile habitats. Its ramifications depends exclusively on the primary axis. No adventitious roots are developed and therefore *E. nanum* is a strictly non-clonal species like many tap-rooted Fabaceae. The basically 2-carpellate ovaries of the members of the borago family develop maximally four individual nutlets per flower which are separately dispersed and for which in the following text the term "seed" will be used. Population density and seed production of *E. nanum* were studied in 69 plots of 1 m² which were established at 17 different sites in the Italian, Swiss, Austrian, and Slovenian Alps (Table 1, Fig. 1).

### POPULATION DENSITY AND SEED NUMBERS

The permanent plots were marked by short metallic sticks and/or stable rocks, both of which were sprayed with yellow paint. In order to make our investigations comparable, we used a metallic frame on which we stretched a nylon cord, dividing 1 m² surfaces into one hundred 1 dm² sections (Zoller et al., 2001). In the field, the position and size of every *E. nanum* plant were accurately projected on paper copies of a 100 dm² grid (scale 1:10). By tracing the sizes on transparent graph paper, the area of each cushion could be determined in cm². By this method it was possible to evaluate the total area of *E. nanum* in relation to the surface of the whole plot (m²). From the total surface (cm²) covered by *E. nanum* its population density per m² could be determined as % cover. To test if population density changed with altitude we measured the total surface of the *E. nanum* cushions in plots of 1 m² sections (Zoller et al., 2001). In the field, the position and size of every *E. nanum* plant were accurately projected on paper copies of a 100 dm² grid (scale 1:10). By tracing the sizes on transparent graph paper, the area of each cushion could be determined in cm². By this method it was possible to evaluate the total area of *E. nanum* in relation to the surface of the whole plot (m²). From the total surface (cm²) covered by *E. nanum* its population density per m² could be determined as % cover. To test if population density changed with altitude we measured the total surface of the *E. nanum* cushions in plots of 1 m² sections (Zoller et al., 2001).

### SEED WEIGHTS

Altogether we weighed 468 seeds of *E. nanum* originating from sites 2, 3, 6, 9, and 10 (about 90 seeds per site) and 30 seeds of two species in the closely related genus *Lappula: L. squarrosa* (Retz.) Dumort. and *L. deflexa* (Wahlenb.) Garcke from different sites in Switzerland. Furthermore, we weighted the seeds of several important neighboring species, such as *Cerastium uniflorum* Clairv., *Minuartia sedoides* (L.) Hiern., *Saxifraga bryoides* L., and *S. exarata* Vill. The seeds of the latter four species originated from three different and far distant sites in the Swiss Alps (n = 30).

### Results

#### POPULATION DENSITY

At sites including most of the geographic distribution of *Eritrichium nanum*, population density (% cover) was always in-
from 0.45% at 2705 m a.s.l. to 2.9% at 3310 m a.s.l. ($R^2 = 0.58$, $P < 0.001$); among the 13 permanent plots from 0.84% at 2500 m a.s.l. (Passo Scuro site 4 in Fig. 1) to 5.6% at 2960 m a.s.l. ($R^2 = 0.74$, $P < 0.001$); among 27 plots from the Eastern Alps from 0.65% at 2170 m a.s.l. to 2.7% at 2760 m a.s.l. ($R^2 = 0.47$, $P < 0.001$), and in 100 m sections between 2100 m and 3200 m a.s.l. from 0.2% to 3.2% ($R^2 = 0.66$, $P < 0.001$).

SEED PRODUCTION

The average number of seeds per fruit in the control plots of a selfing experiment at Passo Scuro was only 1.44 (Zoller et al., 2001, 2002). Nevertheless, we recorded an annual production of 368 seeds/m² (mean ± 354) from the 13 permanent plots over a period of 2 (Piz Lagalb, Piz Nair) to 5/6 yr (Passo Scuro, Claudio e Bruno), respectively, whereas the mean number of seeds per rosette of *E. nanum* amounted to 1.23 during the same period (Table 2). It is noteworthy that the maximal seed production of 1354 per m² (plot 5 at Claudio e Bruno, 1994) was about 450 times higher than the minimum of 3 seeds/m² (plot 2 at Passo Scuro, 1996). An even higher variability was noted for fertilized flowers (maximum about 900 times higher than minimum). Smaller but nevertheless considerable differences were recorded for the flower numbers (maximum about 110 times higher than minimum) and for the inflorescences (maximum 50 times higher than minimum). A significantly greater number of seeds was produced at higher altitudes (Fig. 3). Undoubtedly this increased seed production is parallel to the rising population density with increasing elevation. On the other hand, the seed production per rosette of 1 cm² surface is independent from the altitude ($R^2 = 0.017$, $P = 0.673$, $n = 13$).

