

Population dynamics of a long-lived alpine plant with sexual and clonal reproduction

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Table of contents

Table of contents	3
Chapter 1	
General introduction.....	5
Chapter 2	
The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant <i>Geum reptans</i>	17
Chapter 3	
Variation of sexual and clonal reproduction in the alpine <i>Geum reptans</i> in contrasting altitudes and successional stages.....	37
Chapter 4	
Does pre-dispersal seed predation limit reproduction and population growth in the alpine clonal plant <i>Geum reptans</i> ?	55
Chapter 5	
General summary	71
Acknowledgements	81
Curriculum vitae	83

Chapter 1

General introduction

The aim of this thesis

This thesis focuses on the demography, reproduction, and pre-dispersal seed predation of the clonal plant *Geum reptans*, an alpine pioneer species of glacier forelands. *G. reptans* regularly reproduces by flower heads and above-ground stolons both developing from the same axial meristems. This species is very well suited for studying the impact of environmental gradients on reproduction since it occurs in usually high abundance over a broad altitudinal gradient of 1950–3800 m a.s.l. (Weber 1995). Furthermore, *G. reptans* belongs to the first invaders after glacier retreat (Braun-Blanquet 1948) and shows long successional persistence (Lüdi 1921). Additionally, many populations of this species suffer from heavy infestation by a host-specific seed predator.

I addressed the following main questions:

- (1) How are population dynamics of an alpine plant determined by life-cycle stages and reproductive transitions? In particular, what is the relative importance of sexual and clonal reproduction for population growth? (Chapter 2)
- (2) Does the relationship between sexual and clonal reproduction in an alpine plant vary in contrasting habitats that differ in altitudinal position and successional age? (Chapter 3)
- (3) Does pre-dispersal seed predation limit reproduction and population growth of an alpine clonal plant? (Chapter 4)

Plant life in alpine environments

Alpine environments with their strikingly steep gradients of altitude and climatic conditions shaping the environment and constraining plant life provide various opportunities to study the ecology of alpine plants in natural experiments (Körner 2003). Within a distance of a few meters, small-scale differences in relief affecting solar radiation, wind, and snow cover may create distinct microclimates resulting in considerable heterogeneity of sites. Alpine plants are usually subject to short and cold growing seasons, desiccating winds, and high solar radiation which may restrict growth and reproduction and determine species' life-history and spatial distribution. Nevertheless, the biological richness of mountain areas (Klötzli 1997) and the high amount of endemic species occurring in alpine habitats (Bliss 1971 and references therein) impressively demonstrate that alpine plants may be very well adapted to these apparently harsh environmental conditions.

The uniqueness of alpine plants lies in their ability to persist successfully at considerably low temperatures enabling them to metabolise, to grow, and even to reproduce. In contrast, species from

forests, grasslands, and cold deserts of the middle latitudes also can tolerate extremely low temperatures during the dormant season but require higher temperatures to complete their life-cycles (Billings & Mooney 1968). Besides morphological characteristics enabling plants to withstand such hard conditions, reproduction is expected to be especially adapted to climatic conditions and frequent disturbances occurring in alpine habitats and persistence of species may become of increasing importance (Hartmann 1957; Billings & Mooney 1968; Bliss 1971; Billings 1974). Nevertheless, in addition to abiotic factors determining species' performance, biotic interactions with predators limiting reproductive success and plant abundance (Janzen 1971) may also have substantial impact in alpine habitats (Molau *et al.* 1989).

Population dynamics of alpine plants

Life-history theory predicts, that perennality and polycarpic reproduction will be favoured in habitats where off-spring survival is low (Charnov & Schaffer 1973), or unpredictable (Murphy 1968). In fact, life-cycles of plants adapted to alpine environments are usually characterised by slow growth, longevity, and clonal reproduction (Hartmann 1957; Billings & Mooney 1968; Bliss, 1971). Many alpine plants start their first sexual reproduction only after an elongated juvenile period of many years

(Morris & Doak 1998; Forbis 2003). Longevity is an important feature of plants subject to alpine environments and some of them were found to persist even for centuries (Molau 1997; Morris & Doak 1998). The ability to reproduce by clonal structures promotes growth and persistence still under distinct environmental unpredictability, and thus, enabling species to persist for long times, exceptionally even for several hundred years (Steinger *et al.* 1996). But what role plays sexual reproduction for population growth in alpine plant species?

Clonal growth is an outstanding characteristic of plants living in alpine habitats (Hartmann 1957; Klimeš *et al.* 1997). Clonal plants are often characterised by reduced sexual reproduction and rare seedling recruitment (Crawley 1990; Schmid 1990; Silvertown *et al.* 1993; Eriksson 1997) compared to non-clonal species (Abrahamson 1980; Callaghan & Emanuelsson 1985; Cook 1985; Eriksson 1989, 1992). Consequently, local population dynamics of many species are considered to be strongly dominated by clonal growth (Callaghan 1976; Crawley 1990; Eriksson 1992; Silvertown *et al.* 1993). In fact, there is large evidence, that in alpine plants, seedling recruitment is especially rare (Bliss 1971; Jolls & Bock 1983; Urbanska & Schütz 1986; Scherff *et al.* 1994; Chambers 1995; Forbis 2003). On the other hand, clonal plants from alpine habitats reveal similar genetic variation as lowland species, suggesting at least occasionally recruitment from seeds

(Bingham & Ranker 2000; Till-Bottraud & Gaudeul 2002). Moreover, sexual seed reproduction promotes not only the linkage of isolated populations via pollen and seeds but also the colonisation of new sites, which is of particular importance in the fragmented alpine landscape.

However, despite some demographic studies of alpine plants (e.g. Callaghan 1976; Erschbamer 1994; Molau 1997; Erschbamer *et al.* 1998; Morris & Doak 1998; Diemer 2002; Dinnétz & Nilsson 2002), the role of sexual and clonal reproduction for population growth in alpine plants still remains largely unclear and is a main focus in this thesis, particularly of chapter 2.

Sexual and clonal reproduction in alpine plants

Clonal growth is among the most essential features in plants adapted to cold environments. The capacity of clonal reproduction to assure rapid population growth and persistence even under harsh environmental conditions may explain why it tends to increase with altitude (Bliss 1971; Klimeš *et al.* 1997). A comparatively high fraction of alpine clonal plants occurs not only in late successional grasslands but also in extremely hostile habitats like pioneer communities on screes (Hartmann 1957; Stöcklin 1992; Klimeš *et al.* 1997).

The ability of many plant species to develop clonal structures potentially becoming independent has important

consequences for their life-history and enables them to successfully interact with their local environment (Herben *et al.* 1994). While the development of floral structures and ripening of seeds intensively consumes resources, the costs of self-sustainable ramets are comparatively low (Harper 1977), being of high relevance in habitats where resources are limited. The physiological integration of mother and daughter modules ('ramets'), at least for some time, allows foraging of nutrients and translocation to other modules of the plant, thereby increasing the genets' fitness (Callaghan 1988; Jónsdóttir & Callaghan 1988). This 'post-natal care' of young ramets provides an increase in survival probability, which may be particularly important in the highly variable alpine environment (Callaghan & Emanuelsson 1985). In contrast, especially in high altitudes, the onset of flowers is associated with the large risks of pollinator limitation or seed loss due to environmental unpredictability (Molau 1993). Moreover, abiotic factors occurring in high altitudes allow only few seedlings to survive (Bliss 1971; Urbanska & Schütz 1986; Scherff *et al.* 1994). In alpine habitats, seedling establishment is mainly associated with frequent disturbances as well as with reduced competition in open habitats and early successional stages (Ryvarden 1971; Chambers 1993; Diemer & Prock 1993). The importance of recruitment from seeds declines with successional age (Matthews 1992) and in late successional alpine communities, recruitment of new genets is

rare or even absent (Steinger *et al.* 1996). Consequently, clonal reproduction should be particularly favoured in high alpine habitats and late successional communities. On the other hand, the advantage of sexual reproduction lies in providing genetic variation as a prerequisite for adaptation to long-term environmental changes and in the production of seeds which may promote dispersal in time and in space (Nathan & Muller-Landau 2000).

Interestingly, sexual reproduction is often reduced in clonal plants compared to non-clonal species (Crawley 1990; Schmid 1990; Silvertown *et al.* 1993; Eriksson 1997). Since resources are usually limited, an investment in clonal reproduction implies a trade-off with sexual reproduction (Harper 1977; Watson 1984). However, trade-offs not only concern resource allocation, but could also involve structural constraints like meristems, sexual and clonal organs compete for (Watson 1984; Eriksson 1985). The balance between sexual and clonal reproduction may have major consequences for demography, population genetic structure, and dispersal (van Kleunen *et al.* 2002) and is likely to vary depending on environmental conditions (Loehle 1987). However, a variable ratio between sexual and clonal reproduction as a response to changing environments could also result from phenotypic plasticity (Sultan 2000; Fischer & van Kleunen 2002), thereby masking or even preventing genetic effects from selection pressures.

The strong gradients of altitude and succession are considered to be the most striking environmental effects that alpine plants may experience. It is expected, that the balance between sexual and clonal reproduction should vary in species occurring along these gradients. With increasing altitude, clonal reproduction should be favoured while the importance of sexual reproduction may therefore decrease. In the fragmented alpine landscape with frequent disturbances and continuous creation of open soils, sexual reproduction should be favoured in early successional stages, whereas the importance of clonal reproduction should increase with increasing successional age. However, only little is known of the impact of these gradients on the relationship between sexual and clonal reproduction (Douglas 1981; Peroni 1994; Piquot *et al.* 1998). The influence of contrasting altitudes and successional stages on the variation of sexual and clonal reproduction is the topic of chapter 3.

Pre-dispersal seed predation and population dynamics

Given the ubiquity of seed consuming insects often occurring at high densities and predominantly showing host-specificity, pre-dispersal seed predation provides the potential to strongly influence plant reproductive performance. Accordingly, it has often been shown that consumption of seeds prior to dispersal can substantially influence the relative reproductive success

of individuals by limiting seed production (e.g. Janzen 1971; Louda 1982; Hendrix 1988; Louda & Potvin 1995; Briese 2000; Leimu *et al.* 2002). Furthermore, herbivory may play a role in the evolution of semelparous life-history in perennial plants (Klinkhamer *et al.* 1997).

Theory predicts that pre-dispersal seed predation should have notable consequences, not only for individual reproduction, but also for population dynamics if seed supply reduces recruitment to below the sustainable density (Harper 1977). Some studies demonstrated a direct impact of seed consumption on population growth (e.g. Kelly & Dyer 2002; Fröborg & Eriksson 2003), but consequences of pre-dispersal seed predation on population dynamics are still controversially discussed. Nevertheless, particularly in environments characterised by short vegetation periods restricting the possibility of predator escape, seed feeding herbivores may have substantial impact on population growth (Molau *et al.* 1989).

Clearly, differences in life-history largely determine how strong a plant may respond to seed losses. The existence of a seed bank (Parker 1985; Crawley 1990), immigration of seeds from other patches (Roff 1974; Eriksson 1996), or the ability to clonal reproduction may balance potential seed losses in predated populations. Also a species' life-span, particularly, whether it is semelparous or iteroparous, is of high importance in assessing the role of pre-dispersal seed predation for local population dynamics (Briese 2000). How-

ever, since most studies focus on seed consumption in annual plants (Szentesi & Jermy 2003) or short-lived perennials (e.g. Louda & Potvin 1995; Briese 2000), data concerning the influence of seed predation on population growth in long-lived species are scarce.

Pre-dispersal seed predation may be of particularly high relevance for population dynamics in high alpine habitats, where seedling recruitment strongly can be limited by environmental conditions (Urbanska & Schütz 1986; Scherff *et al.* 1994; Gold & Bliss 1995; Forbis 2003). Data on alpine pre-dispersal seed predation and its influence on reproduction and population growth in a clonal perennial plant are presented in chapter 4.

Experimental approach

Three different approaches were used for this thesis: Firstly, in a demographic field study, marked individuals of *Geum reptans* were followed assessing their survival, growth, and reproduction. Data were used to calculate transition matrices to model yearly population growth rates (λ) as a basis for stochastic simulations. Secondly, in contrasting altitudes and successional stages, variation in the relationship between sexual and clonal reproduction was measured in the field to assess this environmental influence on reproductive behaviour in *G. reptans*. Thirdly, a predator exclusion experiment using an insecticide on a field population

was used to study the effects of pre-dispersal seed predation on reproduction and population growth of *G. reptans*.

Outline

Chapters 2, 3, and 4 are written for publication in peer-reviewed scientific journals. Below, a short outline of each chapter is given. Also, co-authorship and cited reference of each publication are indicated therein.

Chapter 2

The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*

T. Wepler, P. Stoll & J. Stöcklin

Journal of Ecology 94: 869–879, 2006

The aim of this study was to determine the role of sexual and clonal reproduction in the life-history of an alpine clonal plant. Furthermore, I assessed which aspects of the life-history may contribute most to population dynamics in this plant and how variation among years and populations affects the population growth rate. I established permanent plots in two populations of *Geum reptans* in the Swiss Alps. In three consecutive years, I measured survival, growth, and reproduction of 579 and 301 individuals, respectively. Establishment of sexual and clonal off-spring was also obtained directly from field observa-

tions. Matrix modelling was used to calculate yearly population growth rates (λ) for each population. Elasticity analyses allowed the simulation of relative contributions of life-cycle components to population dynamics.

Chapter 3

Variation of sexual and clonal reproduction in the alpine *Geum reptans* in contrasting altitudes and successional stages

T. Wepler & J. Stöcklin

Basic and Applied Ecology 6: 305–319, 2005

The aim of this study was to assess the influence of altitude and successional age on the relative frequency of sexual *vs.* clonal reproduction and the frequency of life-cycle stages in the alpine clonal plant *Geum reptans*. In 20 populations of *G. reptans* situated in the Swiss Alps, I studied the reproductive behaviour in plants of different sizes ($N = 907$). I compared the relative frequency of clonal reproduction between populations from low *vs.* high altitudes and from early *vs.* late successional stages and tested for differences in population structure due to habitat type. Implying a meristem trade-off between both reproductive modes, this approach allows testing if the relative importance of clonal reproduction increases with altitude and if it is also favoured in late successional stages.

Chapter 4

Does pre-dispersal seed predation limit reproduction and population growth in the alpine clonal plant *Geum reptans*?

T. Wepler & J. Stöcklin
Plant Ecology 2005, in press

The aim of this study was to determine the effects of seed predation prior to dispersal on sexual and clonal reproduction and consequences for population growth in an alpine clonal plant. In a population of *Geum reptans* situated in the Swiss Alps, I conducted a two-years exclusion experiment using insecticide to prevent consumption of seeds by a host-specific seed predator ($N = 122$). Differences in seed number and seed weight and effects on clonal reproduction were compared between protected and non-protected plants. Seed viability due to predation was tested by a greenhouse germination experiment. Effects of seed loss on population growth were simulated using the matrix model of *G. reptans* (see chapter 2).

In chapter 5, a general summary concluding the most important findings of this thesis is presented.

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Chapter 2

The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*

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Summary

Demographic studies in natural habitats are important for understanding the life-history and mechanisms of population persistence of particular species. For plants living in high-alpine habitats, it is of significant importance to what extent sexual or clonal reproduction contribute to population growth, but respective data are scarce. We studied the demography of *Geum reptans*, an alpine plant which reproduces by seeds and by vegetative rosettes formed at the ends of above-ground stolons. In three consecutive years, growth, survival, and reproduction were measured in two populations with 579 and 301 individuals, respectively. The two resulting transition matrices per population were used to calculate population growth rates (λ) and elasticities, and to perform stochastic simulations to assess the relative importance of sexual *vs.* clonal reproduction for population growth. Population growth rates (λ) varied from 0.999 to 1.074 among years and populations. The frequency of seed and stolon production was relatively constant over the years. However, there was inter-annual variation in seed germination (0.7–2.4%) and in establishment of clonal off-spring (53–74%). Elasticity analysis showed that changes in the survival of adults had the largest effect on λ , confirming the importance of longevity and persistence in the life-history of *G. reptans*. Stochastic simulations showed that *in G. reptans* independently of location and year, both sexual and clonal reproduction did not significantly differ in their contribution to the population growth rate λ . Establishment from seeds contributes to population growth particularly in favourable years, while the more regularly occurring reproduction by clonal off-spring may ensure population growth in less favourable years. Sexual reproduction in clonal plants is frequently explained by the short- and long-term benefits of genetic variation and the need for dispersal and colonization, for which seeds are better suited than vegetative organs. Our results, however, show the importance of sexual reproduction in a clonal plant for local dynamics as well, and prove the power of matrix models to evaluate the relative contributions of the two reproductive modes.

