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Effect of elevation on sexual reproduction in alpine populations of *Saxifraga oppositifolia* (Saxifragaceae)

Abstract Self-compatibility in high arctic and alpine areas is regarded as an adaptation to low pollinator abundance. However, high genetic variability as a consequence of outcrossing is, with regard to population persistence, favorable in highly stochastic environments such as tundra habitats. To evaluate these contradictory scenarios, I performed in situ pollination experiments to examine the breeding system of the predominant outcrosser *Saxifraga oppositifolia* in ten populations at two different elevations in the Swiss Alps. Pollinator limitation was detected at both elevations, but fruit set in naturally pollinated flowers was only slightly less at the higher elevation. Increased pollinator limitation at high compared with low elevation thus could not be demonstrated in this experiment. Hand-crossings yielded equal mean proportion seed set at both elevations, and so did hand-selfings. This constant pattern of the breeding system in *S. oppositifolia* indicates selective factors that lead to the maintenance of a high level of outcrossing even in high-elevation populations. Based on sex allocation models, it was expected that a high ovule number should be selectively advantageous in a plant-pollinator system where chance visitation or selfing play important roles. However, female reproductive offer in terms of ovule number per flower did not change from low to high elevation. Since neither increased pollinator limitation nor increased seed set in selfed flowers was found at high compared with low elevation, the prerequisites for testing the hypothesis were not given. This study contradicts the hypothesis that inimical environmental factors in alpine or arctic habitats necessarily select for increased selfing rates in a preferentially outcrossing species like *S. oppositifolia*.

Key words Alpine plants · Elevation · Breeding system · Reproduction · Self-pollination

Introduction

The general view about plant reproduction along the macrogradient from temperate to arctic regions predicts increasing self-compatibility, apomixis, polyploidy, and vegetative reproduction, all of which tend to promote the genetic uniformity of populations (Mosquin 1966). Corresponding changes are described for elevational gradients in alpine areas, though knowledge about the breeding systems is often derived from phenological rather than experimental observations (Schröter 1926; Bliss 1962). The same gradient is thought to be recognized both at the species and at the community level. Observations in *Polygonum viviparum* conform to this trend, as plants allocate more resources to vegetative bulbils relative to flowers with increasing latitude and elevation (Bauert 1993, 1994b). However, in a survey at high-arctic northeastern King Christian Island (Northwest Territories, Canada), only one-third of the species were found to be able to reproduce vegetatively, and only three species appeared reasonably successful in dispersing their vegetative organs (Bell and Bliss 1980). To my knowledge, no comparable data are available for alpine areas. In addition, arctic or alpine species usually reported to reproduce exclusively by vegetative means have been found to produce seeds (e.g., *Saxifraga cernua*, *S. foliolosa*, and *P. viviparum*; Molau 1992; Bauert 1993). Though seed set is rare in these species, it is sufficient to result in considerable genetic variability within some populations (Bauert 1994a; T.M. Gabrielsen and C. Brochmann, unpublished data). The same holds true for the rhizomatous *Carex curvula*. This species dominates alpine grasslands on silicate bedrock, but so far has never been observed to establish through seeds.

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Nevertheless, different clones could be delimited by means of RAPDs (Steinger et al. 1996). These investigations demonstrate that reproductive strategies such as vegetative spreading may also conserve extant genetic diversity.

At high elevations and latitudes, reduced pollinator abundance because of inimical abiotic conditions (e.g., low temperatures; Heinrich 1993), and decreased length of the growing season (Bliss 1971; Ellenberg 1988) are recognized as constraints which promote adaptations for self-pollination such as self-compatibility or homogamy (Müller 1881; Bliss 1962; Richards 1986). Such a strategy should ensure fast pollination in the little time available for seed development. Despite these expectations, *S. oppositifolia*, the most abundant species at the very northern limit of growth of higher plants, which also grows in the upper nival zone in the Alps (Jones and Richards 1956; Bay 1992; Kaplan 1995), is a protogynous, entomophilous, predominantly outcrossing, and diploid plant (Kevan 1972; Tikhmenev 1984; Stenström and Molau 1992). Furthermore, populations of sexually reproducing plant species in arctic and alpine areas, i.e., *S. oppositifolia*, *Silene acaulis*, or *Primula* spp., indeed display high genetic variability, indicating considerable outcrossing rates for these species (Miller et al. 1994; Abbott et al. 1995; Gabrielsen et al. 1997; own, unpublished data). These observations suggest that the various selective constraints may act antagonistically, and that the general predictions about plant reproduction in arctic and alpine environments need reconsideration.