The annual number of inflorescences, i.e., generative rosettes, was noticeably constant, whereas the production of flowers and seeds was much more irregular over the years (Fig. 4a–c). Especially in 1996, the amounts of fertilized flowers and seeds were extremely low in all the eight plots of Passo Scuro, Piz Nair, and Piz Lagalb. In the year after this depression (1997) the sexual performance measured in the four plots of Passo Scuro reached again similar levels as before 1996 or was even higher (Fig. 4c). However, in the plots of Claudio e Bruno no

**TABLE 2**

<table>
<thead>
<tr>
<th>Organ</th>
<th>Minimum</th>
<th>Average ± SD per plot (m²)</th>
<th>Maximum</th>
<th>Mean number per rosette of <em>E. nanum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflorescences</td>
<td>16</td>
<td>203 ± 240</td>
<td>777</td>
<td>0.77</td>
</tr>
<tr>
<td>Flowers</td>
<td>27</td>
<td>780 ± 692</td>
<td>3648</td>
<td>2.84</td>
</tr>
<tr>
<td>Fertilized flowers</td>
<td>3</td>
<td>325 ± 318</td>
<td>2709</td>
<td>1.23</td>
</tr>
<tr>
<td>Seeds (nutlets)</td>
<td>3</td>
<td>368 ± 354</td>
<td>1354</td>
<td>1.40</td>
</tr>
</tbody>
</table>

* Based on a mean rosette size of 1 cm².

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corresponding depression of the generative reproduction was observed (values not shown).

**SEED WEIGHTS**

The seed weights of *E. nanum* varied between 0.4 mg and 1.4 mg, with an average value of 0.76 mg. The seeds of *E. nanum* are significantly heavier than those of its most frequent neighboring species (*Saxifraga bryoides*, *S. exarata*) up to 0.24 mg (*Cerastium uniflorum*) and 0.35 mg in *Silene acaulis* (L.) Jacq. (Chambers, 1995), respectively. On the other hand, the seed weights of *Lappula deflexa* and *L. squarrosa*, closely related to *E. nanum* but living at lower altitudes, amounted to more than 1 mg. Obviously they are distinctly heavier than the seeds of *E. nanum* (Fig. 5). Among the seeds of *E. nanum* we observed a significant trend of decreasing mean weight associated with increasing altitude ($R^2 = 0.51$, $P < 0.01$, $n = 13$; Fig. 6).

**FIGURE 2.** Population density of *Eritrichium nanum* in plots of 1 m² (% cover) with altitude in the European Alps. (a) Zwischbergenpass: data of 1996. The population density increases significantly with increasing altitude ($R^2 = 0.581$, $n = 16$, $P < 0.001$). (b) Permanent plots: data of 1995; Claudio e Bruno, 1996. The population density increases significantly with increasing altitude ($R^2 = 0.741$, $n = 13$, $P < 0.001$). (c) Eastern Alps: data of 1996; Triglav, 1997; Mangart, 1998. The population density increases significantly with increasing altitude ($R^2 = 0.471$, $n = 27$, $P < 0.001$). (d) Summary: mean per 100 m section. Data of 1995; Passo Cristallina, 1994; Zwischbergen, Claudio e Bruno, Dolomits, and Austrian Alps, 1996; Triglav, 1997; and Mangart, 1998 (see Table 1). The mean population density per 100 section increases significantly with increasing altitude ($R^2 = 0.659$, $n = 11$, $P < 0.01$).
Discussion

Since Müller (1881), Stäger (1913), and Günthart (1926) suggested that alpine forbs produce more flowers and accordingly higher numbers of possible descendants than lowland plants, this opinion has never been tested by systematic studies. The trend can be caused either by increasing allocation to flowers or by increasing population density. We found increasing population densities in Eritrichium nanum from dense grasslands at the lower alpine belt to open screes near the permanent snow line. We thereby confirm for the first time quantitatively the above suggestions by Müller (1881). In the case of Eritrichium nanum, the increasing population density was investigated over an altitudinal range of more than 1000 m (2170–3310 m) and is probably explained by the distinctively diminishing competition from other species in the open screes at higher altitudes. In particular, sedges and grasses such as Carex curvula All. and Festuca halleri All. or Elyna myosuroides (Vill.) Frötsch, which are typical for dense grasslands, are more and more disconnected above 2700–2800 m. It seems likely that by using a similar method, a corresponding trend could be found for other cushion plants disconnected above 2700–2800 m. It seems likely that by using a similar method, a corresponding trend could be found for other cushion plants closer to six times denser than the lowest of this species. However, their total cover reaches rarely more than 15%.