Key-words: clonal plants, demography, glacier foreland, pioneer plant, population growth rate, population projection matrix, recruitment, seeds, stochastic simulation, stolons

Introduction

Demographic studies using matrix projection models have been applied to a variety of plant species differing in life-history and environment, but there are few demographic surveys of species from arctic-alpine habitats, although examples are *Carex bigelowii* (Callaghan 1976), *Carex curvula* ssp. *curvula* and *C. curvula* ssp. *rosae* (Erschbamer 1994; Erschbamer & Winkler 1995; Erschbamer *et al.* 1998), *Diapensia lapponica* (Molau 1997), *Silene acaulis* (Morris & Doak 1998), *Ranunculus glacialis* (Diemer 2002), and *Saxifraga cotyledon* (Dinnétz & Nilsson 2002). Alpine environments are stressful habitats, characterized by severe climatic constraints, such as short and cold growing seasons, high solar radiation and strong winds (resulting in desiccation of the topsoils), which may limit growth and reproduction. Slow growth combined with longevity and clonal life-cycles are prominent features of alpine species (Hartmann 1957; Billings & Mooney 1968; Bliss 1971). Little is known, however, about the role of sexual reproduction in clonal plants of alpine habitats for local population growth and persistence.

Clonal reproduction is thought to increase with altitude, resulting in a particularly high predominance of clonal plants in alpine environments, not only in closed grasslands but also in pioneer and late-successional communities (Hartmann 1957; Stöcklin 1992; Klimes *et al.* 1997). Clonal plants are often characterized by

reduced sexual reproduction compared with non-clonal species (Crawley 1990; Silvertown *et al.* 1993; Eriksson 1997), and recruitment from seeds is thought to be infrequent (Abrahamson 1980; Callaghan & Emanuelsson 1985; Cook 1985; Eriksson 1989, 1992). In some species, a trade-off between sexual and clonal reproduction has been shown (e.g. Sutherland & Vickery 1988; Piquot *et al.* 1998). Consequently, local population dynamics of many species may depend heavily on clonal reproduction (Callaghan 1976; Eriksson 1992; Silvertown *et al.* 1993).

There is plenty of evidence for infrequent germination and low seedling survival in alpine habitats (Bliss 1971; Urbanska & Schütz 1986; Scherff *et al.* 1994; Chambers 1995; Forbis 2003). Nevertheless, genetic studies have revealed a genetic variation in alpine plants similar to that in lowland species, which indicates that recruitment from seeds does occur at least occasionally (Bingham & Ranker 2000; Till-Bottraud & Gaudeul 2002). In a long-lived plant, even a low rate of seedling establishment may be sufficient for the maintenance of significant genetic variation (Jelinski & Cheliak 1992; Watkinson & Powell 1993). Sexual reproduction is also important for the linking of isolated populations via pollen and seeds and for colonisation of new habitats. Both are particularly relevant in patchy alpine landscapes, but we still do not know much about how important seedling establishment actually is for population growth in alpine habitats. The combination of high

colonisation abilities with extreme longevity and clonal growth is a particularity of pioneer species of glacier forelands, and therefore the respective relative importance of sexual or clonal reproduction modes is crucial for their dynamics.

In this study, we use matrix projection models to study the demographic development of two field populations of the alpine pioneer plant *Geum reptans* L. in the Swiss Alps. The application of matrix projection models on life-cycle components combines both structure and dynamics of populations (Law 1983; Caswell 1985, 2001). Analysis based on projection matrices allows prediction of short- and long-term consequences of demographic parameters for population growth as well as evaluation of hypothetical changes in the life-cycle (Caswell 1985, 2001; van Groenendael *et al.* 1988, 1994; van Tienderen 1995; de Kroon *et al.* 2000). Calculation of sensitivities or elasticities reveals the respective contributions of life-cycle components to population dynamics (e.g. de Kroon *et al.* 1986; van Tienderen 1995; Benton & Grant 1999; Caswell 2001). *G. reptans* is a widespread, slow-growing rosette plant mostly occurring on glacier forelands. It regularly reproduces by flower heads and daughter rosettes formed at the tip of above-ground stolons. We studied growth, survival, and reproduction of this species in two populations and calculated population growth rates (λ) over 3 years to predict the long-term consequences of different life-history traits for population growth. We addressed

the following main questions: (1) What is the relative importance of sexual *vs.* clonal reproduction for population growth? (2) To what changes in life-cycle components is λ most sensitive? (3) How does variation among years and populations affect λ ?

Materials and methods

The study species

Geum reptans L. (Rosaceae) is a clonal perennial rosette plant widely distributed from the Central Alps eastwards to the Carpathian Mountains and Macedonia. This species is usually found on moist moraines and alluvial soils of glacier forelands, on screes, and on mountain ridges, preferring lime-deficient rocks. It shows an altitudinal distribution between 1950 and 3800 m a.s.l. (Conert *et al.* 1995). In the Swiss Alps, population abundance is highest between 2300 and 2800 m (our personal observation). *G. reptans* is among the first pioneer species invading protosols after glacier retreat (Braun-Blanquet 1948) and is frequently found on wet alpine screes. With ongoing succession, grasses and dwarf shrubs dominate the vegetation (Lüdi 1921). Weak competitive ability and dependence on high soil moisture content may explain why *G. reptans* is never found in closed grasslands (Rusterholz *et al.* 1993).

As a hemicryptophyte, *G. reptans* forms clumps of 1–7 (exceptionally more) rosettes sprouting from a taproot in spring.

Growth of an individual results in an increase in the number of side rosettes from the same taproot. The age of first reproduction largely depends on environmental conditions. It ranges from about 5 years in late-successional populations to about 10 years in early-successional populations (A.R. Pluess, unpublished data). In spring, both flower heads and stolons develop at the same time from axial leaf buds that were initiated in the previous year. Clonal daughter rosettes are formed at the tip of stolons, which can grow up to 1 m in length. In late summer, the rosette roots and the connection to the mother plant will wither (clonal reproduction). In contrast to the production of daughter rosettes at the end of stolons, the production of new side rosettes from the same taproot never leads to independent plants. As a consequence of clonal reproduction, genets of *G. reptans* have the potential to live forever, and individual plants are ramets. Flower heads are hermaphroditic or male (rarely), contain about 100 ovaries (Conert *et al.* 1995 and our personal observation) and are predominantly fly-pollinated (Heß 2001). The nutlets exhibit an elongated hairy style and are mainly dispersed by wind. A dispersal model showed that about 99.9% of the seeds of *G. reptans* are dispersed over less than 10 m (O. Tackenberg & J. Stöcklin, unpublished data). *G. reptans* forms no

persistent seed bank (Schwienbacher & Erschbamer 2002).

Study sites

Demographic data were collected in two geographically distinct populations of *Geum reptans* in the Swiss Alps, which were approximately 115 km apart. These sites were selected for their size, their intermediate altitudinal position, at which population abundance of *G. reptans* is highest, and for presenting plants in an intermediate successional stage. Both populations were situated on rocky glacier forelands and showed similar vegetation cover (50–60%). The population size of Vadret da Porchabella (2650 m) was approximately 15 000 individuals (estimate obtained by measuring the size of the area and multiplying it by an average density estimate of the population). The study site was a WNW exposed slope of 18° inclination (Swiss-national grid reference 786964/168168), from which the glacier retreated at least 45 years ago. The population size of Furkapass (2500 m) was approximately 5000 individuals. The study site was a NW-exposed slope of 28° inclination (Swiss-national grid reference 674636/156624), from which the glacier retreated at least 90 years ago.

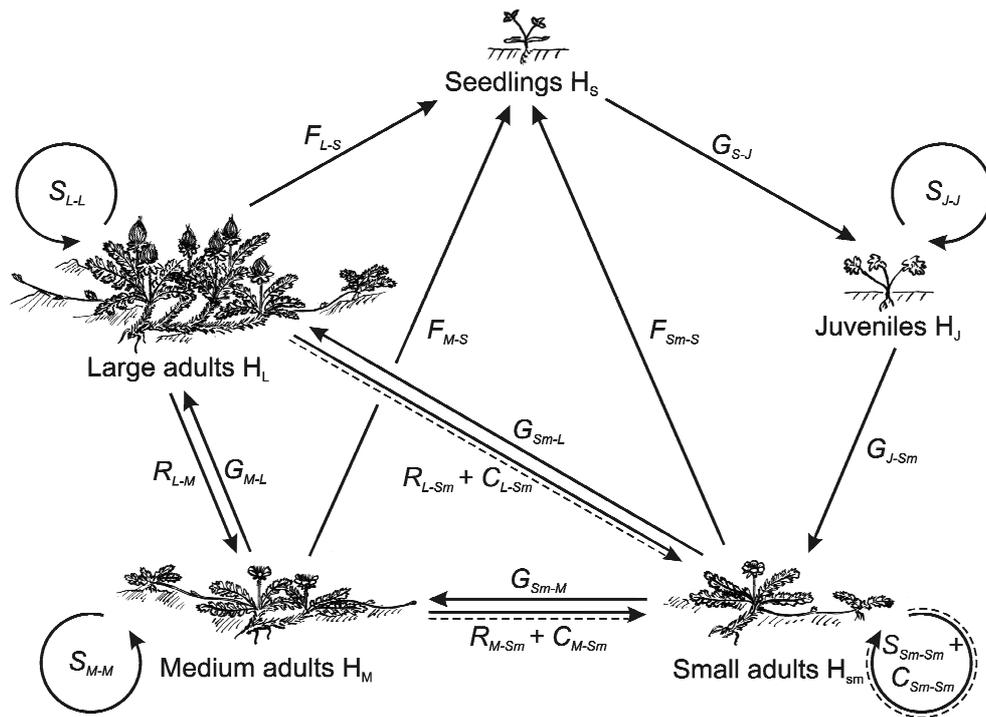


Fig. 1 Life-cycle of *Geum reptans* with five stages (H_s , seedlings; H_j , juveniles; H_{sm} , small adults; H_m , medium adults; H_l , large adults). Transitions between stages represent: G, growth; S, stasis; R, retrogression; F, sexual reproduction. Clonal reproduction (C) is included in the transitions S_{sm-sm} , R_{m-sm} and R_{l-sm} and is represented by a dashed line. Note that the life-cycle corresponds to the matrix population model (see methods for details).

Classification of life-cycle stages

In *Geum reptans* as in many perennial plants, age estimation based on above-ground morphological traits is not possible. Due to field observations and a previous study by Rusterholz *et al.* (1993) we distinguished the following life-cycle stages (Fig. 1):

1. *Seedlings* with cotyledons and generally one pair of leaves. Seeds germinate soon after snowmelt in the spring following their production.
2. *Juveniles* are young plants that have originated from sexual reproduction and have more than one pair of tender leaves. They can be distinguished from adult plants by the shape of their leaves and

from seedlings by the absence of cotyledons.

3. *Small adults* have one leaf rosette. Leaves are rather thick and exhibit distinct adult leaf morphology. Small adults may develop from sexually produced juveniles or from clonal daughter rosettes produced via stolons by small, medium or large adults.
4. *Medium adults* have two or three leaf rosettes.
5. *Large adults* have four or more leaf rosettes.

Demography and calculation of transition probabilities

For data collection, randomly located permanent plots were established in the centre of each population. In 2000, at Vadret da Porchabella, 30 permanent plots of 1 m² were established over an area of 50 × 30 m. In 2001, at the Furkapass study site, 15 permanent plots were set up in an area of 25 × 20 m. The populations were examined over a period of 3 years. In each population, one main census per year was conducted. In late July (Furkapass) or early August (Vadret da Porchabella), all individuals of *Geum reptans* were mapped. For each plant, the life-history stage, the number of rosettes, and the number of flower heads and stolons were recorded. On a second visit in September, seedlings were counted again so as not to miss late germinants. At this time, the position of daughter rosettes at the end of stolons was also mapped. Thus, in the following year, successful establishment of clonal offspring could be determined despite withering of stolons.

Transition probabilities from one life-cycle stage to another were calculated for each stage as the proportion of individuals remaining in that stage or having changed to respective other stages after an interval of 1 year (Caswell 2001). From the data collected in 3 years, two transition matrices for each population were calculated. For estimating percentage germination, we assumed that the number of seeds emigrating equalled the number of seeds

immigrating into the population. Therefore, for each year, the number of seedlings observed was divided by the total number of seeds (S) produced in the previous year (anonymous births). The total number of seeds produced was calculated by multiplying the number of annually produced flower heads per stage i (H_i) by the stage-specific mean number of seeds per flower head (s_i), summed over all stages i (small, medium and large adults): $S = \Sigma(s_i \cdot H_i)$. The mean number of seeds per flower head (s_i) was determined once in each population (in 2001), to which end 10 small, medium and large fruiting plants were randomly selected. The number of seeds in one flower head representing mean seed production of the individual was counted and the mean number of seeds per flower head was calculated for each size class. Sexual reproduction of adult stages was calculated by dividing the number of annually produced seeds in each stage by the number of individuals in each stage, and multiplying the result by the annual percentage germination. Clonal reproduction was calculated for each stage class as the stage-specific annual establishment of daughter rosettes divided by the number of stolons produced. With regard to transitions to the stage of a small adult, two components had to be considered (Fig. 1): the survival of adults (their remaining small adults or retrogressing to that stage) and clonal reproduction (leading to the development of small adults). Thus, according to Caswell (2001), clonal fecundity of adult stages was added

to the transition probabilities of small, medium and large adults remaining in or retrogressing to the stage of small adults, respectively. Because individuals of *G. reptans* grow very slowly, we assumed that survival and growth of adults did not differ between plants that developed from juveniles or from stolons. The resulting four transition matrices are given in Table 1.

The precision of matrices can be increased with equal numbers of individuals in stages compared with plot-based methods (Münzbergová & Ehrlén 2005). Although unbalanced designs can lead to unreliable results in this type of analysis, that is unlikely to be a problem with sample sizes as large as those in this study.

Data analysis and simulation of population growth

For each of the four transition matrices, the population growth rate (λ) and the species' average life span were calculated by means of the program package Ramas EcoLab 2.0 (Sinauer Associates, Inc.), based on observed stage abundance. For each population, the stable stage distribution was computed for a model that averaged two transitions per population, and was compared with the distributions of stages based on the mean (across-years) of observed individual abundance (Table 1), using Keyfitz's Δ . This standard measure quantifies the distance between observed and stable distributions, with

values ranging from 0 to 1, equating to maximum similarity and maximum difference, respectively (cf. Caswell 2001).

The elasticities (proportional sensitivities) of λ to changes in elements of the transition matrix were calculated separately for each year and population. Elasticities of matrix elements comprising multiple components (i.e. stasis/retrogression and clonal fecundity in the transition probabilities of small, medium and large adults to small adults) were calculated separately for each component. In a first step, elasticities were calculated for the sum of the composed elements, and then separately for the first component (stasis) of the composed transitions. Only one matrix element at a time was varied. Elasticities for clonal reproduction were calculated by subtracting the stasis component from the total elasticity. Because elasticities of a matrix total 100%, a change of one element resulted in small changes of other matrix elements. As we observed only minor absolute changes in sensitivities of other life-cycle elements (in most cases by less than 5%), such changes were not considered further. Elasticities of matrix elements comprising multiple components are given separately for each component in Table 1. To account for stochasticity introduced through sampling, population growth rates $\lambda \pm 95\%$ confidence intervals were estimated by a bootstrapping procedure for each transition in both populations (Caswell 2001). Sampling was simulated by calculating transition probabilities of a random

Table 1 Transition and elasticity matrices of two populations of *Geum reptans* (Vadret da Porchabella, Furkapass) during a study period of 3 years each. Transition matrices for each population contain the life-cycle stages (seedlings, juveniles, and small, medium and large adults), the initial individual abundance per stage (n), and the probabilities of individuals remaining in the same stage or changing to another stage, respectively, within one year. For each transition, an elasticity value (%) is calculated. Probabilities of transitions to the stage of a small adult and respective elasticities are based on values for survival of small adults or retrogression of medium or large adults from the previous year (first value) or production of new small adults via clonal reproduction (second value in bold type, see Methods for details). Transition probabilities and elasticities reflecting sexual reproduction are given in italics.

