



Flower longevity and duration of pistil receptivity in high mountain plants

Gerlinde Steinacher, Johanna Wagner*

Institute of Botany, Faculty of Biology, University of Innsbruck, Sternwartestraße 15, A 6020 Innsbruck, Austria

ARTICLE INFO

Article history:
Received 21 March 2009
Accepted 11 June 2009

Keywords:
Alpine plants
Floral longevity
Floral plasticity
Pollen germination
Reproductive success
Stigmatic receptivity

ABSTRACT

Flowers of high mountain plants are generally long-lived to compensate for the low frequency of pollinator visits at higher altitudes. However, nothing is known about floral plasticity when pollinators are absent because of unsuitable weather conditions. We investigated both, actual longevity of naturally pollinated flowers and potential flower longevity, the capacity to prolong corolla life-time and pistil receptivity when pollination is retarded. Seven high mountain plant species from different elevations in the European Alps were tested: *Gentianella germanica*, *Ranunculus alpestris* and *Saxifraga caesia* are restricted to the alpine zone, *Cerastium uniflorum*, *Ranunculus glacialis*, *Saxifraga bryoides* and *Saxifraga moschata* occur from the higher alpine to the glacier zone.

Flower longevity differed greatly among species, according to their taxonomic background and their gender sequence type. Actual flower longevity ranged from a few days (*G. germanica*, *C. uniflorum*, *R. alpestris*) to more than two weeks (*saxifrages*, *R. glacialis*). Unpollinated flowers generally increased longevity, but the plasticity of single floral functions was quite different. Stigma receptivity could be maintained longest. Pollen adhesion was enabled during the full stigma life-time. High levels of pollen germination and pollen tube growth were still possible 29 days after anthesis (DAA) in *R. glacialis*, and 23 DAA in *S. bryoides*. In the remaining species this ability was gradually lost or, in *C. uniflorum*, abruptly ended around 10 DAA. The overall pistil receptivity primarily depended on the duration of ovule receptivity, which in most species ended between 16 and 20 DAA. Corolla life-time was significantly prolonged in *S. bryoides*, *S. moschata* and *G. germanica*. In the remainder of species mean corolla longevity did not differ from the actual longevity, and thus any prolongation of female functions over the corolla life-time would not contribute to reproductive success. The maximal potential longevity of individual flowers with fresh corolla and receptive pistils were 21 d in *S. moschata* followed by *S. caesia* (19 d), *S. bryoides*, *R. glacialis* (18 d) and *G. germanica* (14 d). *R. alpestris* (8 d) and *C. uniflorum* (8 d) exhibited the shortest potential overall flower longevity. Contrary to our expectations, flower longevity did not significantly differ between the alpine and the high-elevation species.

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Introduction

Flower longevity, the period during which a flower is fully open and functional, varies greatly among the different plant species ranging from a few hours to weeks or even months (Primack, 1985; van Doorn, 1997). The length of time a flower is functional may be an important determinant of male and female reproductive success (e.g. Evanhoe and Galloway, 2002; Itagaki and Sakai, 2006; Makrodimos et al., 2008; Rathcke, 2003). In insect pollinated flowers, the probability of efficient pollinator visits increases with longevity, as this increases the amount of own pollen exported and foreign pollen imported (Ashman and Schoen, 1994). However, maintaining a flower involves costs such as nectar production (Harder and Barrett, 1995), transpirational water loss mainly through the perianth (Galen et al., 1999; Galen,

2000), and metabolic costs (respiration of reproductive tissues; Ashman and Schoen, 1994). This has led to the assumption that flower longevity is a compromise between the benefit of successful pollen dispersal and receipt, and the costs of flower maintenance (Ashman and Schoen, 1994, 1996; Primack, 1985; Webb and Littleton, 1987). It is further assumed that floral longevity is heritable and can be optimized by natural selection in response to the pollination environment (Ashman and Schoen, 1994). This means that in environments with abundant, predictable pollinators plants would show shorter floral durations than in environments where pollinator activity is low.

Alpine habitats are among those habitats where, due to a harsh and stochastic climate, pollinators are sparse or uncertain (Arroyo et al., 1985; Muñoz and Arroyo, 2006 and citations therein; Primack, 1978). Nevertheless, insect pollination is far more important than wind pollination in alpine ecosystems (Arroyo et al., 1982; Bingham and Ranker, 2000; Müller, 1881; Totland, 1993). Several studies have shown that flower longevity generally increases with altitude (Arroyo et al., 1981; Bingham and Orthner, 1998; Blionis and Vokou,

* Corresponding author. Tel.: +43 512 507 5932; fax: +43 512 507 2715.
E-mail address: Johanna.Wagner@uibk.ac.at (J. Wagner).

2002; Primack, 1978), which, according to Ashman and Schoen (1994), may reflect an adaptation to low pollinator visitation rates but may additionally be the result of a slower development because of cooler temperatures (Primack, 1985).

Within a plant, flower longevity is not a fixed trait but plastic and may be extended or shortened in response to short-term environmental variations (Arathi et al., 2002; Clark and Husband, 2007; Evanhoe and Galloway, 2002; Lundemo and Totland, 2007), temperature and pollinator activity being the most important factors. Cool temperatures increase the longevity of a flower because progamic flower development (e.g. anther dehiscence, style elongation, stigma expansion) slows down (Ladinig and Wagner, 2005, 2007). In contrast, higher temperatures mostly shorten flower development (Evanhoe and Galloway, 2002 and citations therein). Temperature may also affect pollination. Low temperatures cause low pollinator activity which retards pollen removal from stamens and pollen deposition on the stigma (Arroyo et al., 1985; Itagaki and Sakai, 2006; Primack, 1985; Robertson and Lloyd, 1993) whereas warmer weather may allow more reliable levels of pollinator visitation (Primack, 1985).