Winn and Gross (1993) summarize results about the effect of elevation or latitude on seed mass or size. They point out that these variables react inconsistently to the environmental change along elevational or latitudinal gradients. Empirical investigations into the influence of increasing elevation or latitude on the breeding systems of plant species are very scarce. Cruden (1972) found that proportion seed set in naturally bee-pollinated Lamiaceae is lower in high-elevation than in mid-elevation populations in Mexico. Similarly, seed set in *Trifolium pallescens* and *T. thalii* decreases from low- to high-elevation populations in the Alps (Hilligardt 1993), but proportion seed set in the annual *Gentianella caucasea* does not differ among alpine to subnival populations in the Caucasus (Akhalkatsi and Wagner 1996). It is not known in these studies, however, whether seed set resulted from self or cross pollen. Experimental pollinations with *Pedicularis lapponica* indicate a change in the breeding system from low to high elevation in northernmost Sweden, with a higher seed set after hand-selfing at high than at low elevation when compared to seed set after hand-crossing (Eriksen et al. 1993). On the other hand, seed set in self-pollinated relative to cross-pollinated plants of *Espeletia schultzii* does not change along an extended elevational gradient in the Venezuelan mountains (Sobrevila 1989). Unfortunately, however, elevation as a treatment factor has not been replicated in these studies.

In each of five different regions in the central Alps of southeastern Switzerland, I examined the breeding system of *S. oppositifolia* at two elevations differing by 320–455 m. *Saxifraga oppositifolia* shows great morphological variation in relation to the wide range of different habitat types in arctic and alpine environments (Crawford et al. 1995; Kaplan 1995), which demonstrates its potential for local adaptation. It may therefore be expected that populations of *S. oppositifolia* are also able to adapt to selective pressure on its breeding system. *Saxifraga oppositifolia* depends on pollinator visits for seed set in the Arctic as well as in the Alps (Kevan 1972; Tikhmenev 1984; Stenström and Molau 1992; Gugerli 1997b). Reduced pollinator activity should accordingly lead to decreased reproductive output due to low fruit and seed set (see Anderson and Beare 1983).

I investigated the effect of elevation on the fruit set of naturally pollinated *S. oppositifolia*, testing the hypothesis that fruit set is lower in high- than in low-elevation populations. If pollinator activity is reduced at high elevations compared with low elevations, this constraint should select for higher self-compatibility. As a consequence, reduced inbreeding depression should be detectable. Current theory suggests that inbreeding depression in outcrossers is mainly expressed in early stages of the life cycle such as seed formation (Husband and Schemske 1996). I therefore wanted to know whether the seed set of self-pollinated compared with cross-pollinated flowers of *S. oppositifolia* increases from low- to high-elevation populations, which would eventually lead to a shift towards self-pollination in the breeding system of *S. oppositifolia*.

A higher number of ovules (= female reproductive offer; Urbanska 1989) relative to a fixed number of deposited pollen grains should enhance fertilization success, given that (1) seed set is independent of the degree of incompatibility, and (2) more ovules per flower increases the genetic diversity among ovules (due to meiotic recombination) and thus the coincidence of female and male gametes compatible for fertilization. An increased selfing rate also leads to a higher allocation to female relative to male function, whereas reduced pollen transfer probability, e.g., because of low pollinator activity, should counteract this trend (Brunet and Charlesworth 1995). In a comparison of two closely related species, Gugerli (1997b) shows that geitonogamous selfing seems to be more important in *Saxifraga biflora* than in *S. oppositifolia*. Concordantly, *S. biflora* has more ovules per fruit than does *S. oppositifolia*. Thus I hypothesized that ovule number per fruit is higher at high than at low elevation.