	Transition matrix					Elasticity matrix				
	Seedlings	Juveniles	Small adults	Medium adults	Large adults	Seedlings	Juveniles	Small adults	Medium adults	Large adults
Vadret da Porchabella, 2000–2001 ($\lambda = 1.070$)										
n	23	31	351	104	70					
Seedlings	–	–	<i>0.02</i>	<i>0.08</i>	<i>0.21</i>	0	0	<i>0.5</i>	<i>0.6</i>	<i>2.0</i>
Juveniles	0.96	0.39	–	–	–	3.1	1.8	0	0	0
Small adults	–	0.52	0.87 + 0.03	0.12 + 0.08	0.00 + 0.09	0	3.1	32.9 + 1.1	1.2 + 0.8	0 + 1.2
Medium adults	–	–	0.09	0.70	0.03	0	0	5.9	12.5	0.7
Large adults	–	–	–	0.17	0.94	0	0	0	3.9	28.7
2001–2002 ($\lambda = 1.031$)										
n	31	34	365	108	84					
Seedlings	–	–	<i>0.02</i>	<i>0.07</i>	<i>0.23</i>	0	0	<i>0.4</i>	<i>0.2</i>	<i>0.7</i>
Juveniles	0.94	0.74	–	–	–	1.3	3.1	0	0	0
Small adults	–	0.12	0.90 + 0.03	0.27 + 0.07	0.00 + 0.19	0	1.3	48.0 + 1.6	2.7 + 0.7	0 + 1.6
Medium adults	–	–	0.06	0.64	0.10	0	0	4.4	8.7	1.1
Large adults	–	–	0.01	0.07	0.90	0	0	1.5	1.9	20.8
Furkapass, 2001–2002 ($\lambda = 1.074$)										
n	40	11	195	34	21					
Seedlings	–	–	<i>0.08</i>	<i>0.21</i>	<i>0.39</i>	0	0	<i>2.0</i>	<i>1.1</i>	<i>1.3</i>
Juveniles	0.88	0.55	–	–	–	4.5	4.7	0	0	0
Small adults	–	0.36	0.87 + 0.02	0.18 + 0.21	0.00 + 0.05	0	4.5	39.9 + 0.9	1.8 + 2.1	0 + 0.3
Medium adults	–	–	0.06	0.68	0.19	0	0	5.5	13.3	2.3
Large adults	–	–	0.01	0.12	0.81	0	0	1.1	2.8	11.9
2002–2003 ($\lambda = 0.999$)										
n	32	42	189	39	23					
Seedlings	–	–	<i>0.20</i>	<i>0.45</i>	<i>0.22</i>	0	0	<i>1.5</i>	<i>0.8</i>	<i>< 0.1</i>
Juveniles	0.91	0.64	–	–	–	2.3	4.2	0	0	0
Small adults	–	0.05	0.82 + 0.02	0.23 + 0.23	0.09 + 0.04	0	2.3	47.6 + 1.2	3.3 + 3.3	0.1 + < 0.1
Medium adults	–	–	0.06	0.74	0.17	0	0	7.6	23.3	0.5
Large adults	–	–	–	0.03	0.65	0	0	0	0.7	1.2

sample of 50% of the available individuals in each life-cycle stage. Fecundity was simulated by randomly selecting 50% of individuals reproducing by flower heads and 50% of individuals reproducing by stolons. The λ values of 1000 replications were then averaged and 95% confidence intervals calculated, using the percentiles of the distribution. The confidence intervals calculated using percentiles were virtually identical to confidence intervals based on normal theory [i.e. ± 1.96 standard error estimated from the distribution, cf. Caswell (2001, p. 307)]. The stochastic simulation of λ was then used to analyse the effects of a gradual reduction in sexual or clonal reproduction on population growth rates, separately for each population and each transition. For that purpose, the matrix elements representing either sexual or clonal reproduction were reduced in steps of 25%, 50% and 100% in all four matrices. The resulting growth rates were compared with simulated stochastic population growth based on observed values of sexual and clonal fecundity and with population growth with both reproductive modes set to zero simultaneously. To test for differences in the impact of gradual reduction of sexual or clonal reproduction on growth rates, a paired *t*-test ($N = 4$) was used. Calculation of elasticities and all stochastic simulations were performed using the program package R version 1.7.1 (Ihaka & Gentleman 1996).

Results

Population structure and reproduction

In the first year, 579 plants were present in the 30 plots at Vadret da Porchabella (about 3.9% of the estimated total population size). At Furkapass, 301 plants were present in the 15 plots (about 6.0% of the estimated total population size). At Vadret da Porchabella, 20.6 ± 1.0 plants (mean \pm SE, range 2–83 individuals) occurred in each permanent plot of 1 m² whereas at Furkapass, 21.8 ± 1.5 plants (range 6–56 individuals) per plot were recorded.

Population structure at the two study sites was similar (Fig. 2). In both cases, small adult plants with only one rosette dominated the population. Vadret da Porchabella showed a higher frequency of medium and large adults than Furkapass. The proportions of seedlings and juveniles were higher at Furkapass. For both populations, the observed frequencies of life-cycle stages were similar to the calculated stable stage distributions ($\Delta = 0.04$ for Vadret da Porchabella and $\Delta = 0.12$ for Furkapass; Fig. 2). Calculated average life-span of individual plants (ramets) was 31.1 ± 3.5 years (mean \pm SD) at Vadret da Porchabella and 18.4 ± 2.4 years at Furkapass.

Both populations reproduced sexually and clonally in all three years under study, but the frequency of reproducing adults was low ($7.9 \pm 0.9\%$ for Vadret da Porchabella and $8.5 \pm 0.5\%$ for Furkapass). Within the study plots at Vadret da

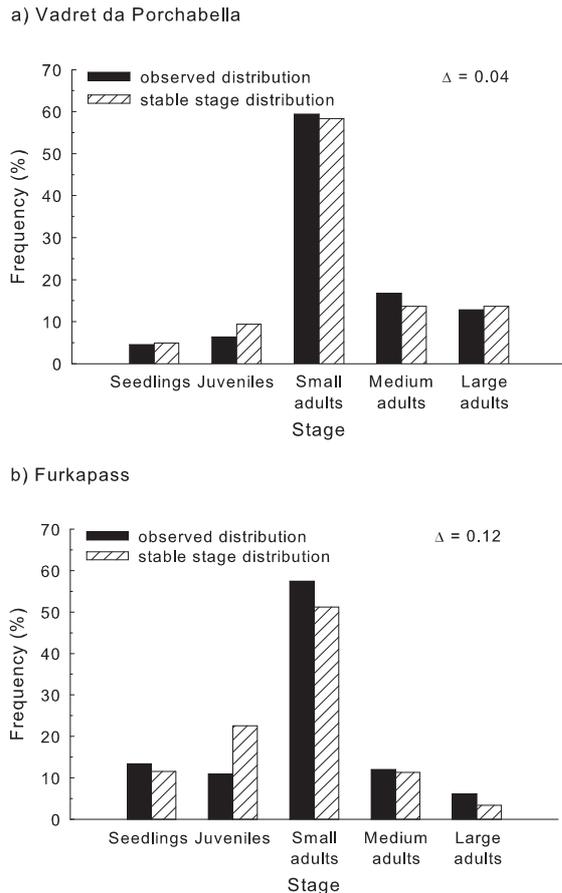


Fig. 2 Observed and stable stage distributions of life-cycle stages (seedlings, juveniles, and small, medium and large adults) and Keyfitz's Δ as a measure of the difference between the two distributions in each population of *Geum reptans*. Stable stage distributions were calculated in each population from a mean model, i.e. from transition matrices averaged over the years: (a) Vadret da Porchabella, (b) Furkapass.

Porchabella, 3126 ± 1159 seeds and 51 ± 8 stolons were produced. Within the study plots at Furkapass, 2529 ± 86 seeds and 18 ± 4 stolons were produced. At Vadret da Porchabella, the number of seeds per reproductive adult increased with increasing plant size, but at Furkapass, there was no such trend. In both populations, the number of stolons did not increase with plant size (Table 2).

Whereas the proportion of reproductive plants remained rather similar over the years under study, reproduction of individual plants differed largely from year to year. From 63 plants initially reproducing in both populations, only 14 (22.2%) reproduced every year. Even large plants did not produce flower heads and stolons simultaneously in each year and there was no significant correlation between the production of flower heads and stolons ($P > 0.05$). In the first year, 46.7% of all large reproducing adults showed sexual and clonal reproduction simultaneously. In the following year, only 13.3% of these individuals reproduced again by both reproductive modes.

In both populations, percentage germination was lowest during period 2001–02 and varied by nearly 200% among years (Table 3). At both study sites, at least 50% of clonal off-spring established in each time step, and at Furkapass, from 2002 to 2003, even three of four daughter rosettes survived (Table 3).

In both populations, relative mortalities of seedlings and juveniles were higher than percentage mortalities of adult plants and showed little inter-annual variation (Table 3). The only exception was at Furkapass, where during 2002–03 relative mortalities were comparably high for four of five life-cycle stages.

Table 2 Seed and stolon production in two populations of *Geum reptans* (Vadret da Porchabella, Furkapass). Values are means (\pm SE) for small, medium and large reproductive adults over 3 years. The effect of plant size on reproduction was tested by means of Kruskal–Wallis tests.

	Small adults	Medium adults	Large adults	<i>P</i>
Vadret da Porchabella 2000–02				
Seeds	46.3 \pm 10.6	59.4 \pm 11.8	108.3 \pm 28.8	0.04
Stolons	1.0 \pm 0.1	1.0 \pm 0.1	1.4 \pm 0.2	0.49
Furkapass 2001–03				
Seeds	125.6 \pm 24.0	95.4 \pm 25.9	150.8 \pm 47.1	0.43
Stolons	0.7 \pm 0.1	1.2 \pm 0.2	0.9 \pm 0.2	0.21

Population dynamics

Except for the period 2002–03 at Furkapass, the population growth rates (λ) of *Geum reptans* were positive, varying between 0.999 and 1.074 (Table 1). Population growth at the same site varied among years (3.6% variation at Vadret da Porchabella and 7.0% variation at Furkapass), but between the two populations, growth rates based on mean transitions varied only little (0.2%).

In both populations, establishment of sexual off-spring occurred regularly. The probability of seedlings becoming juveniles was high (88–96%; Table 1). At Vadret da Porchabella, the probability of juveniles remaining in the same stage doubled from one year to another whereas at the same time the proportion of juveniles developing into small plants decreased by a factor of four. At Furkapass, the proportion of juveniles showing stasis increased slightly, but from 2002 to

2003, only 5% of juveniles progressed into small plants, as compared with 36% in the first year.

At Vadret da Porchabella as well as at Furkapass, the probabilities of small, medium and large adults remaining in the same stage after one year were much higher (64–94%) than the probabilities of their progressing (3–17%) or retrogressing (3–27%) into other stages (Table 1). In both populations, a small proportion of small adults (1%) directly developed into large adults in only one year.

Elasticities of lambda

Elasticity analysis revealed that changes in the proportion of small, medium and large adults remaining in the same stage had the highest effect on the population growth rate (λ). The elasticity of λ was, in both populations, particularly pronounced with respect to the survival of small adults (elasticities of 33–48% with regard to small adults, 9–23% medium adults and 1–29% large adults; Table 1). Remarkably, a change in recruitment from seeds and from clonal off-spring produced via stolons only slightly affected λ (elasticities regarding seedlings < 0.1–2% and regarding clonal off-spring < 0.1–3.3%; Table 1). Except for Furkapass during 2001–02, the summed elasticities of λ to clonal reproduction were slightly higher than those to sexual reproduction. The elasticities of λ to progression (0–7.6%) or retrogression (0–3.3%) of adults were of minor importance.

Table 3 Establishment and mortality in two populations of *Geum reptans* (Vadret da Porchabella, Furkapass) over 3 years: (a) number of seedlings and percentage germination (number of seedlings per total number of seeds in the previous year), and number of stolons and percentage clonal establishment (number of established daughter rosettes per total number of stolons in the previous year); and (b) mortality of seedlings, juveniles, and small, medium and large adults. For each population, values are given for two transitions.

	Vadret da Porchabella		Furkapass	
	2000–01	2001–02	2001–02	2002–03
(a) Establishment				
Number of seedlings	31	33	31	61
Sexual establishment	1.69%	0.71%	1.28%	2.40%
Number of daughter rosettes from stolons	25	33	11	14
Clonal establishment	53.2%	53.2%	50.0%	73.7%
(b) Mortality				
Seedlings	4.4%	6.5%	9.4%	12.5%
Juveniles	9.7%	14.7%	9.1%	31.0%
Small adults	4.0%	4.1%	6.2%	11.1%
Medium adults	1.0%	2.8%	2.9%	0
Large adults	2.9%	1.2%	0	8.7%

The relative importance of sexual vs. clonal reproduction for population growth

Stochastic simulations of the population growth rate (λ) showed that, independently of location and of years within one location, there was no difference in the relative decrease of λ in response to a reduction of either sexual or clonal reproduction (Table 4). Tested over both populations and all transitions, a reduction in either sexual or clonal reproduction by 25% resulted in a respective decrease of λ by 0.72% or 1.08% (n.s., $P = 0.24$, paired t -test, $N = 4$), a reduction by 50% resulted in a respective decrease of λ by 1.40% or 1.84% (n.s., $P = 0.46$), and a reduction by 100% resulted in a decrease of λ by 3.21% or 3.84%, respectively (n.s., $P = 0.59$).

When both reproductive modes were set to zero simultaneously, the mean relative decrease of λ was 8.26%, and population size would decrease slowly in all cases.

Discussion

Our results demonstrate that in *Geum reptans*, a high-alpine plant, sexual reproduction plays an equally important role for population growth as reproduction by clonal off-spring formed by above-ground stolons. Sexual and clonal reproduction occurred regularly in both studied populations, but in contrast to the consistently high establishment of clonal off-spring, the establishment of new plants from seeds varied largely among years and was always much lower than establishment from

clonal daughter rosettes.

Table 4 Observed stochastic population growth rate (a) and effects of stepwise reduction (by 25%, 50% or 100%) of sexual (b) or clonal (c) reproduction on the population growth rate ($\lambda \pm 95\%$ confidence interval), in two populations of *Geum reptans*, at (i) Vadret da Porchabella and (ii) Furkapass, over 3 years. Relative reduction in λ (%) was obtained by comparing reduced growth rates with population growth of the full model. The last column (d) gives stochastic growth rates based on a model with total reduction in sexual and clonal reproduction. Simulations were performed by a bootstrap procedure based on transition probabilities of randomly selected individuals in each population and each period (see Methods for details).

(i) Vadret da Porchabella		2000–01		2001–02	
Simulation	Percentage reduction	Growth rate ($\lambda \pm$ CI)	Reduction in λ (%)	Growth rate ($\lambda \pm$ CI)	Reduction in λ (%)
(a) Full model		1.067 \pm 0.065		1.033 \pm 0.065	
(b) Reduction in sexual reproduction	-25	1.058 \pm 0.063	-0.88	1.030 \pm 0.062	-0.28
	-50	1.051 \pm 0.064	-1.52	1.026 \pm 0.062	-0.69
	-100	1.027 \pm 0.066	-3.76	1.017 \pm 0.061	-1.56
(c) Reduction in clonal reproduction	-25	1.059 \pm 0.062	-0.74	1.022 \pm 0.061	-1.03
	-50	1.051 \pm 0.063	-1.50	1.014 \pm 0.063	-1.82
	-100	1.034 \pm 0.064	-3.10	0.992 \pm 0.060	-3.89
(d) Reduction in sexual and clonal reproduction	-100	0.974 \pm 0.071	-8.70	0.972 \pm 0.057	-5.899
(ii) Furkapass		2001–02		2002–03	
Simulation	Percentage reduction	Growth rate ($\lambda \pm$ CI)	Reduction in λ (%)	Growth rate ($\lambda \pm$ CI)	Reduction in λ (%)
(a) Full model		1.062 \pm 0.128	–	0.994 \pm 0.17	
(b) Reduction in sexual reproduction	-25	1.054 \pm 0.120	-0.78	0.984 \pm 0.110	-0.95
	-50	1.038 \pm 0.111	-2.33	0.983 \pm 0.111	-1.06
	-100	1.009 \pm 0.119	-5.02	0.969 \pm 0.113	-2.52
(c) Reduction in clonal reproduction	-25	1.053 \pm 0.127	-0.91	0.977 \pm 0.114	-1.66
	-50	1.046 \pm 0.127	-1.51	0.969 \pm 0.113	-2.52
	-100	1.026 \pm 0.132	-3.38	0.944 \pm 0.115	-4.99
(d) Reduction in sexual and clonal reproduction	-100	0.960 \pm 0.124	-9.66	0.906 \pm 0.111	-8.80

Population dynamics

Although there was considerable variation in growth rates (λ) among years, the dynamics of both populations of *Geum reptans* were similar. Population growth was positive in three of four transitions and negative in one transition, but nevertheless very close to equilibrium. In the three years under study, the population sizes at Vadret da Porchabella and Furkapass increased only by 13% and 18%, respectively. Slow growth and long life spans are typical features of many alpine species [e.g. *Carex curvula* (Steinger *et al.* 1996; Erschbamer *et al.* 1998), *Diapensia lapponica* (Molau (1997) and *Silene acaulis* (Morris & Doak 1998)]. *G. reptans*, as a species of alpine protosols with frequent disturbances, is expected to show persistence at the expense of rapid population growth. But populations exhibiting rather slow increase ($\lambda < 1.15$) are likely to be sensitive to environmental stochasticity (Menges 1998). Thus, the population size of *G. reptans* may rapidly decrease if recruitment does not balance higher mortalities in unfavourable years or after catastrophic events, which was indeed the case in the period 2002–03 at Furkapass, when λ was equal to 1.

