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Sexual reproduction of the high mountain plant *Saxifraga moschata* Wulfen at varying lengths of the growing season

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Abstract

Flowering phenology, dynamics of seed development and reproductive success of *Saxifraga moschata* Wulfen, occurring from the alpine to the nival zone, was investigated in three climatically varying years on early- and late-thawing sites at 2340 m a.s.l. in the Austrian Alps. The growing season was particularly short in 2001, about normal in 2002 and exceptionally long and warm in 2003. *S. moschata* is a mid-season flowering species, which started to bloom about 1 month after snowmelt. From onset of anthesis until seed maturity an individual flower required 6–7 weeks, and all individuals of a site 9–11 weeks. In 2001, late flowering individuals lost about 40% of the seed crop because of too early snowfalls in autumn. No clear relationship could be found between thermal time and the length of different reproductive phases, which indicates that temperature was not a limiting factor for reproductive development in the growing seasons 2001–2003.

Plants from the earliest-thawing site produced about double the reproductive structures (reproductive shoots per individual, number of flowers per inflorescence, number of ovules per ovary), and had a significantly higher reproductive output (number of fruits and mature seeds per inflorescence) compared with individuals from the late-thawing site. Reproductive success was additionally affected by the seasonal climate and was lowest in the warm and dry summer of 2003. Fruit/flower ratio ranged between 0.6 and 0.8, seed/ovule ratio between 0.4 and 0.5 and relative reproductive success (RRS) between 0.3 and 0.4, depending on the site and year.

Different from our expectations, it took *S. moschata* relatively long to undergo reproductive development; however, its phenological plasticity and ability to continue seed maturation even under snow are most advantageous for a life at higher altitudes.

Keywords: *Saxifraga moschata*; Alpine plant; Flowering phenology; Reproductive success; Seed development

Introduction

The length of the growing season is the most important factor limiting plant life in high alpine and arctic habitats (Billings and Bliss, 1959; Kudo, 1991, 1992; Molau, 1996a). Depending on relief and snow accumulation in winter, plants in the mountains of the temperate zone have 3–5 months in the alpine belt and 1–3 months in the nival belt for growth and reproduction (Larcher, 1980). Mountain plant species have evolved various strategies to adjust their life cycle to a short growing season in a cold climate. To ensure reproduction by seeds, most species carry out flower

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preformation, which enables them to start flowering soon after snowmelt in spring (Billings and Mooney, 1968; Diggle, 1997; Sørensen, 1941). Extended anthesis of individual flowers compensates for lower pollinator frequency (Bingham and Orthner, 1998; Fabbro and Körner, 2004; Primack, 1985). Depending on the species and climatic conditions, the period for seed development ranges between 22 and 70 days (Billings and Bliss, 1959; Kudo, 1991; Stenström and Molau, 1992; Wagner and Reichegger, 1997), with late flowering *Gentianella* species showing a particularly short reproductive period (Akhalkatsi and Wagner, 1996; Wagner and Mitterhofer, 1998).

In spite of various adaptations to a short period of active growth, only a few species cope with the demands at the limits of higher plant life. In the European Alps, species richness drastically decreases from about 200 species at 3000 m a.s.l. to about 20 species at 4000 m (Grabherr et al., 1995). The long-living cushion plant *Saxifraga moschata* is one of the few species reaching the upper limits of distribution for flowering plants. It has been reported to occur even at 4200 m a.s.l. in the Swiss Alps (Heer, 1885) and at 3900 m a.s.l. in the Caucasus (Nakhutsrishvili, 2003; Nakhutsrishvili and Gagnidze, 1999). The lower limit of its distribution is at about 1600 m a.s.l. (Landolt, 1992).

Because of this wide range of vertical distribution, we expected *S. moschata* to be highly plastic in its reproductive development and that seeds could be produced within a short period of time. The aim of the present study therefore was to characterize the reproductive performance of this species under different climatic site conditions. We investigated flowering phenology, dynamics of seed development, and reproductive success on early snow-free sites and in a north-exposed hollow with deep winter snow accumulation and late thawing-dates. The main questions addressed were: (1) are there species-specific strategies of reproductive development which enable *S. moschata* to advance to the highest altitudes reached by plant life? and (2) what impact would climate change have on the reproductive output of this species?

Materials and methods

Study species

S. moschata Wulfen inhabits most European mountain systems (Pyrenees, Alps, Carpathians, Apennines, Balkan mountains), the Caucasus, and the Altai mountains (Kaplan, 1995). This pioneer species prefers base-rich substrates and grows on stable and unstable scree and in rocky swards from the subalpine to the nival zone.

Study sites

The investigations were carried out in the northern calcareous mountain range of the Tyrolean Alps during the growing seasons of 2001–2003. The study area was located on the northern side of Mt Hafelekar (2334 m a.s.l., 47°42′N, 11°29′E), at the upper margin of a scree. The area is highly structured; differences in declination and exposure lead to variable snow accumulation in winter. Three microsites were selected:

Early-thawing site (E-site): East to south facing slope with 35° inclination, becoming free of snow early in May. *S. moschata* cushions are distributed among unstable calcareous scree. On this site only reproductive success was determined, because a steep snowfield prevented access earlier in the season.

Mid-thawing site (M-site): Flat area of about 20 m^2 above E-site. The surface is covered with stable scree. On this site, snowmelt starts about 2–3 weeks later than on the E-site.

Late-thawing site (L-site): This is a nearly flat, north-facing hollow of about 15 m^2 with 10° inclination. Due to snow drifts, a huge winter snow-pack accumulates which melts up to 4 weeks later than on the M-site. *S. moschata* cushions are distributed among rocky outcrops.

S. moschata individuals showed a marked morphological variability on the different sites. E-site plants developed long leaves, forming large open rosettes of 10.7 ± 3.2 mm diameter. Flowering stems grew up to 12 cm in height and bore 1–7 flowers. On the L-site, most cushions consisted of small, compact rosettes of 7.4 ± 3.0 mm diameter. Flowering stems remained short and mostly developed only 1–2 small flowers. M-site plants were intermediates with a mean rosette diameter of 8.7 ± 1.9 mm and 1–5 flowers per inflorescence. The differences in rosette diameter and number of flowers are statistically significant (one-way ANOVA, $p < 0.004$, $n = 100$ rosettes and inflorescences per site).

Climate measurements

Plant temperatures were recorded continuously on M-site and L-site throughout the whole investigation period 2001–2003, using small data loggers (TIDBIT, Onset, Bourne, MA, USA). Loggers were installed among rosettes so that the sensors were shaded by leaves. Thermal time, i.e. cumulative degree-days, was calculated by summing up the daily mean air temperature above the temperature threshold of 0 °C (Cannell and Smith, 1983), both for the whole growing season and for distinct reproductive phases. Macroclimate databases were available from standard weather stations at the same elevation a few kilometers away.