Materials and methods

Study species

The semi-evergreen, long-lived *S. oppositifolia* L. is widespread throughout its circumarctic-alpine distribution area (Hultén and Fries 1986; Kaplan 1995). The species even grows as far north as

vascular plants can be found (Cape Morris Jesup, Greenland; Bay 1992). The elevational range of *S. oppositifolia* in the Alps reaches from 580 to 3800 m above sea level (a.s.l.), but it is most abundant between 1800 and 2800 m a.s.l. (Kaplan 1995). In the investigated regions, the main elevational zone of *S. oppositifolia* extends over approximately 500 m. Populations of *S. oppositifolia* are found in almost any tundra habitat type, e.g., in crevices of rock walls, on scree slopes, or even in late-thawing snowbeds. This allows one to distinguish not only various subspecies (Webb and Gornall 1989), but also different ecotypes at a small spatial scale (Crawford and Abbott 1994; Crawford et al. 1995). The plants used for this study can all be recognized as the robust, semi-erect form of *S. oppositifolia* ssp. *oppositifolia*. The species is also ubiquitous with regard to acidity of the bedrock, though it is more abundant on calcareous substrates (Webb and Gornall 1989). Bumblebees are the main pollinators of *S. oppositifolia* (Stenström 1995; own, personal observation), but dipteran and lepidopteran species are also among the potential pollinators (Müller 1881; Schröter 1926; Stenström 1995; own, personal observation). Because most populations of *S. oppositifolia* flower very early in the season, pollinator limitation is often pronounced (Stenström 1995; Gugerli 1997b).

Study sites

All sites were located in the Canton of Grisons, eastern Switzerland (Fig. 1, Table 1). In each of the five regions I selected one population at each of two elevational levels: (1) at approximately 2500 m a.s.l. and (2) at approximately 3000 m a.s.l. (Table 1). These represented the lower and higher zones, respectively, where *S. oppositifolia* grows in abundance in these areas. The low sites belonged to the alpine zone, the high sites to the subnival zone. The habitat

Fig. 1 Locations of the study sites in the Canton of Grisons, eastern Switzerland

types of the selected locations resembled each other to minimize uncontrolled environmental variations that could obscure the effect of the experimental treatments. Though a greater elevational difference would be desirable, small population sizes at the border of the distribution zone would have genetic effects beyond those that were intended to be detected with the experiment.

Experiments

The design included two elevational treatments in each of five regions (see study sites) and three pollination treatments: (1) natural pollination (= control), (2) hand-crossing (= artificial xenogamy), and (3) hand-selfing (= artificial geitonogamy). In each population I selected ten genets by throwing a marker and choosing the first plant in the direction of the marker tip. Only genets with sufficient numbers of unpollinated flowers and at least some flowers with open anthers for self-pollinations could be included. To avoid maternal effects, I randomly assigned four flowers to each of the three pollination treatments within a genet. I tied threads of different colors for each treatment around the flower pedicels, which allowed me to identify the fruits at the time of collection. This resulted in a total of 1200 treated flowers on 100 plants.

Pollinations took place between 4 and 17 June 1996. Populations belonging to the same regions were always visited on consecutive days to minimize the effect of pollination time on the results. For hand-crossings I applied pollen from freshly collected stamens. Selfed flowers received pollen from within the same genet (geitonogamous selfing), but not from the same flower, because flowers are protogynous, and stigmatic receptivity declines at the beginning of the male phase (Stenström and Molau 1992; Gugerli 1997b). The stigmas of all treated flowers were fully covered with pollen. Untreated control flowers served to estimate the frequency of natural pollination. Stigmas of all selected flowers were checked prior to treatment to ensure that no pollen had been deposited beforehand. The bright orange pollen can be seen easily with a hand lens. All plants remained unbagged to avoid microclimatic impacts on fruit development (Gross and Werner 1983; Young and Young 1992). This method does not absolutely exclude the possibility that hand-selfed flowers received naturally applied outcross pollen after treatment. Self pollen already covering the entire stigmatic surface, however, should prevent germination of pollen arriving later on hand-pollinated flowers. The ripe fruits were collected in Eppendorf tubes and stored dry at room temperature before the seeds and ovules were counted under a stereo lens.