G. reptans showed a very low frequency of reproductive adults in both populations. Even large well-established plants did not reproduce every year, suggesting that reproductive costs are high, which leads to an annually varying availability of resources for reproduction. Annual varia-

tion in reproduction is very common in long-lived herbs (Webb & Kelly 1993; Kelly 1994). Because climate is often a determining factor for high-reproduction years, at higher altitudes, where environmental unpredictability may constrain growth and reproduction, plants are expected to have even more variable seed yields (Webb & Kelly 1993).

The relative importance of sexual vs. clonal reproduction for population growth

In many studies of long-lived clonal plants, seedling recruitment was found to be of minor importance for population growth (e.g. Sarukhan 1974; Thomas & Dale 1975; Eriksson 1985; Damman & Cain 1998; Kiviniemi 2002) while others found evidence of high sexual reproduction and repeated recruitment from seeds (e.g. Suzuki *et al.* 1999; Guàrdia *et al.* 2000; Berg 2002). This study clearly shows that the role of sexual reproduction in clonal plants at high altitudes is not restricted to the maintenance of genetic variation or long-distance dispersal. In *Geum reptans*, sexual and clonal reproduction contributed similarly to population growth. Both reproductive modes are important, as the absence of either sexual or clonal reproduction may result in low population growth or even in no growth at all (Table 4).

According to Stöcklin & Bäumler (1996), a high production of many small

seeds is typical of alpine pioneer species, but seed recruitment may frequently be restricted to safe sites. In both populations of *G. reptans* studied here, seed production was high, germination occurred regularly in all years under study and survival of seedlings was high (at least 88%). Thus, recruitment from seeds may be common in *G. reptans* and is not restricted to rare safe sites, founding events or 'windows of opportunities' related to disturbances (cf. Eriksson 1989, 1997; Jelinski & Cheliak 1992). The observed variation in percentage germination was due to a highly variable germination success, indicating that also in *G. reptans* germination may be particularly susceptible to environmental variation and weather conditions (e.g. Jolls & Bock 1983; Urbanska & Schütz 1986; Scherff *et al.* 1994; Chambers 1995). The probability of a seedling surviving the first winter was, on average, 1.6 times higher than that of a clonal daughter rosette becoming established (Table 3). This suggests that wet soil conditions and low competition on the glacier foreland may be relatively favourable for seedling establishment, whereas the successful establishment of a daughter rosette at the end of a stolon is relatively risky because there is no guarantee for the daughter to root on fertile ground and because the connection to the mother plant withers at an early stage. A recent study reported high seedling densities and survival in several other alpine species (Forbis 2003).

Clonal establishment showed less temporal variation than seedling establishment. Although connections of above-ground stolons wither and therefore do not provide continuous support by the mother plant (e.g. Callaghan & Emanuelsson 1985), the high and relatively constant clonal establishment in *G. reptans* may provide a large buffering capacity against environmental variation. Clonal off-spring may develop faster and become reproductive more quickly, and may therefore shorten the extremely long juvenile period of many alpine plants (Morris & Doak 1998; Forbis 2003).

Even though both sexual and clonal reproduction contributed to population growth, they may have a slightly different role for the dynamics of *G. reptans*. The fact that establishment from clonal off-spring is constantly higher than establishment from seeds suggests that clonal propagation may serve as a low risk alternative to the more unpredictable and insecure establishment from seeds. Germination success varied by nearly 200% among years in both populations, indicating that seedling recruitment may depend on variable environmental conditions to a higher degree than clonal establishment.

Elasticities of lambda

Three study years, and two transitions each for two populations, are rather short to understand the demography of a long-

lived plant. Nevertheless, elasticity analysis can be used to test the robustness of λ regarding changes in specific demographic parameters (e.g. de Kroon et al. 2000; Caswell 2001). In *Geum reptans*, the elasticity of λ was highest to changes in the proportion of small, medium and large adults remaining in the same stage (Table 1). The value of λ was far more sensitive to changes in adult survival than to changes in growth or reproductive parameters, a fact that is well known from woody species (Silvertown *et al.* 1993). According to Grime (1977), the life-history of plants living in stressful environments is expected to focus on stasis of adults at the expense of growth and fecundity. *G. reptans*, as a species of glacier forelands, has to cope with a highly unpredictable environment. As a long-lived species (maximum life span of about 30 years; A.R. Pluess, unpublished data) with low recruitment rates, *G. reptans* may be particularly vulnerable to adult mortality. The outstanding importance of adult survival could be seen at Furkapass, where during the period 2002–03 recruitment was not sufficient to balance the exceptionally high adult mortality of nearly 20%, which led to a negative growth rate. This result corresponds with results from other species of stressful habitats (Forbis & Doak 2004).

Thus, it can be concluded that even in the harsh alpine environment, population growth of a long-lived plant does not rely on clonal reproduction alone. In *G. reptans*, reproduction by seeds is an im-

portant contributor to population growth in favourable years but is also highly sensitive to environmental variation. Reproduction by clonal off-spring occurs more steadily, thus ensuring persistence. Both reproductive modes are important for population growth. Adult survival is crucial in the life-cycle of *G. reptans*, as it serves as a buffer against temporal variation, a condition of particular relevance in disturbed habitats such as alpine scree or glacier forelands.

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Chapter 3

Variation of sexual and clonal reproduction in the alpine *Geum reptans* in contrasting altitudes and successional stages

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Summary

We studied the relative proportion of sexual *vs.* clonal reproduction in 20 populations of the alpine pioneer plant *Geum reptans* in response to altitude (low and high) and succession (early and late). Additionally, the proportion of life-cycle stages, the proportion of reproducing adults, seed size, and seed number per flower head were determined. With increasing plant size, the probability of producing both flower heads and stolons increased ($P < 0.001$). Individuals of all size classes tended to produce more flower heads than stolons. Stolon production was more frequent only if plants reproduced by one reproductive mode ($P < 0.05$). The significant difference among populations in sexual reproduction and of seed number per flower head was not explained by habitat type. However, clonal reproduction was higher in populations at low and high altitude compared to populations at intermediate altitude ($P < 0.05$). High altitude populations were characterised by a tendency of small plants to decline and an increase in the proportion of large plants ($P < 0.05$) whereas the proportion of reproducing adults did not change with altitude. This indicates not only lower recruitment but also, that after successful establishment, growth and reproduction in *G. reptans* are not generally restricted, even above 2850 m. Our results suggest that variation in the proportion of sexual and clonal reproduction in *G. reptans* is probably more shaped by individual, i.e. plastic responses to local environmental conditions than by environmental gradients.

Key-words: clonal growth, glacier foreland, pioneer plant, plasticity, stolons, succession, trade-off

Introduction

Prominent features of alpine ecosystems are the steep gradients of altitude and climatic conditions shaping the environment and affecting alpine plant life. The natural fragmentation of alpine habitats created by small-scale differences in relief interacting with abiotic factors may influence a species' life-history and spatial distribution. Plants capable of growing in alpine environments are usually considered to be long-lived and to rely on clonal growth (Hartmann 1957; Billings & Mooney 1968).

Generally, the importance of clonal growth tends to increase with altitude (Bliss 1971; Klimeš *et al.* 1997) leading to a comparatively high fraction of clonal species occurring in extremely hostile habitats like pioneer communities on screes as well as in late successional alpine grasslands (Hartmann 1957; Stöcklin 1992; Klimeš *et al.* 1997; Klimeš 2003).

Clonal plants often show reduced sexual reproduction compared to non-clonal species (Crawley 1990; Schmid 1990; Silvertown *et al.* 1993; Eriksson 1997) and frequently seedling recruitment has been

considered to be rare (Eriksson 1989, 1992). Local population dynamics of many species are strongly dominated by clonal growth (Callaghan 1976; Crawley 1990; Eriksson 1992; Silvertown *et al.* 1993) assuring population growth and species' persistence during phases lacking sexual reproduction and increasing the fitness of established genotypes. Recruitment of seedlings is often restricted to founding events, 'windows of opportunities' or is closely linked to habitat disturbances (Jelinski & Cheliak 1992; Eriksson 1997). Nevertheless, seedling recruitment of clonal plants is easily underestimated (Eriksson 1989). Many studies revealed considerable genetic variation not only in clonal species in general (Ellstrand & Roose 1987; Hamrick & Godt 1989) but also in clonal plants from alpine habitats (Bingham & Ranker 2000; Till-Bottraud & Gaudeul 2002; Reisch *et al.* 2005). Sexual reproduction not only provides genetic variation as a basis for adaptation to long-term environmental changes but also promotes dispersal in time and space (Nathan & Muller-Landau 2000).

Plants may vary in their allocation to sexual and clonal reproduction and an investment in clonal growth may imply a trade-off with sexual reproduction (Cody 1966). Such trade-offs have been demonstrated for a variety of species (e.g. Law *et al.* 1983; Sutherland & Vickery 1988; Ronsheim & Bever 2000). Trade-offs also could involve structural constraints like the utilisation of the same meristems for sexual and clonal organs (Watson 1984;

Eriksson 1985). If a particular reproductive mode is favoured in a specific environment, selection is expected to act on the relationship between sexual and clonal reproduction (Loehle 1987). However, plants are also able to respond to changing environmental conditions by phenotypic plasticity, which may also be under selection (Sultan 1987). The relationship between sexual and clonal reproduction may be highly plastic in response to different environments (Sultan 2000; Fischer & van Kleunen 2002) leading to a variable ratio between both reproductive modes.

Here, we consider different altitudes and successional stages as the most striking environmental effects that alpine species may experience. The effect of altitude on the relationship between sexual and clonal reproduction is poorly understood. If the importance of clonal growth increases with altitude, one would expect relatively more allocation to clonal meristems and a decrease in allocation to sexual meristems in plants from high altitude. With increasing successional age, metapopulation theory predicts counterselection for dispersal traits (e.g. Olivieri *et al.* 1990; Olivieri *et al.* 1995; Harrison & Hastings 1996; Husband & Barrett 1996): Traits that enhance dispersal should be favoured in recently established populations since they are more likely founded by genotypes with high dispersal ability. As population age proceeds, within-population selection should favour persistence resulting in a decrease in allocation to

sexual reproduction whilst clonal reproduction increases. Selection for long-distance dispersal in early compared to late successional populations has been shown by Peroni (1994). Piquot *et al.* (1998) demonstrated opposing selection pressures for sexual and clonal reproduction in newly founded and old populations of *Sparganium erectum*, but similar studies on alpine plants in naturally fragmented environments are lacking. Additionally, we consider plant size as a possible factor influencing the relationship between sexual and clonal reproduction since it may be favourable to secure persistence first by clonal reproduction and to invest in the more nutrient-demanding seed production (Harper 1977; Watson 1984) only when a certain plant size has been reached.

We focused on the variation between sexual and clonal reproduction in *Geum reptans* L., a widespread alpine pioneer species of glacier forelands. *G. reptans* regularly produces above-ground stolons and flower heads both generated by the same axial meristems. This species belongs to the first colonisers after glacier retreat and shows long persistence and continuous seedling recruitment as succession proceeds. We compared the relative allocation of meristems to flower heads and stolons among populations of low and high altitude and of early and late successional stage for plants of different sizes. We addressed the following hypotheses: (1) The relative importance of clonal reproduction, i.e. the number and

proportion of clonal meristems producing stolons increases with altitude and successional age. (2) Small plants invest more in clonal reproduction than larger plants. (3) Furthermore, because we expect a general decrease in recruitment not only from seeds but also from clonal off-spring during succession due to ageing of populations and increasing competition and with altitude due to more severe climatic conditions, (4) we also checked for changes in the frequency of life-cycle stages among habitats.

Material and methods

The study species

Geum reptans L. (Rosaceae) is a clonal perennial rosette plant distributed in the Central Alps, the Carpathians, and the Mountains of North Albania, Montenegro, and South West Bulgaria. It usually occurs between 1950 and 3800 m a.s.l. on moist moraines, alluvial soils, block fields, and mountain ridges especially of lime deficient rocks (Weber 1995). Most populations are to be found between 2300 and 2800 m (personal observation). After glacier retreat *G. reptans* belongs to the first pioneer species on protosoils (Braun-Blanquet 1948). In tens to hundreds of years, succession proceeds to a vegetation type dominated by grasses and dwarf shrubs (Lüdi 1921). Strong competition and water stress may explain why *G. reptans* being a bad competitor is never

Table 1 Location (field name and canton abbreviation), elevation, co-ordinates, and number of studied individuals of 20 populations of *Geum reptans* from low and high altitude, or early and late successional stage, respectively. Sample size (*N*) contains individuals collected in three size classes (small, medium, large), total sample size is 907 plants.

Location	Population	Elevation (m a.s.l.)	Co-ordinates*	<i>N</i>
a) Low altitude				
Flueseeli, BE	Flu	2053	604602/139547	71
Lötschental, VS	Loe	2079	635850/144168	15
Steinlimigletscher, BE	Ste	2097	674927/173739	80
Val Roseg, GR	Ros	2149	786210/142475	19
Val Fex, GR	Fex	2162	781267/137535	59
b) High altitude				
Fuorcla Pischa, GR	Pis	2847	794256/149679	45
Diavolezza/Sass Queder, GR	Dis	2876	794483/143479	45
Flüela Schwarzhorn, GR	Sch	2976	791360/178541	33
Diavolezza/Munt Pers, GR	Dip	3006	793815/143434	45
Piz Languard, GR	Lan	3029	793020/151184	45
c) Early successional stage				
Scalettagletscher, GR	See	2534	791500/175270	45
Muttgletscher, VS	Mut	2594	674721/156252	45
Vadret da Radönt, GR	Rad	2650	792457/178423	45
Keschhütte, GR	Kee	2675	787020/167947	45
Vadret da Grialetsch, GR	Gri	2680	793449/175021	45
d) Late successional stage				
Scalettagletscher, GR	Scl	2267	790842/175706	45
Val dal Cambrena, GR	Cam	2329	797068/142237	45
Flüelapass, GR	Flp	2430	791623/180174	45
Keschhütte, GR	Kel	2523	785918/168435	45
Blauberg, VS	Bla	2550	674981/157897	45

* co-ordinates follow Swiss national grid

found in closed grasslands (Rusterholz *et al.* 1993).

Individuals of *G. reptans* consist of clumps of one to seven (rarely more) leaf rosettes emerging from a taproot. Axial leaf buds are used either for flower head or stolon production. Rusterholz (1992) found, that c. every fifth axial leaf bud is used for sexual reproduction producing a flowering stem while stolon production is

less regular. Buds for stolons and flower heads are initiated in the previous year and emerge in the following spring. Stolons can grow up to 1 m in length, forming a daughter rosette at the end, which roots and establishes in late summer when the connection to the mother plant dies back. Flower heads are hermaphroditic or rarely male and contain numerous ovaries (Weber 1995 and per-

sonal observation). Pollination predominantly occurs by flies, self-pollination results in non-viable seeds (Rusterholz *et al.* 1993). According to the elongated hairy style the nutlets are mainly dispersed by wind.

Sampling

In 2001, 20 populations of *Geum reptans* were selected in the Swiss Alps covering an area of 200 km (E-W) x 40 km (N-S), (Table 1, Fig. 1). Five populations were situated below 2160 m (low altitude) and five populations above 2850 m (high altitude). Additionally, five early successional and five late successional populations were selected at intermediate altitudes (around 2500 m). Early succession habitats had sparse vegetation on bare soil (cover $25\% \pm 1.6\%$ (mean \pm SE)) and by comparison of old topographical maps (Meyer 1796-1802; Eidg. topographisches Bureau 1845-1939, 1870-1949; Bundesamt für Landestopographie 1952-2004) glacier retreat can be dated c. 52 ± 8.7 years back. The presence of *Salix*-species and distinct higher vegetation cover ($79\% \pm 2.9\%$) characterised late successional sites from which the glacier retreated c. 151.8 ± 26.8 years ago. Populations from low and high altitude were selected from intermediate successional stages. However, there was a tendency for the low altitude populations to be of slightly later stages than the high altitude populations. Populations were of similar slope and exposure and except for altitude

and successional stage, there were no fundamental differences among them. The minimal distance between selected populations was 500 m. In each population, individuals of *G. reptans* were grouped into size classes (small, medium, large). Small plants had one leaf rosette, medium plants consisted of 2–3 leaf rosettes and large plants contained ≥ 4 leaf rosettes. In 2001, 15 reproducing individuals per size class were randomly chosen along a transect across each population. In three low altitude populations additional plants were sampled to compensate for the low numbers of individuals in other populations of the same category. The number of leaf rosettes and the numbers of stolons and flower heads of each plant were counted. In total, 297 small, 304 medium, and 306 large individuals were selected, resulting in a total sample size of 907 plants reproducing either by flower heads only, by stolons only or by flower heads and stolons simultaneously (Table 2). In 2002, 10 fruiting plants per size class were randomly selected within each population and the seed number of the largest flower head per plant was counted. In 2001, air-dried seed weight was measured in five populations (Bla, Flu, Gri, Mut, Scl; see Table 1).