SEED NUMBERS

It is common in studies dealing with sexual reproduction of plants to calculate the number of developed seeds in relation to shoots, individual rosettes, or the seed bank in the soil. Seed production of Eritrichium nanum seems to be clearly correlated with its population density and is therefore best counted in defined surfaces (e.g., 1m² plots). Corresponding to the increase in population density at higher altitudes, the numbers of seeds were also increasing (Fig. 3). Undoubtedly this increasing number of seeds is related to the increasing surface covered by E. nanum. On the other hand, by calculating the seeds per cm² surface of E. nanum, it could be shown that the seed production per rosette is independent of altitude. From this, it follows that the increasing number of seeds with altitude is caused by a higher number of rosettes per surface and not by an increased investment in reproduction by single rosettes. The increased seed production at higher altitudes seems to be essential for E. nanum, maintaining stable populations in the subnival belt just below the permanent snow line. Seed numbers/m² at 2950–2960 m at Piz Lagalp were at least two to three times higher than at Passo Scuro at 2550–2605 m (Fig. 3), in spite of the strongly limited seed production per flower within the family of Boraginaceae (maximal 4 seeds/flower), which seems disadvantageous for an obligatory non-clonal species like E. nanum. There are clonal species with up to seven times higher seed production/fruit than E. nanum, such as Epilobium fleischeri Hochst. (Stöcklin and Favre, 1994). Saxifraga bryoides, another clonal species occurring together with E. nanum, produces at least 20 times more seeds per fruit (counting in 2002, mean = 119 ± 43, n = 5). Nevertheless, this taxonomically restricted seed reproduction in E. nanum is sufficient due to the relatively high seed weight guaranteeing a high rate of recruitment (Zoller and Lenzin, 2004).

Day et al. (1999) showed on an Antarctic island that seed weight and seed numbers of the cushion plant Colobanthus quitensis are strongly influenced by temperature. The capsules of this species produced under experimental warming 45% more seeds that were 11% heavier. We did not study cushions of E. nanum under experimental conditions, but our countings (Fig. 4c) make it evident that the seed production of E. nanum is vulnerable and can be affected by unfavorable weather conditions, such as in 1996 when seed production was almost completely suppressed in several plots. According to the 1996 report of the Swiss Central Meteorological Institution (1997), the winter of 1995/1996 was almost without snow even at high altitudes and was followed by an extremely dry spring, then a hot and dry period during June and July which ended abruptly in the second half of August, when a polar air current brought early snow and icy temperatures. These exceptional weather conditions were much more pronounced east of the “Gotthardpass” than farther west. Therefore, it seems plausible that the eastern study sites (Passo Scuro, Piz Nair, and Piz Lagalp) had a heavily depressed seed production in this year, whereas, at the westernmost site (Claudio e Bruno), seed development was unimpaired. Rauh (1939), cited by Körner (1993) and Körner and de Moreas (1979), observed that alpine cushion plants lose only relatively little water from their reduced leaf surface and consequently suffer little from water stress. That E. nanum was not seriously damaged, either by the persistent drought or the sudden frost in 1996, is demonstrated by its high seed production in 1997 at Passo Scuro which reached in all four plots similar levels as in previous years (Fig. 4c). However, it is worth mentioning that the seeds of E. nanum ripen in inflorescences which are often elongated up to 6 cm and therefore less protected than in most alpine cushion plants with their extremely reduced stems and with fruits developing within the cushion or less than 1 cm above its surface, i.e., Minuartia sedoides, Silene acaulis, S. esscapa All., Androsace alpina (L.) Lam., A. helvetica (L.) All., A. vandelli (Turra) Chiov., etc. We suppose that the extreme weather conditions, particularly the general drought to which the inflorescences, flowers, and ripening seeds of E. nanum were exposed during 1996, may have contributed to the unusually low seed production in this year.

SEED WEIGHTS

Evidently diaspore weight is taxonomically constrained (Urban ska and Schütz, 1986; Thompson and Rabinowitz, 1989). Therefore, ecologically significant differences are best studied within the same genus or family. Several factors causing variability in seed weights of alpine plants have been discussed: (1) Pioneer plants are small seeded,

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whereas plants of climax vegetation are heavy seeded (Kerner, 1871; Salisbury, 1974). (2) Late flowering alpine plants produce smaller seeds. Furthermore, it seems conclusive that the seed weights are distinctly lighter in flowers developing three or four seeds than in those with only one (Zoller, unpublished).

Recently, Schütz and Stöcklin (2001) observed a distinct trend towards higher seed weight corresponding with increasing altitude in the genera Crepis and Senecio (Asteraceae). Trying to confirm this trend for E. nanum and its most closely related species in the genus Lappula, we found the weights of the lowland species were significantly heavier, i.e., just the opposite of the observed trend among species. Nevertheless, we assume that the significantly higher seed weights in alpine species at the generic level, observed in the Asteraceae and preliminarily in the Apiaceae and Caryophyllaceae reflect a general trend, whereas the inverse trend found in the family Boraginaceae may be rather exceptional. In the relationship of the tribe Eritrichioideae (Fig. 5), it may be connected with the life span of the cushions of E. nanum which is much longer than in the annual or short perennial Lappula species.

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**FIGURE 5.** Mean seed weight of Eritrichium nanum, of related species (Lappula squarrosa and L. deflexa, to the left) and of species from the same habitat (Leucanthemopsis alpina, Moehringia ciliata, Silene acaulis, Cerastium pedunculatum, Achillea moschata, Minuartia sedoides, Cerastium uniflorum, Saxifraga oppositifolia, Saxifraga exarata and Saxifraga bryoides, to the right).

**FIGURE 6.** Mean seed weight (mg, n = 50) of Eritrichium nanum in 13 plots of 1 m$^2$ in relation to altitude in the European Alps (data of 1990–2001; R$^2$ = 0.52, n = 13, P < 0.01).


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