Statistical analysis

To test the effect of elevation and pollination treatment on proportion fruit set per plant (ratio of fruits/flowers per plant = Fr/Fl) and on mean proportion seed set of the developed fruits (ratio of seeds/ovules, means of four fruits per plant = mean S/O) I applied a hierarchic two-way ANOVA (split-plot design). The error model consisted of the five regions as main blocks, locations as
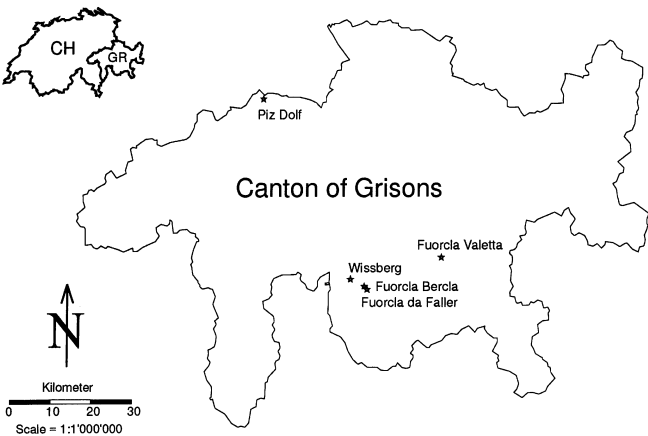
Table 1 Site description parameters for locations included in the experiment on the effect of elevation on the breeding system of *Saxifraga oppositifolia*

Location	Elevational level	Elevation (m above sea level)	Aspect	Coordinates (Swiss grid)
Fuorcla da Faller	Low	2520	NE	764′400/149′200
	High	2900	E	765′000/147′975
Fuorcla Bercla	Low	2480	W	764′950/149′600
	High	2920	W	763′100/149′100
Wissberg	Low	2550	ENE	760′800/151′450
	High	2970	ENE	760′450/150′875
Piz Dolf	Low	2565	W	738′800/194′750
	High	3020	E	739′275/196′350
Fuorcla Valetta	Low	2540	–	783′800/156′800
	High	2860	NE	782′300/156′325

plots within regions, genets as subplots within locations, and the four flowers per pollination treatment as sub-subplots within genets; the treatment model consisted of the factors elevation and pollination (Payne et al. 1993). These treatment factors were tested at the location level and the pollination-subplot level within genets, respectively. I could not take single fruits as experimental units because too many flowers did not develop into fruits or were lost to herbivore activity. Comparisons among pollination treatments were tested with linear contrasts. For between-elevation comparisons within single pollination treatments I used means and standard errors of difference of means from the ANOVA for t-tests (Payne et al. 1993). Data were angle-transformed so that the visual inspection of residual distributions indicated no violation of assumptions for ANOVA. The same split-plot ANOVA was applied to mean ovule number per fruit (including ovule numbers from undeveloped fruits; log-transformed means of four flowers per plant). The variation among regions (R stratum) turned out to be negligible in the analyses, whereas among-plant variation (R × L × G stratum) was high (own unpublished data; for abbreviations see Table 3). I consequently included the block effect of regions within the level of locations, but separately fitted the block effect of plants in all analyses. The split-plot design applied in this experiment should minimize maternal influence on the effect of pollen source (Travis 1992). Data analyses were performed using the ANOVA procedure of Genstat 5 (Payne et al. 1993).

Results

Mean ovule number per fruit increased by 10% from low to high elevations (overall means of three treatment means; Table 2), but the difference was not significant (Fig. 2a; elevation: $P > 0.3$, Table 3). Mean ovule number per fruit did not vary among the three pollination treatments (Fig. 2a; pollination treatment: $P > 0.9$, Table 3).

Proportion fruit set per plant of naturally pollinated plants at the higher locations was reduced by 15% compared with the lower locations (Table 2). With large variation, however, no significant difference was detected between the two elevations (Fig. 2b; $df = 8$, $t = 0.943$, $P > 0.05$). Artificial xenogamy resulted in a significantly higher proportion fruit set than did natural pollination (Table 2; Fig. 2b; control vs. artifical xenogamy: $P < 0.01$, Table 3), but this difference was independent of the elevational level [elevation × (control vs. artifical xenogamy): $P > 0.05$, Table 3].