Four plants per population and size class were selected. One flower head per plant was randomly chosen and mean individual seed weight was calculated from the total weight of 30 seeds. In 2002, 100 individuals per population were randomly selected along a transect. These plants

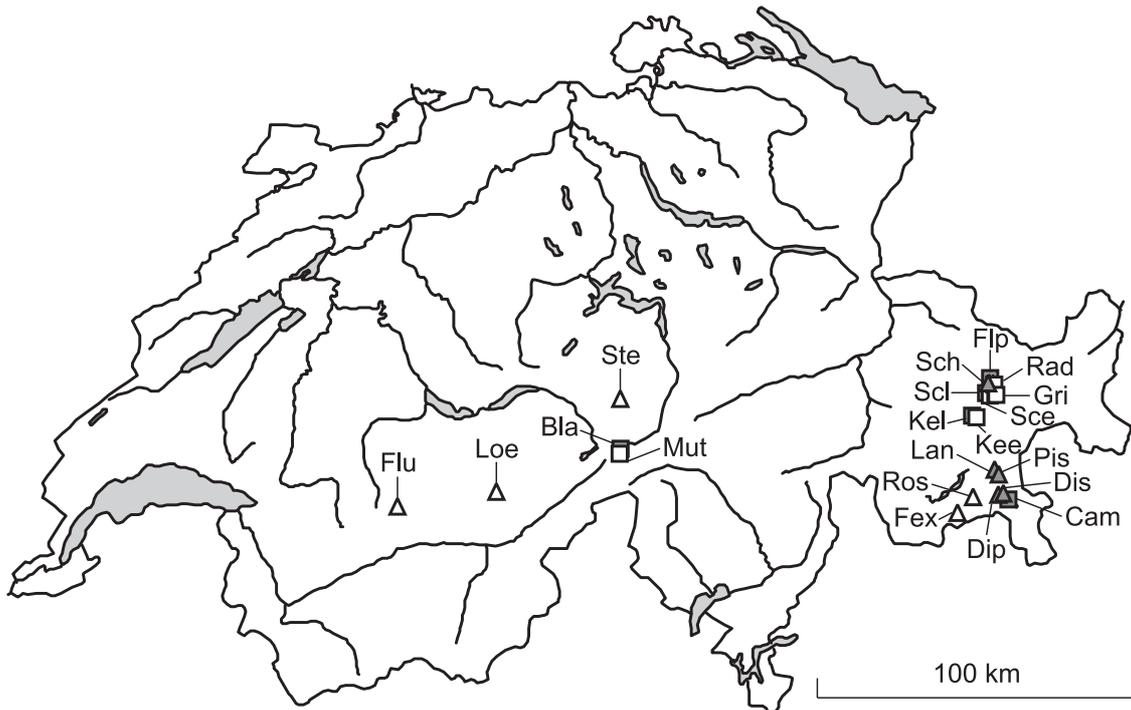


Fig. 1 Location of the 20 studied populations of *Geum reptans* in the Swiss Alps. Triangles: altitudinal position (white: low altitude populations, stippled: high altitude populations), squares: successional stage (white: early successional populations, stippled: late successional populations). Population abbreviations refer to Table 1.

were classified into juveniles, which were distinguished from adults by a different leaf shape, reproducing and non-reproducing adults. Adults were further subdivided into the three size classes. Seedlings were not considered.

Due to data structure (counts with zero values) reproductive measures were averaged at the level of population and size class. The reduced data set ($N = 60$) was used to test for effects of habitat type (populations of low and high altitude and of early and late successional stage), population, and size class on mean number of stolons and flower heads and the proportion of stolons by ANOVA (JMP 4.0, SAS Institute Inc.). Habitat type was tested against population ($F_{3,16}$), effects of population and size class, and size class \times

habitat type were tested against the remaining residual (population was considered as a random effect; Table 3). *A priori* contrasts were used to compare low *vs.* high altitudinal populations and early *vs.* late successional populations. All data were log-transformed.

Preferences of plants from the three size classes to produce stolons only, flower heads only or both simultaneously were analysed using χ^2 tests.

To test for habitat type effects on life-cycle stages, arcsine-transformed proportions of juveniles, small, medium, and large plants as well as the proportion of reproducing adults were analysed using one-way ANOVA. Effects of early *vs.* late succession and low *vs.* high altitude were tested with *a priori* contrasts.

Table 2 Number of small, medium, and large plants from 20 populations of *Geum reptans* which showed reproduction by flower heads only, by stolons only, or which reproduced by flower heads and stolons simultaneously.

	Small plants	Medium plants	Large plants
Flower heads only	65	59	32
Stolons only	127	70	75
Flower heads + stolons	105	175	199
Total	297	304	306

Data analysis

The effects of habitat type, population, and size class on seed number were tested by ANOVA with log-transformed data. The effect of habitat type was tested against population, the effect of size class was tested against the interaction of size class x population (population was considered as a random effect). Data of 478 individuals from 18 populations were available for this analysis.

Results

Effects of plant size on sexual and clonal reproduction

Plant size strongly influenced sexual and clonal reproduction. The probability of producing flower heads and stolons simultaneously increased with increasing plant size ($P < 0.001$; Table 2). If plants reproduced only by one reproductive mode, stolon production was more frequent ($P < 0.05$; Table 2). Both mean stolon and flower head production increased with increasing plant size

($P < 0.001$ for both stolons and flower heads; Table 3; Fig. 2). Thus, large plants generated almost three times more stolons and flower heads than small plants. On average, individuals of all size classes tended to produce more sexual than clonal meristems (% flower heads of total reproductive meristems, $P = 0.09$): Small plants produced $51.9\% \pm 3.9\%$ (mean \pm SE), medium plants $56.8\% \pm 4.2\%$, and large plants $53.2\% \pm 5.2\%$ sexual meristems. If only individuals with both reproductive modes in all three size classes were considered, sexual meristems prevailed with $55.3 \pm 0.81\%$.

Effects of altitude and succession on sexual vs. clonal reproduction

Among all populations, large variation in sexual ($P < 0.05$) and clonal reproduction occurred (Table 3, Fig. 3). Population averages ranged from 2.4 to 5.9 reproductive meristems per individual. Population averages of mean number of stolons per individual varied from 1.1 to 2.7 and mean number of flower heads per plant ranged from 0.9 to 3.4.

Table 3 Results of ANOVAs on the influence of habitat type (altitude, successional stage), population, and size class on mean number of stolons per plant, flower heads per plant, and mean proportion of stolons per plant in *Geum reptans* (see methods for model specification).

Source of variation	DF	Parameter tested					
		Stolons		Flower heads		% Stolons	
		SS	F	SS	F	SS	F
Habitat type	3/16	0.0384	0.8525	0.0330	0.6245	0.0355	1.7963
Contrast low <i>vs.</i> high	1/16	0.0025	0.1668	0.0002	0.0123	0.0015	0.2250
Contrast early <i>vs.</i> late	1/16	0.0148	0.9868	0.0028	0.1602	0.0025	0.3750
Population (habitat type)	16/32	0.4466	1.8570	0.7463	2.6501	0.1823	1.7317
Size class	2/32	2.1079	70.1236	1.8812	53.4432	0.0217	1.6494
Size class x habitat type	6/32	0.0342	0.3789	0.1999	1.8930	0.0507	1.2849
Error	32	0.4810		0.5632		0.2106	

Neither altitude nor successional stage significantly influenced the relative proportion of stolon and flower head production in reproducing plants of *Geum reptans* (Table 3, Fig. 4). Interestingly, there was a significant difference between low + high populations *vs.* early + late populations ($P < 0.05$): Populations of marginal altitudinal range (low + high altitude) produced on average 10% more stolons than early + late successional populations at intermediate altitude (Fig. 4).

Effects of altitude and succession on population structure and proportion of reproducing adults

Population structure of *Geum reptans* differed between low and high altitude habitats (Fig. 5a): There was a higher proportion of small plants at low altitude compared to high altitude populations ($P = 0.07$). In contrast, the proportion of large plants increased from low altitude to

high altitude sites ($P < 0.05$). A similar shift in population structure was observed between early and late successional stages (Fig. 5b): Compared to early successional populations, the proportion of small plants declined in late successional populations ($P = 0.05$), whereas the proportion of large plants showed an increase with successional age ($P < 0.05$).

The proportion of reproducing adults was neither significantly influenced by altitudinal position nor by successional stage of populations (Fig. 5).

Effects of altitude and succession on seed number and seed size

There was no effect of altitude on the number of seeds per flower head of *Geum reptans*. However, a significant interaction between size class and habitat type (Table 4) indicated that seed number of small plants from early successional habitats was increased compared to small

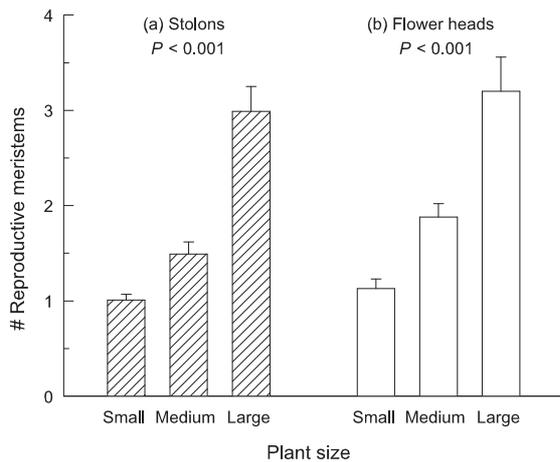


Fig. 2 Clonal and sexual reproduction in small, medium, and large reproducing individuals of *Geum reptans*: (a) number of stolons (mean ± SE), (b) number of flower heads (mean ± SE). The same individuals were used for both investigations.

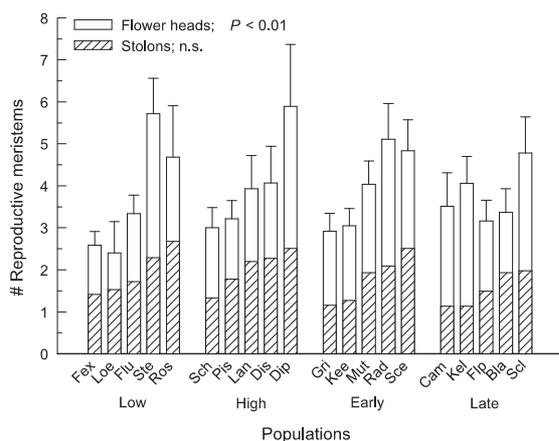


Fig. 3 Mean number of stolons and flower heads (\pm SE for reproductive meristems) in 20 populations of low and high altitude and early and late successional stage of *Geum reptans*. Populations within habitat type are grouped by increasing mean number of stolons.

plants of late successional habitats ($P < 0.05$ from *a priori* contrast), while this was not the case for medium and large plants. There was significant variation among populations in the number of seeds per flower head ($P < 0.05$). With the above mentioned exception, the number of seeds

was not influenced by plant size or by the interaction between plant size and population. In average, small plants produced 104.1 ± 2.2 (mean \pm SE, CV = 25.6), medium plants 105.0 ± 2.3 (CV = 27.2), and large plants 108.9 ± 2.2 (CV = 26.0) seeds per flower head. Individual seed weight was only available for five populations ($0.39 \text{ mg} \pm 0.02 \text{ mg}$) and did not differ between size classes (data not shown).

Discussion

Sexual and clonal reproduction both have an important role in the life-history of the alpine pioneer *Geum reptans*. Individuals of all size classes produced slightly more flower heads than stolons. Plants reproducing by one reproductive mode reproduced significantly more by stolons than by flower heads. Contrary to expecta

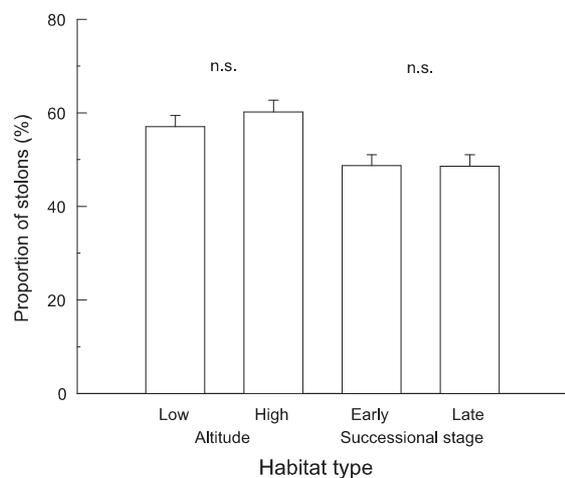
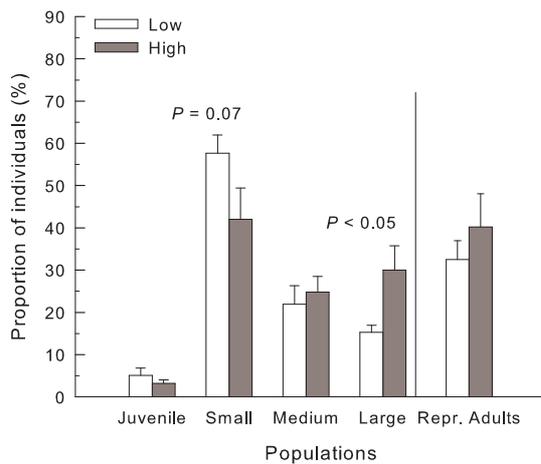


Fig. 4 Influence of habitat type (altitude, successional stage) on the proportion of stolons (mean \pm SE) in *Geum reptans*.

(A) Altitude



(B) Successional stage

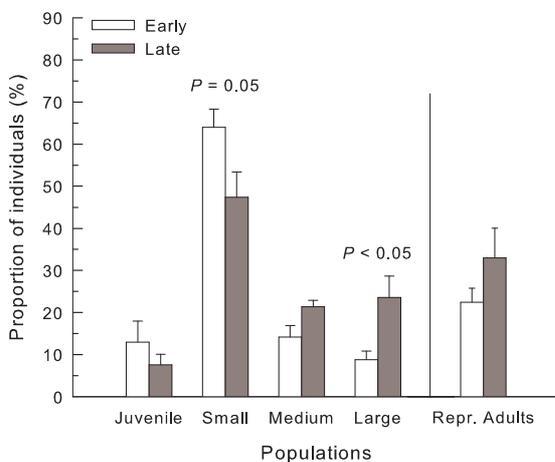


Fig. 5 Effects of (A) altitude and (B) successional stage on the proportion of juveniles, small, medium, and large adults and the proportion of reproducing adults (mean \pm SE) in *Geum reptans*.

tion, the number and relative importance of clonal and sexual reproduction did not change due to contrasting successional stage or altitude. But there was large variation in the proportion of stolons and flower heads among populations. Interestingly, the proportion of clonal reproduction was higher in marginal populations (low + high altitude) compared to populations at intermediate altitude (early + late successional stage).

Effects of plant size on sexual and clonal reproduction

According to Samson & Werk (1986) and Stöcklin & Favre (1994), many plant species show a linear correlation between size and reproductive biomass. In *Geum reptans*, the number of reproductive meristems as well as the probability of producing flower heads and stolons simultaneously increased with size. Seed production is considered to be more nutrient-demanding than clonal reproduction (Harper 1977; Watson 1984). This may explain why small plants invested preferentially in clonal reproduction while larger plants having more resources available invested into both reproductive modes tending to prefer sexual reproduction. Thus, in *G. reptans* individuals may alter their reproductive behaviour depending on size. Yearly variation in resources available for reproduction may explain why even in the largest size class one third of all individuals reproduced only by one reproductive mode. Yearly variation in reproductive yield is common in herbs (Kelly 1994; Kelly & Sork 2002) and probably particularly frequent at high altitude, where the short growing season and low temperatures limit growth and storage.

Table 4 Results of ANOVA on the influence of habitat type (altitude, successional stage), population, and size class on the number of seeds per flower head of *Geum reptans* (see methods for model specification).

Source	DF	SS	MS	F	P
Habitat type	3	2731.98	910.66	0.68	0.58
Population (habitat type)	14	18145.18	1296.09	1.77	< 0.05
Size class	2	2060.54	1030.27	1.32	0.28
Size class x habitat type	6	11675.31	1945.89	2.65	< 0.05
Size class x population (habitat type)	27	21047.57	779.54	1.06	0.38
Error	425	311709.55	735.43		

Effects of altitude and succession on sexual vs. clonal reproduction

Environmental heterogeneity is considered to promote genetic variation in life-history traits (Stratton 1994; Linhart & Grant 1996; Prati & Schmid 2000). Large-scale environmental gradients are well known to result in locally adapted genotypes (Clausen *et al.* 1947; Linhart & Grant 1996). Successional change can lead to modifications in selection pressures that act on life-history (Cody & Overton 1996). Piquot *et al.* (1998) found opposing selection pressures for sexual and asexual reproduction in young and old populations of *Sparganium erectum*. Altitudinal variation also has been shown to be sufficient altering the reproductive outcome of plants. With increasing altitude, (Young *et al.* 2002) showed higher importance of clonal growth in *Rutidosis leiolepis*.