So far, data in the literature on flower longevity in mountain plants concern the actual longevity under given weather and pollination conditions during the observation period. However, the extent to which the duration of a flower may be prolonged when pollinators are rare or absent – this is a situation which might be expected when many days are unsuitable for flower visits – is not known. In our study we therefore investigated both the actual flower longevity of naturally insect pollinated flowers and the potential flower longevity, i.e. the capacity to increase corolla longevity and pistil receptivity when pollination is retarded. A detailed analysis of pistil receptivity (stigma, style and ovule receptivity) should reveal how long the different female functions can be maintained and whether the visual appearance of a flower (freshness of corolla and stigma) indicates its functionality. Seven abundant plant species with different altitudinal distributions in the European Alps were studied. Three species are mainly restricted to the alpine zone (*Gentianella germanica* (Willd.) Börner, *Ranunculus alpestris* L., *Saxifraga caesia* L.), the latter four species (*Cerastium uniflorum* Clairv., *Ranunculus glacialis* L., *Saxifraga bryoides* L., *Saxifraga moschata* Wulfen) occur from the higher alpine to the nival zone (i.e. the glacier zone) where they colonize ice-free areas.

We addressed the following questions. (1) What is the actual longevity of naturally pollinated flowers, and to what extent can corolla longevity and length of female functions be increased

(potential flower longevity) to ensure maternal fitness – i.e., when can the latest pollen deposition occur so that seeds will still be formed? (2) Are there differences in the longevity of corolla and pistil functions? Which is the limiting function? (3) How is capacity to prolong flower functions affected by altitudinal distribution of a species? Do nival species tend to maintain flower functions longer than their alpine counterparts when pollinators are absent? We examined the corolla life-span and the changes in pistil receptivity and female reproductive capacity with floral age and explored the differences among species.

Materials and methods

Study species and experimental sites

Study species and characteristics are summarized in Table 1. The investigations at alpine sites took place in 2005 in the northern calcareous mountain range on Mt Hafelekar (2334 m a.s.l., 47°42'N, 11°23'E) and in the Tyrolean Central Alps on Mt Patscherkofel (2250 m a.s.l., 47°12'N, 11°27'E), near Innsbruck. The study area on Mt Hafelekar is highly structured with varying declination and exposure. *R. alpestris* was growing on a north facing slope in alpine turf. The studied individuals of *Saxifraga caesia* and *Saxifraga moschata* were distributed among unstable, calcareous scree with patchy vegetation. Microsite aspects varied between N, NW and S. Experiments on *G. germanica* were carried out on Mt Patscherkofel in a W-facing alpine pasture (Poion alpinae). Investigations at subnival sites were carried out in 2007 in the forelands of two northeast facing glaciers in the Tyrolean Central Alps: the Hintertux Glacier (2650 m a.s.l., 47°04'N, 11°39'E, Zillertal Alps) and the Stubai Glacier (2880 m a.s.l., 46°59'N, 11°07'E, Stubai Alps). Study sites were established about 100–200 m below the rims of the glaciers in unstable scree on a rocky slope (*R. glacialis*) and on flat, rocky plateaus (*S. bryoides*, *C. uniflorum*).

At each site, plant temperatures were recorded during the investigation periods with small temperature loggers (Tidbit, Onset, USA) which were mounted 1–2 cm above the ground in plant cushions. Sensors were shaded with white plastic grids to avoid radiation errors. Additionally, flower temperatures were measured using data loggers (EasyLog, Lascar Electronics, UK) with thermocouples which were mounted inside the flowers.

Table 1
Characteristics of study species.

Species	Geographical distribution	Mountain belt	Study site	Flowering time	Gender sequence	Flower size (diameter in mm ± SD, n=30)
<i>Cerastium uniflorum</i>	European Alps	Subnival–nival	StG	mid-late	Protandrous	17.0 ± 2.1
<i>Gentianella germanica</i> (alpine ecotype)	Alpine grasslands in Western and Central Europe	Subalpine–alpine	PK	late	Adichogamous	19.2 ± 2.9
<i>Ranunculus alpestris</i>	European Mountains	Alpine	HK	early-mid	Adichogamous	14.0 ± 1.8
<i>Ranunculus glacialis</i>	Arctic-alpine, European Mountains	Subnival–nival	StG, HTxG	early-mid	Adichogamous	22.9 ± 3.3
<i>Saxifraga bryoides</i>	European Mountains	Subnival–nival	StG, HTxG	mid-late	Protandrous	12.6 ± 1.5
<i>Saxifraga caesia</i>	European Mountains	Alpine	HK	mid-late	Protandrous	9.8 ± 1.4
<i>Saxifraga moschata</i>	Eurasian Mountains	Alpine–nival	HK	mid	Protandrous	7.8 ± 0.8

Notes: *R. glacialis*, *S. bryoides* and *S. moschata* reach altitudes above 4000 m a.s.l. in the European Alps (Zimmermann, 1975; Kaplan, 1995).

Mountain belt: subnival=alpine–nival ecotone, nival=glacier zone.

Study site: HK=Mt Hafelekar, PK=Mt Patscherkofel, HTxG=Hintertux Glacier, StG=Stubai Glacier.

Flowering time: early=May–June; mid=June–July, late=August and later.

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