Mean proportion seed set per fruit was highest in fruits of xenogamous hand-pollination (Table 2, Fig. 2c). The overall mean decreased by 66% in fruits of
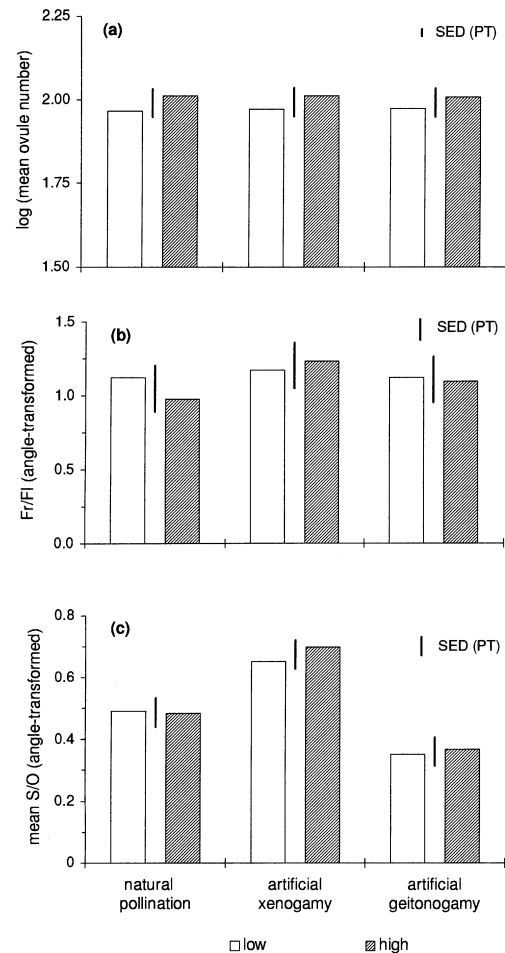
Fig. 2 Effect of elevation and pollination treatment on mean ovule number per fruit (**a**), proportion fruit set per plant (*Fr/Fl*) (**b**), and mean proportion seed set per fruit (mean *S/O*) (**c**) of *Saxifraga oppositifolia* in the Swiss Alps. *Vertical lines between bars* represent standard errors of difference of means between elevational levels within the same pollination treatment; *SED (PT)* represents standard errors of difference of means among levels of pollination treatments. Means and standard errors of difference of means were derived from ANOVA; note that transformed values are presented

Table 2 Mean ovule number per fruit, proportion fruit set per plant, and mean proportion seed set per fruit from different pollination treatments in low- and high-elevation populations of *S. oppositifolia*. Means ($\bar{x}$), minimum (*Min*), maximum (*Max*), and sample number (*n*) are presented from pooled raw data

Elevation		Mean ovule number		Proportion fruit set		Mean proportion seed set	
		Low	High	Low	High	Low	High
Natural pollination	$\bar{x}$	95.9	106.8	0.73	0.62	0.23	0.22
	Min	55.0	49.3	0.00	0.00	0.01	0.01
	Max	185.5	174.3	1.00	1.00	0.74	0.55
	n	44	48	49	49	45	43
Artificial xenogamy	$\bar{x}$	97.2	106.2	0.76	0.80	0.37	0.40
	Min	55.0	59.0	0.00	0.00	0.04	0.09
	Max	175.5	166.0	1.00	1.00	0.87	0.83
	n	46	49	48	50	43	47
Artificial geitonogamy	$\bar{x}$	96.6	106.4	0.71	0.70	0.12	0.14
	Min	61.3	36.0	0.00	0.00	0.01	0.01
	Max	160.0	189.7	1.00	1.00	0.55	0.56
	n	46	48	48	48	44	46

Table 3 ANOVA table (split-plot, including contrasts) of effect of elevation and pollination treatment on mean ovule number per fruit (log-transformed), proportion fruit set per plant (angle-transformed), and mean proportion seed set per fruit (angle-transformed) in alpine populations of *S. oppositifolia*. Blocking factors: *R* region, *L* location, *G* genet, *P* pollination-subplot within genet; treatment factors: elevation, pollination treatment; *df* degrees of freedom, *SS* sum of squares, *F* variance ratio. Total *df* are less than 299 because of missing values