Accordingly, we expected an increase in the relative importance of clonal reproduction with successional age and altitude in *Geum reptans*. However, the variation in reproductive behaviour of populations (Fig. 3) was not explained by contrasting

habitats. There are two mutually not exclusive explanations for this result: First, reproductive differences of populations may reflect mainly small-scale variation in environmental conditions not related to altitude or succession overriding the effects of gradients. Second, if genotypes of *G. reptans* are characterised by high phenotypic plasticity, this might restrict or even prevent adaptation to contrasting environmental conditions. Several studies with species dispersed across broad geographic and environmental ranges indicated comparatively little genetic or morphological differentiation but genetically similar populations of highly plastic genotypes (Williams *et al.* 1995; Hermanutz & Weaver 1996; Sultan 2000). Particularly, colonising species have been found to be highly plastic, enabling them to spread into new habitats without experiencing adaptation through selection (Williams *et al.* 1995). If a species is composed of genotypes with the capacity of broad plastic responses, no selection for locally adapted genotypes is expected to occur (Schlichting 1986; Sultan 1987, 1995). A further reason why we detected

no effect of contrasting habitats on reproductive behaviour could result from the high inter-annual individual variation in stolon and flower head production. In a parallel demographic study with *G. reptans* (Weppeler *et al.* 2006) only 28% of the initially reproducing 40 individuals reproduced continuously during all three years of the study. Taken together, our results suggest that the observed variation among populations in reproduction largely results from differences in local environmental conditions. This conclusion is supported by a common garden experiment with *G. reptans*. There as well, in spite of significant variation, differences in reproductive behaviour were not explained by population origin from successional gradients (Pluess & Stöcklin 2005).

Unexpectedly, clonal reproduction increased in populations from low and high altitudes compared to populations at intermediate altitudinal position (Fig. 4). The reasons for this increase of clonal reproduction at the upper and lower end of the altitudinal distribution in *Geum reptans* are probably not identical. The upper limits of a species' distribution are determined by abiotic factors while biotic factors control the lower limits of alpine plants (Billings & Mooney 1968). Conditions like topsoil desiccation, high surface temperature at bare soils, night-time ice-needle formation, and cryogenic processes may explain low seedling survival at high altitudes (Bliss 1971; Urbanska & Schütz 1986; Scherff *et al.* 1994). But why should clonal reproduction also increase in popu-

lations at the lowest sites compared to populations from intermediate altitude? Certainly, alpine habitats at lower altitude are often characterised by higher inter-specific competition, one of the possible reasons for the lower distributional limits of such species (Rochow 1970). *G. reptans* is very susceptible to competition (Pluess & Stöcklin 2005), and seedlings lacking the support of established adults (in contrast to vegetative off-spring) may be particularly vulnerable to crowding. Thus, the increase in clonal reproduction at low altitude could also act as a sort of escape to small-scale competition.

Effects of altitude and succession on population structure and proportion of reproducing adults

As expected, we observed relatively fewer small adults and an increase in large adults in high altitude populations of *Geum reptans* indicating lower recruitment, but also longevity of well established individuals even in habitats above 2850 m. Safe-sites at such altitudes are scarce and seedling mortality is high (Urbanska & Schütz 1986; Chambers 1995). Establishment of clonal off-spring may also be critical in comparison with lower sites for the same reasons. The constant proportion of reproducing adults also illustrates that even if recruitment of new individuals may be low, reproduction in *G. reptans* is not restricted at high altitudes.

The increase of large plants from early to late successional habitats reflects the expected ageing of populations during succession. Increased competition and water stress are likely in reducing recruitment of *G. reptans* in late successional populations (Rusterholz *et al.* 1993).

Effects of altitude and succession on seed number and seed size

We detected no influence of contrasting altitudes or successional stages on the number of seeds or seed weight per flower head in *Geum reptans* with the exception that seed number of small plants was increased in early successional habitats compared to late successional habitats. This result was probably due to different habitat conditions and did not result from selection for higher seed number in early succession habitats since otherwise, seed number of medium and large plants would have been also affected by successional stages. Although seed size and number per flower head are generally well preserved traits (Smith & Fretwell 1974; Harper 1977), most species vary their seed output depending on availability of resources (Westoby *et al.* 1992). Totland & Birks (1996) and Totland (1997) demonstrated a considerable decline in seed weight and number with altitude in populations of *Ranunculus acris* suggesting that climatic conditions may negatively influence reproduction. Competition as a factor related to succession could also result in increased

abortion rates of seeds (Lee 1988; Stöcklin 1997). As for the proportion of clonal reproduction, populations differed in the number of seeds per flower head indicating once more that spatial variation among sites not related to altitude or succession is more pronounced than the effects of gradients.

To conclude, in spite of the prominent role of reproduction by stolons in *G. reptans*, more meristems are used for sexual reproduction, particularly in large plants, indicating the importance of seeds for this species. The considerable difference in the relative importance of flower head production among the 20 study populations could not be explained by environmental gradients but is probably largely a result of plastic responses to the highly heterogeneous habitat conditions in the alpine landscape.

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Chapter 4

Does pre-dispersal seed predation limit reproduction and population growth in the alpine clonal plant *Geum reptans*?

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Summary

We studied the impact of the seed damaging gall midge larva *Geomyia alpina* on its perennial alpine host plant *Geum reptans*. We analysed the effect of seed predation on reproduction by seeds, i.e. seed number, seed mass, and seed viability and on growth and clonal propagation of non-protected plants in comparison to plants protected from predation by an insecticide. Additionally, we assessed the consequences of seed predation for population growth using matrix projection modelling. Seed predation resulted in a decrease in total seed mass per flower head by 23.8% in non-protected plants ($P < 0.05$). Individual seed mass decreased with increasing infestation intensity ($P < 0.05$). Seed number remained unaffected because the sucking feeding behaviour by gall midge larvae does not evoke seed abortion. Percent germination of seeds from non-protected plants was reduced by 97.9% compared to seeds from protected plants. According to reduced seed viability, modelling revealed a decrease in population growth rate from $\lambda = 1.055$ to $\lambda = 1.041$. Predation did neither influence total plant biomass nor biomass fractions. But stolon dry-weight of non-protected plants increased by 24.1% ($P < 0.05$), which may indicate a trade-off between sexual reproduction and clonal propagation. Our results demonstrate that despite substantial reduction of viable seeds, predation by gall midge larvae only slightly affected population growth of *G. reptans* suggesting that in this alpine species, persistence by longevity and clonal propagation can balance potential seed losses by predation, at least for local population growth.

Key-words: clonal growth, gall midge, *Geomyia alpina*, herbivory, matrix projection modelling

Introduction

Pre-dispersal seed predation is well known to have substantial impact on the relative reproductive success of individuals by limiting the number of viable seeds (e.g. Hendrix 1979; Louda 1982; Louda & Potvin 1995; Briese 2000; Leimu *et al.* 2002) and altering flowering phenology (e.g. Janzen 1971; Eriksson 1995; Louda & Potvin 1995; Albrechtsen 2000; Mahoro 2002; Russell & Louda 2004). Predation of seeds prior to dispersal is experienced

by a variety of plant species in different habitats throughout the world. Most pre-dispersal seed predation is caused by small insects showing high host-specificity (Crawley 1992). These predators cause damage to a variable degree by attacking whole fruits, feeding on individual seeds, or sucking on tissue of ovules (Crawley 1997). Theoretically, it is expected that pre-dispersal seed predation should have consequences not only for individual reproduction but also for growth and dynamics of populations if seed supply

reduces recruitment to below the sustainable density (Harper 1977). Louda (1982) and Louda & Potvin (1995) were among the first who demonstrated a direct effect of inflorescence-feeding herbivores on recruitment, plant demography, and fitness by limiting total seed output. However, even despite an increasing number of studies associating seed predation and population growth (e.g. Briese 2000; Kelly & Dyer 2002; Fröborg & Eriksson 2003), effects of pre-dispersal seed predation on population dynamics of most host-plants are still poorly understood and controversially discussed.

In fact, the persistence of many plant populations does not always depend critically upon current seed production (Cohen 1968; Eriksson 1996). Differences in life-histories largely determine how strong a plant may respond to seed losses or not. The existence of a persistent seed bank may buffer potential seed losses by seed consumers in time (Parker 1985; Crawley 1990). Also a species' life-span, particularly whether it is semelparous or iteroparous, is considered to be an important aspect in assessing the role of pre-dispersal seed predation for population dynamics (Briese 2000). Immigration of seeds from other patches may balance low seed availability in predated populations (Roff 1974; Eriksson 1996). Nevertheless, since seed production of most plants is large, increasing mortality of seeds during germination can have substantial effects on the number of surviving seedlings in a population (Crawley 1992).

Most studies of the effects of pre-dispersal seed predation on recruitment and population growth focus on annual plants (e.g. Szentesi & Jermy 2003) or short-lived perennials (e.g. Louda & Potvin 1995; Briese 2000). In long-lived perennials, due to the complexity of recruitment, the impacts of seed losses are difficult to determine (Andersen 1989). Clearly, independent of life-history, species must be followed over several years and locations to account for environmental variation. A combination of field measurements and matrix projection modelling may provide a promising approach to assess the impact of seed predators on population growth rate (Fröborg & Eriksson 2003).

Destruction of flowers or immature fruits may induce changes in resource allocation of plants (Hendrix 1988). Compensation for seed losses might particularly evolve in plants subjected to a predictable risk of damage by host-specific herbivores (Crawley 1983; Järemo *et al.* 1996). As a consequence, resources that would have been used for seed and fruit maturation may be stored, may be allocated into compensatory flowers or fruits that would normally be aborted or may be used for the production of non-reproductive tissue (Janzen 1971; Hendrix 1979; Crawley 1997). Accordingly, for clonal plants it could be inferred that the loss of seeds due to predation may alter the balance between sexual reproduction and clonal growth in favour of the latter. Support for this assumption comes from studies detecting a trade-off between

sexual reproduction and clonal propagation (e.g. Law *et al.* 1983; Sutherland & Vickery 1988; Piquot *et al.* 1998; Ronsheim & Bever 2000). However, interestingly, there are only few studies on seed predation in clonal plants considering potential benefits for clonal growth (Doak 1991).

We used an exclusion field experiment to determine the effects of pre-dispersal seed predation on sexual reproduction and clonal propagation in *Geum reptans* L., a long-lived alpine pioneer species occurring on glacier forelands. Furthermore, we simulated the consequences of reduced seed viability due to pre-dispersal seed predation on the population growth rate (λ) of *G. reptans* using a matrix projection model. *G. reptans* is an iteroparous rosette plant producing flower heads and above-ground stolons, but does not form a persistent seed bank. The seeds of this species are damaged by larvae of a recently discovered specialist gall midge (Skuhrová *et al.* 2006). We addressed the following questions: (1) What are the effects of pre-dispersal seed predation on reproduction by seeds, i.e. seed number, seed mass and seed viability? (2) Are other traits, i.e. growth and clonal propagation, also affected by the predation of the gall midge? (3) What are the consequences of pre-dispersal seed predation for population growth rate (λ)?

Material and Methods

Study species

Geum reptans L. (Rosaceae) is a clonal perennial rosette plant occurring between 1950 and 3800 m a.s.l. This pioneer species grows on moist moraines and alluvial soils of glacier forelands, block fields and mountain ridges, particularly on lime-deficient soils. Its distribution ranges from the Central Alps to the Carpathians and the Mountains of Northern Albania and Macedonia (Weber 1995). Individuals of *G. reptans* are about 5–15 cm in height and form clumps of 1 to c. 7 leaf rosettes emerging from a taproot. In spring, axial leaf buds initiated in the previous year give rise to flower heads and c. 2 weeks later to above-ground stolons. Stolons can grow up to 1 m in length. At the end of a stolon, a clonal daughter rosette develops and establishes a new individual in autumn when the connection to the mother plant withers (clonal propagation). Flower heads are generally hermaphrodite and contain c. 100 ovaries, but male flower heads also rarely occur (Weber 1995; T. Weppeler, unpubl.). *G. reptans* is pollinated mainly by flies (Heß 2001); self-pollination of the proterogynous flower heads results in non-viable seeds (Rusterholz *et al.* 1993). Plants produce on average 105.9 ± 11.0 (mean \pm SD) seeds per flower head; abortion of ovules is usually very low ($0.6 \pm 1.8\%$, $n = 60$; Authors, unpubl.). In accordance with the elongated hairy style, the nutlets are mainly wind-dispersed.

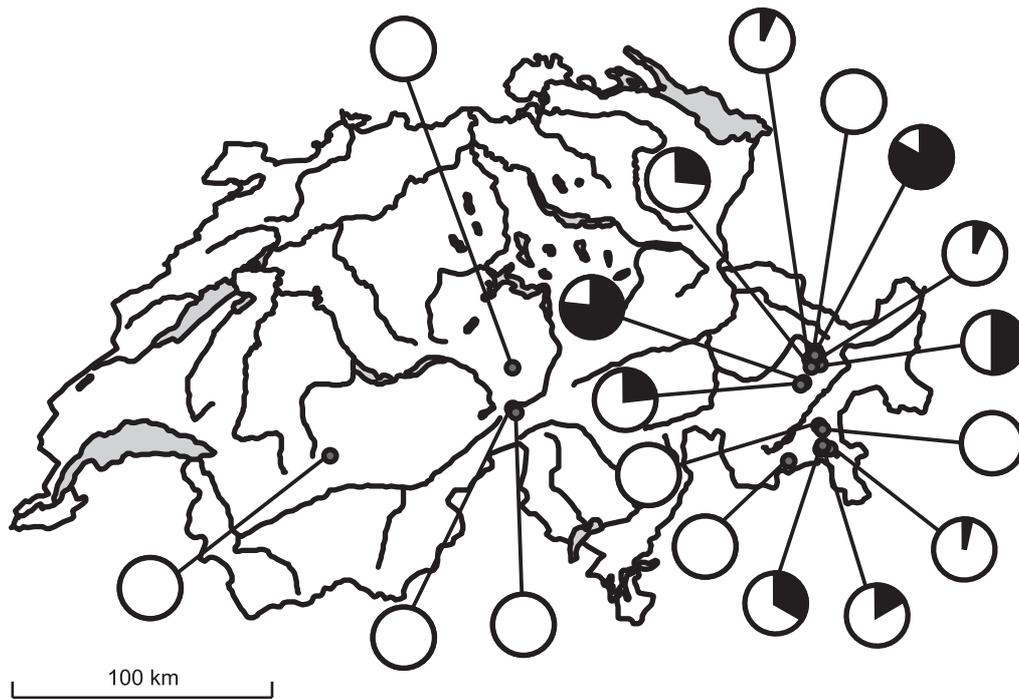


Fig. 1 Location of 18 populations of *Geum reptans* in Switzerland and their frequency of infestation (%) by gall midge larvae. The filled part of pies refers to percent individuals with infested flower heads. Frequency of infestation was independent of altitude and successional stage of populations.

G. reptans forms no persistent seed bank (Schwienbacher & Erschbamer 2002).

Developing seeds of *G. reptans* are damaged by larvae of the recently described gall midge species *Geomyia alpina* Skuhrová (Cecidomyiidae; Skuhrová *et al.* 2006). We observed infestation by gall midge larvae in 10 out of 18 populations of *G. reptans* surveyed in the Swiss Alps (Fig. 1). Infestation of flower heads varied between 3.6% and 83.3%. *G. alpina* does not induce galls but feeding results in small and atrophied seeds sticking to each other (T. Wepler, unpubl.). Adult gall midges emerge in spring, mate and infest the flower heads of *G. reptans* by ovipositing eggs. Larvae hatch after several days and develop inside the flower heads sucking sap of developing nutlets. In autumn, the mature larvae leave the host plant and

overwinter in the soil. Gall midges developing in alpine host plants show usually one generation per year (Skuhrová *et al.* 1984), which is probably also true for the present species.

Study site

The study site is a large population of c. 20'000 individuals of *Geum reptans* on the foreland of Scaletta glacier in Eastern Switzerland (WNW-exposed slope with c. 20° inclination, 2400 m a.s.l., 791335/175478, Swiss national grid). In 1991, Rusterholz (1992) reported heavy infestation of this population by gall midge larvae, resulting in 10–40% seed loss. Gall midge larvae were again observed during 2000–2002 (no data available for 1992–

1999), but we assume that gall midge larvae were continuously present since gall midge populations often remain at constant levels for prolonged periods (Skuhrová *et al.* 1984). No other predators feeding on seeds of *G. reptans* were observed.

Field study

At the end of June 2001, 122 individuals of *Geum reptans* with buds of flower heads were randomly selected so that the minimum distance between individuals was at least 2 m (Table 1). According to life-cycle stages of reproducing plants, individuals were grouped into three size classes: small (1 leaf rosette), medium (2–3 leaf rosettes), and large plants (≥ 4 leaf rosettes). Twice the number of medium-sized plants was selected, because it was planned to harvest half of these plants in autumn 2001.

In half of the plants within each size class (64 plants in total), all flower heads were sprayed with a 0.05% solution of a systemic broad-spectrum insecticide against sucking and herbivorous insects [Perfekthion®, BASF AG, Maag Agro, 8157 Dielsdorf, Switzerland; active ingredient dimethoat (40%)]. Insecticide-treated plants are subsequently referred to as ‘protected’, regardless of whether they were infested. The flower heads of the other half of the plants (58 plants in total) were sprayed with the same amount of water; these plants are subsequently re-

ferred to as ‘non-protected’. The insecticide treatment was first applied on buds of flower heads and repeated fortnightly for 12 weeks. Direct treatment of unpollinated flower heads was avoided. We repeated the treatment on the same plants in 2002. However, due to high inter-annual variation in reproduction typical of *G. reptans* (Wepler *et al.* 2006) and an avalanche partly burying the study site, the number of experimental plants which flowered in the second year was very low. Thus, we mainly present results from 2001, and only a summary of the results from 2002.

The number of stolons and flower heads per plant was counted fortnightly. From mid July to mid August, the intensity of larval infestation was measured fortnightly on a randomly selected flower head per plant and classified as (1) none (uninfested), (2) slightly (by 1–10 larvae infested), (3) heavily (by more than 10 larvae infested; mean larvae number of heaviest infested flower heads was 37.2). If the measures differed among surveys, the highest measured infestation intensity was chosen. Prior to seed-dispersal, all flower heads were bagged separately with small-meshed nylon fabric to avoid loss of mature seeds. At this time, new infestation of flower heads was unlikely. In October, mature seeds were harvested, air-dried, and the number of seeds, individual seed weight, and total seed weight per flower head was calculated. In October 2001, above-ground biomass of half of the medium-sized plants (15 non-protected, 14 protected) were harvested, separated into

Table 1 Number of flower heads and stolons per plant (mean \pm SE) in small, medium, and large individuals of *Geum reptans* in two treatments of an experiment to test for the effects of pre-dispersal seed predation by gall midge larvae.

Plant size	N	Treatment	# Flower heads per plant (mean \pm SE)	# Stolons per plant (mean \pm SE)
Small	17	non-protected	0.65 \pm 0.19	1.47 \pm 0.44
Medium	31	non-protected	1.61 \pm 0.31	1.13 \pm 0.24
Large	10	non-protected	2.50 \pm 0.73	1.90 \pm 1.36
Small	21	protected	0.81 \pm 0.20	0.52 \pm 0.15
Medium	30	protected	1.50 \pm 0.30	1.07 \pm 0.23
Large	13	protected	3.08 \pm 0.89	1.15 \pm 0.36

green leaves, dead leaves, stems, leaf buds, sexual and clonal reproductive organs. After drying at 80°C, the biomass was weighted.

In order to test whether growth of *G. reptans* was affected by the insecticide, 26 clonal off-spring of untreated individuals were randomly selected in 2001 and raised in the greenhouse for 9 months. Thereafter, half of these plants were sprayed with insecticide and the other half was sprayed with the same amount of water (eight weeks; fortnightly applied). Above-ground biomass per plant was harvested, separated into the same fractions as in the field study and weighted after drying at 80°C. The insecticide treatment did not have an effect on any of the collected biomass fractions or on total biomass ($F_{1, 19} < 1.4$, $P > 0.05$ for all biomass fractions and total biomass), confirming that the insecticide did not affect plant growth directly.

Seed viability and effect on population growth rate

To test for seed viability, mature seeds from 5 non-protected and 5 protected plants of *Geum reptans* were collected in 2001 and 2002. Additionally, mature seeds originating from a population at Lötschental not infested with gall midge larvae (SE-exposed slope with c. 24° inclination, 2079 m a.s.l., 635850/144168, Swiss national grid, and 158 km apart from the foreland of Scaletta glacier) were collected in 2002. Seeds collected in 2001 and 2002 were stored at room temperature until spring 2003. After washing in 80% ethyl alcohol, seeds were placed into petri-dishes lined with filter paper (25 seeds per petri-dish), watered and chilled at 4°C for 6 weeks. For the seeds from 2001, 10 petri-dishes per treatment were used, 15 petri-dishes per treatment were used for the seeds from 2002, and 10 petri-dishes were used for the seeds of the not infested population at Lötschental (in total 60 petri-dishes). Afterwards, petri-

dishes were transferred into the greenhouse (mean temperature c. 20°C) and seeds were allowed to germinate for 8 weeks. Germination was detected by penetration of the radicula, and germinated seeds were continually removed. Percent germination was calculated for each petri-dish. Percent germination within treatments did not differ between years (Wilcoxon-rank sum test; $Z = -0.19$, $P > 0.8$) indicating that storage had no effects on seed viability.

To analyse the consequences of pre-dispersal seed predation on population growth rate of *G. reptans*, we used a stochastic matrix model based on demographic data from a nearby population not infested by the gall midge, situated at Vadret da Porchabella (2650 m, 11 km distant from the study site). This specific model was developed to analyse population growth of *G. reptans* in relation to variation in proportions of sexual reproduction and clonal growth (Wepler *et al.* 2006). Here, for the computation of the population growth rate λ , a standard transition matrix was calculated based on demographic data over three years (2000–2002) from observations of 579 plants in 30 permanent plots of 1 m² at Vadret da Porchabella. Calculations of population growth rates were performed with the program package Ramas EcoLab 2.0, Sinauer Associates, Inc. Transition probabilities were calculated between five life-cycle stages (seedlings, juveniles, small adults, medium adults, large adults). During the three years of observation at Vadret da

Porchabella, sexual reproduction and clonal propagation occurred regularly. The numbers of seeds and stolons were counted separately for each stage of adult plants and averaged over the three years. Similarly, the percentages establishment of seedlings and stolons were observed yearly and averaged over the study period. An annual production of 69.8 ± 22.7 seeds (mean \pm SD) and 1.2 ± 0.1 stolons was found per reproducing adult; percentage germination was 1.2%, and percentage of successful clonal propagation of rosettes at the end of stolons was 53.2%. Population growth rate of this population not infested by the gall midge was $\lambda = 1.055$ (Wepler *et al.* 2006). To simulate the effect of seed predation by the gall midge observed in the population at Scaletta glacier on population growth rate, the matrix model described above was modified to take into account the decreased number of viable seeds after predation. Mean calculated seed numbers derived from the population at Vadret da Porchabella were multiplied by the reduction in viable seeds due to infestation frequency observed in the field experiment at Scaletta glacier. The simulated decrease in population growth rate λ was compared with the observed population growth rate in the population not infested by the gall midge and with the growth rate of the same population simulated without any viable seed production allowing only growth by clonal propagation ($\lambda = 1.027$). To evaluate the relative contribution of life-cycle components to population growth rate,

elasticities of matrix elements were calculated using the program package R 2.1.1. The elasticity of λ was highest to changes in survival of adult plants (elasticity 73.7%). The elasticity of λ to changes in growth was 8.8% and elasticities of λ to changes in clonal growth and sexual reproduction were 11.6% and 0.08%, respectively. Long-term effects of population growth were then evaluated with stochastic simulations over 30 years and 1000 replicates (Caswell 2001).

Data analysis

Individual plants were treated as replicates. Aborted flower heads and incomplete stolons were excluded except for the analysis of biomass. If more than one flower head or stolon was present in a plant, means for seed mass and seed number per flower head and stolon number were calculated. If necessary, data were log-transformed to achieve normally distributed residuals and variance homogeneity. Kruskal-Wallis tests were used to compare differences in the number of flower heads and stolons per plant in total and for each size class and to examine the effect of treatment on percent germination. T-tests were performed to test for effects of treatment on plant biomass, stolon dry-weight, seed number per flower head, and total seed mass per flower head. The influence of infestation intensity on the number of seeds per flower head and on individual seed mass was analysed by

one-way ANOVA. To study the effect of gall midge infestation on population growth, population growth rates (λ) were calculated. All statistical analyses were conducted in JMP 4.0, SAS Institute Inc.

Results

Field experiment 2001

In 100% of the flower heads of non-protected plants, living larvae of *Geomyia alpina* occurred whereas only dead larvae were found in 78.6% of the protected plants, (with the rest, 21.4% free of larvae), data that confirm the effectiveness of the insecticide.

The number of flower heads and stolons did not differ between treatments. The number of flower heads significantly increased with increasing plant size (Kruskal-Wallis test; chisquare = 10.4 for protected and 9.8 for non-protected plants, $P < 0.01$), but the number of stolons was not influenced by plant size (Kruskal-Wallis test; chisquare = 2.7, $P = 0.3$ for protected and chisquare = 0.7, $P = 0.7$ for non-protected plants; Table 1).

Predation by gall midge larvae did not affect the number of developing seeds per flower head (85.3 ± 3.2 (mean \pm SE) for protected and 85.0 ± 3.6 for non-protected plants; $F_{1,88} = 0.02$, $P = 0.9$). Seed number per flower head significantly increased with infestation intensity (81.9 ± 4.3 and 93.1 ± 3.9 for slightly and heavily infested flower heads, respectively; $F_{2,87} = 3.5$,

$P < 0.05$). In non-protected plants, total seed mass per flower head was significantly reduced by 23.8% compared to protected plants ($F_{1, 88} = 5.4$, $P < 0.05$; Fig. 2a), and individual seed mass of heavily infested flower heads was significantly lower compared to not infested flower heads ($F_{2, 87} = 5.0$, $P < 0.01$; Fig. 2b).

Total biomass of non-protected and protected plants did not differ (2822.5 ± 469.3 mg for protected and 2462.4 ± 390.3 mg for non-protected plants; $F_{1, 27} = 0.3$, $P = 0.6$). However, stolon dry-weight of non-protected plants significantly increased by 24.1% ($F_{1, 17} = 7.0$, $P < 0.05$; Fig. 3) and stolon length increased by 13.6% ($F_{1, 17} = 3.8$, $P = 0.07$) but the latter was not significant.

Seed viability and effect on population growth rate

Percent germination of seeds from non-protected plants was significantly different from seeds from protected plants (it reduced by 97.9% compared to seeds from protected plants; Kruskal-Wallis test; chisquare = 15.3, $P < 0.001$; Fig. 4) while percent germination of seeds from protected plants did not differ (Kruskal-Wallis test; chisquare = 0.1, $P = 0.8$) when compared with seeds originated from an uninfested population. Simulated population growth rate of *Geum reptans* decreased from $\lambda = 1.055$ to $\lambda = 1.041$ when viable seed number was reduced

according to the observed seed loss due to predation. This would result in a decrease of the predicted population size by 38.1% after 30 years.

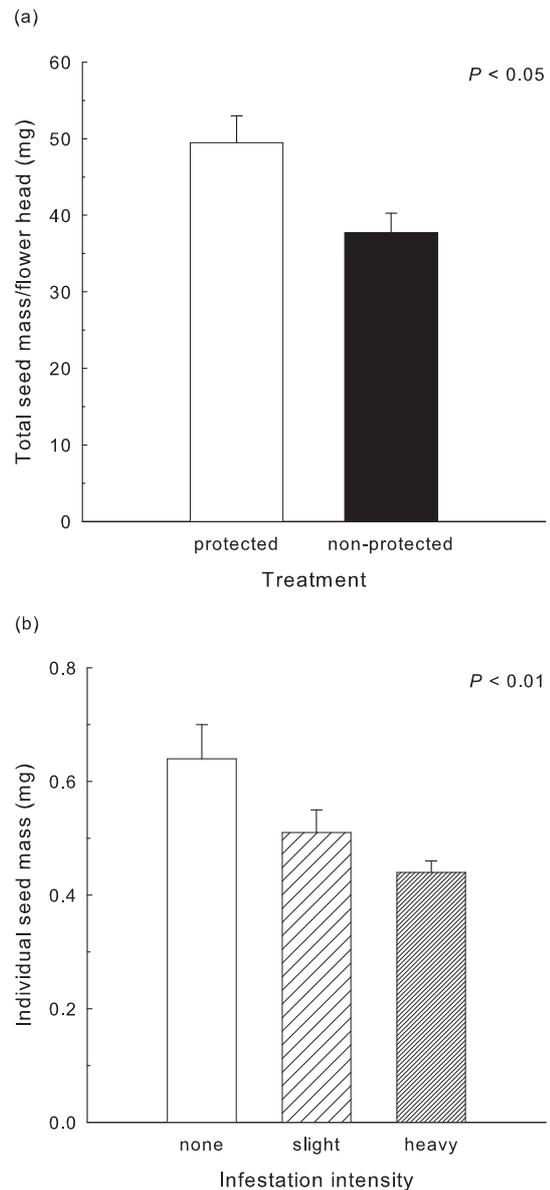


Fig. 2 (a) Effect of pre-dispersal seed predation by gall midge larvae on total seed mass per flower head (mean \pm SE) of *Geum reptans*. (b) Influence of infestation intensity (heavy, slight, none) by gall midge larvae on individual seed mass (mean \pm SE) of *G. reptans*.

Results from 2002

In the second year, the number of flowering plants was very low (21 flowering individuals instead of 58 in non-protected plants, and 14 instead of 64 in protected plants). However, we found similar trends than in 2001, but these were not always statistically significant, probably due to the low number of replicates.

After the onset of flowering in 2002, 74.3% of all the flowering plants showed infestation by larvae of *Geomyia alpina*. Again, predation by gall midge larvae did not affect the number of seeds per flower head ($F_{1, 15} = 0.1$, $P = 0.7$). Seed number per flower head did not differ between slightly and heavily infested flower heads ($F_{1, 15} = 0.1$, $P = 0.7$).

In non-protected plants, total seed mass per flower head was reduced by 19.7% compared to protected plants ($F_{1, 15} = 0.9$, $P = 0.4$), and individual seed mass of heavily infested flower heads was reduced by 23.3% compared to slightly infested plants ($F_{1, 15} = 0.1$, $P = 0.8$).

Percent germination of seeds from non-protected plants was significantly different from seeds from protected plants (it was reduced by 81.7%, compared to seeds from protected plants; Kruskal-Wallis test; chi-square = 6.6, $P < 0.05$), while percent germination of seeds from protected plants did not differ (Kruskal-Wallis test; chi-square = 1.9, $P = 0.2$) when compared with seeds originated from an uninfested population. Simulated population growth rate decreased from $\lambda = 1.055$ to $\lambda = 1.042$

when viable seed number was reduced to model predation. This would result in a decrease of population size by 35.9% after 30 years, confirming results for 2001.

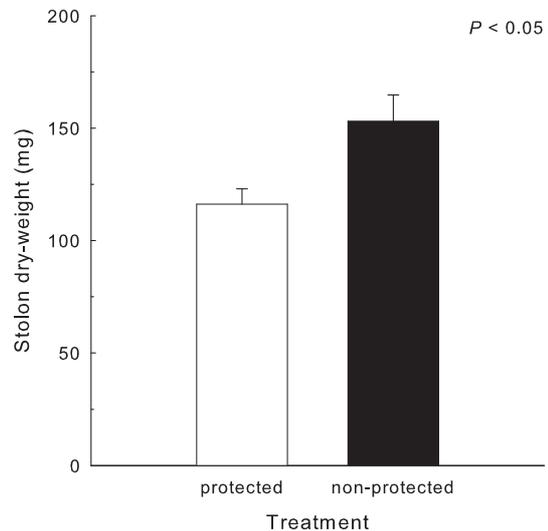


Fig. 3 Effect of pre-dispersal seed predation by gall midge larvae on stolon dry-weight (mean \pm SE) of *Geum reptans* ($N = 29$).

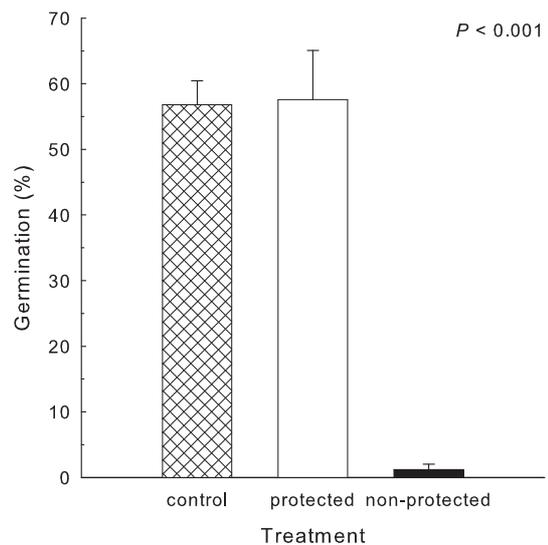


Fig. 4 Effect of pre-dispersal seed predation by gall midge larvae on percent germination (mean \pm SE) of *Geum reptans*. Seeds originating from an uninfested population served as control.