Source of variation	Mean ovule number			Proportion fruit set			Mean proportion seed set		
	df	SS	*F*	*df*	SS	*F*	*df*	SS	*F*
R × L stratum									
Elevation	1	0.115	0.87 n.s.	1	0.173	0.10 n.s.	1	0.020	0.13 n.s.
Residual	8	1.058	5.00	8	14.394	4.64	8	1.292	2.38
R × L × G stratum									
Residual	89	2.355	9.10	89	34.500	2.94	87	5.899	3.08
R × L × G × P stratum									
Pollination treatment	2	0.000	0.08 n.s.	2	1.369	5.19**	2	5.065	114.86***
Control vs. xenogamy				1	1.315	9.97**	1	1.758	79.74***
Xenogamy vs. geitonogamy				1	0.054	0.41 n.s.	1	3.307	149.98***
Elevation × pollination treatment	2	0.003	0.58 n.s.	2	0.507	1.92 n.s.	2	0.070	1.59 n.s.
Elevation × (control vs. xenogamy)				1	0.505	3.83 n.s.	1	0.068	3.10 n.s.
Elevation × (xenogamy vs. geitonogamy)				1	0.002	0.01 n.s.	1	0.002	0.09 n.s.
Residual	178	0.517		189	24.933		167	3.682	
Total	280	3.892		291	74.045		267	14.631	

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; *n.s.* not significant

geitonogamous compared with xenogamous hand-pollinations (Table 2, Fig. 2c; artifical xenogamy vs. artifical geitonogamy: $P < 0.001$, Table 3). Comparisons within pollination treatments showed that mean proportion seed set did not significantly differ between high and low elevations either from geitonogamous hand-pollinations (increase by 11%; Table 2, Fig. 2c; $df = 8$, $t = 0.51$, $P > 0.05$) or from xenogamous hand-pollinations (increase by 11%; Table 2, Fig. 2c; $df = 8$, $t = 1.07$, $P > 0.05$). The differences between mean proportion seed set of the two hand-pollination treatments were thus consistent among elevations [elevation × (artifical xenogamy vs. artifical geitonogamy): $P > 0.7$, Table 3]. Naturally pollinated fruits also yielded a lower mean proportion seed set than did hand-crossed fruits (Table 2, Fig. 2c; control vs. artifical xenogamy: $P < 0.001$, Table 3), but this was still a significantly higher yield than from hand-selfed fruits (Table 2; Fig. 2c; $df = 167$, $t = 6.14$, $P < 0.001$). The elevation did not affect mean proportion seed set in these naturally pollinated flowers (Table 2, Fig. 2c; $df = 8$, $t = 0.52$, $P > 0.05$).

Discussion

The breeding system in *S. oppositifolia* remains constant within its main elevational distribution zone in the investigated area. This finding contradicts the general hypothesis that adverse abiotic environments select for reproductive modes which are independent of pollinator activity (Richards 1986). The preference of *S. oppositifolia* for cross-pollination (Fig. 2c) confirms previous pollination experiments which have been carried out in different arctic and alpine locations (Kevan 1972;

Tikhmenev 1984; Stenström and Molau 1992; Gugerli 1997b). The mean proportion seed set from hand-crossings and hand-selfings remained equal at low and high elevations (Fig. 2c). The non-significant interaction of elevation and hand-pollination treatments (Table 3) demonstrates that the relative difference between these two pollination treatments did not change from low- to high-elevation populations. The few experimental studies that have been carried out so far to test this hypothesis show increased seed set from selfing at high elevations (Eriksen et al. 1993) or no effect at all (Sobrevila 1989). Since the elevational treatment lacked replication in these previous investigations, any detected differences may not be attributable to the effect of elevation (see below). Descriptive studies about natural seed set in plants at different elevations, such as those of Cruden (1972), Hilligardt (1993), or Akhalkatsi and Wagner (1996), have also yielded inconsistent results. Generalizations may thus be misleading, since the same selective constraints may lead to species-specific adaptations.

Proportion fruit set in naturally pollinated plants of *S. oppositifolia*, used as an indicator of pollinator abundance and activity, was slightly reduced in high compared with low elevations (Table 3). Extremely warm temperatures during the flowering period of *S. oppositifolia* in the investigated populations in 1996 (Gugerli 1997a) may have provided exceptional conditions for insect pollinator activity, thus obscuring the trend of a lower fruit set with increasing elevation. Resource limitations, shifts in allocation patterns, or genetically based variation, on the other hand, may further influence fruit set and thus overlie effects due to pollen limitation. Investigating populations at even higher elevations might also lead to a more pronounced

elevational effect on proportion fruit set of naturally pollinated plants than was found in this study. Because of difficult accessibility and small sizes, such populations could not be included in this experiment.

The reduced proportion fruit set and mean proportion seed set in natural pollinations compared with hand-crossings (Fig. 2b, c, Table 3) indicates pollinator limitation independent of the elevation. Synchronous flowering within a genet, protogyny, rapid decline of stigmatic receptivity at the beginning of the male phase, and a low pollen autodeposition rate (in unmanipulated, bagged plants) lead to the conclusion that entomophilous *S. oppositifolia* depends on pollinators for seed set throughout its vast distribution area (Kevan 1972; Tikhmenev 1984; Stenström and Molau 1992; Stenström 1995; Gugerli 1997b). Relative reproductive success (proportion fruit set × proportion seed set; Wiens 1984) of naturally pollinated *S. oppositifolia* is very low compared with other tundra plants (Molau 1993) because of limited pollinator availability early in the growing season (Stenström 1995; Gugerli 1997b). Nevertheless, *S. oppositifolia* remains predominantly outcrossing even at the upper elevational limit of its main distribution area.

Local environmental conditions can obscure the effects of clinal variation on the observed traits in experiments along a gradient (Winn and Gross 1993). A major weakness of both the experimental and descriptive studies about elevational or latitudinal effects on reproduction is that this treatment factor is usually not replicated. Researchers are thus tempted to analyze their data without considering possible pseudoreplication (Hurlbert 1984). In 1995 I performed a preliminary experiment to determine variation at the different levels of the experiment. This experimental design included only two regions (Bercla, Faller), eight genets per population, and two pollination treatments per genet (xenogamous/geitonogamous). *Saxifraga oppositifolia* showed a slightly divergent reaction to elevation and hand-pollinations in the two replicates of elevation as a treatment factor (own, unpublished data). This prompted an extended experimental setup with respect to the number of regions included. The results of the present experiment were still not totally consistent among the five investigated regions, but the *F*-value for the R stratum was very low so that it was not necessary to separately fit this blocking effect.

There was only a trend to a higher mean ovule number per fruit at high compared with low elevation (Fig. 2a, Table 3). Since seed set after selfing and pollen availability did not differ among populations at low and high elevation, the hypothesis of increased allocation to female function due to increased selfing and pollinator activity could not be tested. The mean number of ovules per fruit was equal among pollination treatments (Fig. 2a), since all three types of pollinations were performed on each genet. Among-genet variation, however, was high, as seen from the high *F*-value of the R × L × G stratum (Table 3). The two results imply genetic or microenvironmental influences on ovule number per fruit. They also demonstrate the importance of conducting the three pollination treatments within each genet (Travis 1992).

Over generations, selfing may reduce the inbreeding depression because deleterious alleles should be purged (Husband and Schemske 1996). Ramsey and Vaughton (1996) also argue that pollination limitation raises the threshold of inbreeding depression below which self-fertility evolves. From the point of view of population genetics, however, it is evident that theoretically genetic variability is important for population persistence in a highly stochastic environment (Lande and Shannon 1996). Strict selfing would eventually lead to complete homozygosity (Richards 1986; Maynard Smith 1989). High genetic variability because of predominant outcrossing can thus be regarded as preadaptation to high stochasticity of environmental factors in tundra habitats over a large time scale (Crawford and Abbott 1994). Equal seed set of naturally pollinated fruits of *S. oppositifolia* at the two elevations in this study may be seen as an equilibrium between these opposing selective constraints, as there is a '... general balance between heterotic selection favoring outcross progeny and the transmission bias of selfing genes' (Clegg 1980, p. 818).

Homozygous genotypes are thought to be more susceptible to the adversity of a harsh environment as found in high alpine or arctic areas, whereas heterozygote advantage should be a better buffer against variability within the habitat (Dudash 1990). In addition, longevity of individual plants is favorable for population persistence. This not only enhances the chances that a single plant eventually sets seed, but also increases genetic diversity within a population as several different generations are found at the same time. It seems that the reproductive strategy of *S. oppositifolia,* which retains a high option for fertilization by cross pollen, is very successful in terms of survival at the limit of plant existence in tundra habitats.

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