Discussion

Our results demonstrate that predation by seed damaging larvae of the gall midge *Geomyia alpina* heavily reduced seed mass per flower head in *Geum reptans* and caused seeds to be mostly nonviable. Predation had no influence on the number of developing seeds per flower head. Interestingly, seed predation resulted in an increase in stolon dry-weight which may indicate a trade-off between sexual reproduction and clonal propagation. However, despite substantial reduction in viable seeds, the population growth rate (λ) of *G. reptans* was only slightly affected by pre-dispersal seed predation suggesting that the persistence of this long-lived clonal species did not depend on current seed production alone.

Given the ubiquity of seed consuming insects often occurring at high densities and predominantly showing host-specificity, pre-dispersal seed predation provides the potential to strongly influence plant performance. In some populations of *G. reptans* seeds are subject to heavy predation by larvae of the host-specific gall midge *G. alpina* developing inside the flower heads and thereby sucking on the immature seeds. In the two years of the study, almost 75% of the control plants were infested by larvae indicating the high presence of these predators in the studied population. Exclusion of larvae by the use of an insecticide resulted in a significantly higher seed mass per flower head. Even

more, individual seed mass decreased with increasing infestation intensity affecting heavily the viability of mature seeds and confirming that pre-dispersal seed predation directly has a negative effect on reproduction of *G. reptans*. Reduced reproductive output due to pre-dispersal seed predation has been well documented for a variety of species (e.g. Louda 1982; De Steven 1983; Louda & Potvin 1995; Briese 2000; Kelly & Dyer 2002; Fröborg & Eriksson 2003; Szentesi & Jermy 2003). However, contrary to most other studies concerning seed consuming insects, predation had no influence on the number of developing seeds per flower head. Since gall midge larvae used to suck sap from plant tissues (Skuhrová *et al.* 1984), i.e. developing ovules in case of *G. reptans*, their feeding behaviour explains why seed number, unlike seed mass, remained unaffected by predation.

Interestingly, flower heads with high seed numbers also had highest attack intensities. Thus, female gall midges seemed to prefer flower heads containing more seeds for oviposition, thereby maximising fitness of their off-spring. Selective oviposition on plants with higher seed numbers per flower head has been demonstrated for *Polemonium foliosissimum* predated by an anthomyiid fly (Zimmerman 1979, 1980). Also Molau *et al.* (1989) found evidence for higher predation frequencies by two lepidopteran predators in larger inflorescences of *Bartsia alpina*.

Clearly, developing reproductive structures are a sink continuously requiring the

supply of resources (Lee 1988), and the removal of a fraction of this sink may lead to a change in resource allocation (Hendrix 1988). Removal of seeds has been observed to result in the production of additional flowers or fruits as an effect of reduced floral abortion (Hendrix 1979; Islam & Crawley 1983; Lehtilä & Syrjänen 1995). Nevertheless, compensation in growth due to herbivory is controversially discussed (e.g. Belsky 1986; McNaughton 1986; Järemo *et al.* 1996; Crawley 1997). Positive responses may be associated with release of apical dominance rather than compensating directly for seed losses (Doak 1991). In *G. reptans*, no compensation in vegetative plant biomass due to predation by gall midge larvae occurred. Non-protected plants did not compensate for seed losses, neither by reduced abortion rates nor by production of additional flower heads or stolons. In *G. reptans*, because of the sucking habit of the gall midge larvae, the proportion of saved resources may be low and the short growing season does not allow the onset of additional reproductive organs. Interestingly, we found evidence for an increase of stolon dry-weight in non-protected plants suggesting a change in resource allocation due to seed predation favouring growth of stolons and thereby possibly clonal propagation. Since the higher stolon dry-weight of non-protected plants tended to be associated with an increase in length, this might indicate escape of predation by clonal daughter rosettes spreading away from infested mother plants. However, as

leafy stolons of *G. reptans* may mainly support themselves, it seems unlikely that a higher stolon mass may increase clonal establishment and therefore directly compensate for reduced sexual establishment due to seed losses.

Clearly, pre-dispersal seed predation has the potential to act on the maintenance of populations if their persistence directly depends on the number of available seeds (e.g. Janzen 1971; Harper 1977; Andersen 1989; Crawley 1990, 1992; Louda & Potvin 1995; Kelly & Dyer 2002). Even episodic seed limitation occurring in 2 years out of 10 can lead to significant impacts on population level (Maron & Gardner 2000). In particular, plants with transient or no seed banks are strongly affected from seed loss caused by predation decreasing adult plant density (Louda & Potvin 1995; Maron & Gardner 2000). Remaining of gall midges at relatively constant population levels in a locality for long time periods is most common (Skuhrová *et al.* 1984) and *G. reptans* is not expected to form a persistent seed bank buffering potential seed losses in time (Schwienbacher & Erschbamer 2002). Immigration of seeds from other sites is considered to be very rare (Pluess & Stöcklin 2004). Our results demonstrate that seed viability of non-protected plants was substantially reduced in two consecutive years (at least by 80%) indicating deleterious effects of predation on germination ability of seeds. Simulation of population growth revealed a decrease in population size by c. 36–38% after 30 years due to seed loss, but

population growth rate λ did not drop below the sustainable threshold ($\lambda = 1$). Thus, despite heavy impacts on reproduction, pre-dispersal seed predation does not limit population growth of *G. reptans* heavily as it has been shown for other perennial species (e.g. Andersen 1989; Fröborg & Eriksson 2003, but see Kelly & Dyer 2002). There are two possible reasons for this: Firstly, in long-lived perennials, recruitment may often be related to the availability of safe-sites rather than to seed number (Andersen 1989; Eriksson & Ehrlén 1992). Therefore, predation of even high fractions of seeds may not lower seedling recruitment (cp. Crawley 1992). However, in a demographic study of *G. reptans* (Weppler *et al.* 2006) we did not find evidence for a direct relationship between seed number and seedling recruitment. Thus, recruitment of seeds may be safe-site limited. Secondly, since *G. reptans* regularly produces above-ground stolons, clonal propagation may balance reduced sexual recruitment caused by seed predation. Matrix modelling revealed that sexual reproduction and clonal propagation similarly contributed to population dynamics in this species demonstrating even that clonal propagation alone may be sufficient to maintain population growth of *G. reptans*. Elasticity analysis showed that population growth of *G. reptans* was most sensitive to changes in adult longevity as it has been shown for many long-lived species (Silvertown *et al.* 1993) and assigning only minor

importance of sexual reproduction for population dynamics.

Although pre-dispersal seed predation by host-specific gall midge larvae did not limit population growth of *G. reptans*, the production of viable seeds was substantially reduced. Therefore, infested populations may have reduced amounts of seeds available for dispersal and successful colonisation events of new sites which may be of particular importance for a species growing in the naturally fragmented alpine landscape.

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Chapter 5

General summary

This thesis focuses on the demography, reproduction, and pre-dispersal seed predation of the alpine clonal plant *Geum reptans*. In chapter 2, I studied the population dynamics of *G. reptans*, thereby I particularly addressed the relative importance of sexual *vs.* clonal reproduction for population growth in this long-lived species. In chapter 3, the balance between sexual and clonal reproduction in plants of different sizes and the frequency of life-cycle stages in *G. reptans* were studied in respect to the environmental gradients altitude and succession. In chapter 4, I demonstrated the impact of a host-specific seed predator on reproduction and population growth of *G. reptans*.

G. reptans is a typical pioneer species of recently deglaciated areas showing also high persistence in late successional communities. Since *G. reptans* occurs along broad ranges of altitude and succession, its environment is mainly characterised by high natural fragmentation, frequent disturbances, and sharp gradients of climatic conditions which may constrain growth and reproduction. Many plants adapted to alpine habitats are slow-growing, thereby showing long life-spans and pronounced clonal reproduction (Hartmann 1957; Billings & Mooney 1968; Bliss 1971). Longevity and particularly the ability for clonal growth can result in high individual persistence for centuries or even for hundreds of years (Steinger *et al.* 1996; Molau 1997; Morris & Doak 1998). Generally, the importance of clonal growth

tends to increase with altitude (Bliss 1971; Klimeš *et al.* 1997). Contrary, there is large evidence that recruitment from seeds declines with altitude (e.g. Jolls & Bock 1983) supporting the assumption that in high alpine habitats, local population dynamics of many species are strongly dominated by clonal growth (cp. Crawley 1990; Eriksson 1992; Silvertown *et al.* 1993). However, alpine pioneer species are characterised by high seed production (Stöcklin & Bäumler 1996). Thus, sexual reproduction providing dispersal and colonisation of new sites must be of particular importance for a pioneer species situated in the patchy alpine landscape. Nevertheless, knowledge about population dynamics of alpine plants is scarce and the importance of sexual *vs.* clonal reproduction for population growth remains largely unclear. In a demographic study in two field populations, I focused on the relevance of life-cycle stages as well as on the significance of sexual and clonal reproductive transitions for population dynamics in long-lived *G. reptans* (chapter 2).

Implying a trade-off between sexual and clonal reproduction in *G. reptans* depending on meristem availability, the balance between both reproductive modes is likely to vary depending on different selection pressures. Environmental heterogeneity is considered to promote genetic variation in life-history traits (Stratton 1994; Prati & Schmid 2000) and large-scale environmental gradients are well known to result in locally adapted genotypes (Clausen *et al.* 1947; Linhart &

Grant 1996). The question, if the relationship between sexual and clonal reproduction varies in contrasting altitudes and successional stages is one of the main topics in this thesis (chapter 3). Opposing selection pressures for reproductive traits is predicted by metapopulation theory (e.g. Olivieri *et al.* 1995; Husband & Barrett 1996): In recently established populations, traits that enhance dispersal should be favoured since they are more likely founded by genotypes with high dispersal ability. With increasing population age, within-population selection should act against dispersal resulting in a decrease in sexual reproduction whereas clonal reproduction increases. If the importance of clonal growth increases with altitude, in high altitude plants more allocation to clonal reproduction at the expense of sexual reproduction is expected. In 20 populations of *G. reptans*, I compared the proportion of clonal reproduction in low *vs.* high altitude habitats and in early *vs.* late successional habitats and studied the influence of plant size on reproduction of this species.

Pre-dispersal seed predation can substantially influence the relative reproductive success of individuals by limiting seed production (e.g. Louda & Potvin 1995; Briese 2000). Moreover, evidence is given, that seed consumption prior to dispersal can limit a species population growth and therefore may have severe consequences for its persistence (e.g. Louda 1982; Kelly & Dyer 2002).

However, effects of pre-dispersal seed predation on population dynamics are still poorly understood. A reduction in seed output may be of particular importance in high alpine habitats, where recruitment from seeds can be strongly limited by harsh environmental conditions (Scherff *et al.* 1994; Forbis 2003). Many populations of *G. reptans* show heavy predation by host-specific gall midge larvae feeding on developing seeds. In an exclusion experiment, I used insecticide to study the consequences of pre-dispersal seed predation on reproduction in a population of *G. reptans* (chapter 4). Since this species does not form a persistent seed bank and immigration of seeds from other sites is negligible (Tackenberg & Stöcklin, unpublished), impacts of seed loss are expected to directly affect recruitment. I used a greenhouse germination experiment to test for seed viability due to predation and matrix modelling allowed predicting consequences for population growth based on the observed seed loss.

Population dynamics of *Geum reptans*

Population dynamics of *Geum reptans* are mainly characterised by slow yearly increase and longevity which are typical features of many alpine plants as well as of pioneer species of primary successions. Despite considerable variation in growth rates (λ) among sites and years, dynamics in both populations were very similar.

However, a slightly negative λ in one year out of four mainly resulting from higher adult mortality indicates that population dynamics of slow-growing *G. reptans* are likely to be sensitive to environmental stochasticity.

Sexual and clonal reproduction occurred regularly in both populations during the study period but the frequency of reproducing adults was always low. This was demonstrated for populations of *G. reptans* situated in different environments (chapter 3), suggesting that yearly variable availability of resources for reproduction and the cost of reproduction may cause annually variation in reproductive output similar to mast seeding in trees (Webb & Kelly 1993). Interestingly, in *G. reptans* sexual reproduction plays an equally important role for population growth as the reproduction by stolons. Thus, my results clearly contradict the general assumption, that the role of sexual reproduction in clonal plants from high altitudes is mainly restricted to the maintenance of genetic variation and long-distance dispersal. Nevertheless, the two reproductive modes may have different significance for population dynamics: The constantly higher establishment of stolons compared to seeds suggests that clonal propagation serves as a low-risk alternative compared to more unpredictable and unsecured establishment from seeds. Reproduction by stolons alone may guarantee continuously slow population growth leading to a positive λ and thereby assuring persistence of the population even in

unfavourable periods. Although germination occurred regularly in both studied populations, percent germination varied by nearly 200% among years implying that seed recruitment in *G. reptans* may be particularly susceptible to environmental variation. On the other hand, in favourable years, reproduction by seeds may be an important contributor to population growth.

In *G. reptans*, population growth rate was much more sensitive to changes in the survivorship of adults than to growth or to reproductive parameters confirming the importance of persistence. Long-lived species living in stressful environments and exhibiting low recruitment rates may be particularly vulnerable to adult mortality. Since *G. reptans* as a species of glacier forelands is highly subject to changes in habitat conditions, it is a reasonable strategy for this species to privilege investments to maintenance of adults at the expense of growth and fecundity. Thus, adult longevity is expected to serve as a buffer against temporal variation which may be of particular importance in frequently disturbed alpine habitats. My results indicate that even in harsh alpine environments, population growth of a long-lived species does not rely on clonal reproduction alone.

Variation of sexual and clonal reproduction

In *Geum reptans*, the relationship between sexual and clonal reproduction largely varied among populations. However, the variation in reproductive behaviour could only be explained to a small degree by contrasting altitudes or successional stages. There may be two possible explanations for this result: Firstly, reproductive differences between populations may reflect mainly small-scale variation in environmental conditions not related to altitude or succession overriding the effects of gradients. Secondly, high phenotypic plasticity may restrict or even prevent adaptation to contrasting environmental conditions. Highly plastic genotypes have been demonstrated for species dispersed over broad geographic and environmental ranges showing little genetic or morphological differentiation (Williams *et al.* 1995; Hermanutz & Weaver 1996). Accordingly, *G. reptans* as a colonising species may have the capacity of broad plastic responses allowing rapid spread into new habitats without experiencing adaptation through selection. Additionally, high individual variation in stolon and flower head production could add to population variability which was also detected in chapter 2.

Nevertheless, in comparison with intermediate populations, clonal reproduction increased in populations at high altitude as well as at low altitude which was partly in accordance with my expectations. The

higher frequency of stolons at high altitudes demonstrates that abiotic environmental conditions may restrict seedling establishment leading to a higher fraction of clonal reproduction. At low altitudes, habitats are often characterised by increased inter-specific competition and *G. reptans* is very susceptible to competition (Pluess & Stöcklin 2005). Additionally, seedlings lacking the support of adults in contrast to vegetative off-spring may be particularly vulnerable for crowding what might explain the higher proportion of stolons also found in low altitude habitats. However, sensitivity analysis of matrix projection models can reveal the direction and intensity of selection on life-history characteristics of species (van Groenendaal *et al.* 1988). Since sensitivity of λ was highest to stasis of small adults and very low to reproductive transitions (chapter 2), it is expected that in *G. reptans*, traits promoting persistence may be stronger under selection compared to reproductive behaviour. In a common garden experiment studying the effects of population origin and environment in *G. reptans*, in spite of high variation, differences in reproductive behaviour were not explained by population origin from successional gradients supporting the assumption that adaptation in reproductive behaviour to contrasting habitats is limited in this species (Pluess & Stöcklin 2005). My results suggest that the observed variation among populations in the frequency of clonal reproduction largely results either from differences in local environmental

conditions and probably also from random drift among populations.

Another factor altering the relationship of sexual and clonal reproduction was plant size. In *G. reptans*, the number of reproductive meristems as well as the probability of producing flower heads and stolons simultaneously increased with the number of rosettes. Accordingly, small plants being rather limited in resources invested preferentially in low-cost stolon production. Larger plants having more resources available invested into both reproductive modes thereby tending to prefer sexual reproduction confirming once more the importance of sexual reproduction for a clonal alpine plant (chapter 2).

Pre-dispersal seed predation

Pre-dispersal seed predation by gall midge larvae heavily decreased seed mass in *Geum reptans* causing seed viability to be substantially reduced (-98%). However, matrix modelling revealed that the population growth rate (λ) was only slightly affected by the observed seed loss suggesting that persistence of *G. reptans* does not depend on seed production alone.

In natural habitats, sexual reproduction and seedling establishment are very likely to show high inter-annual variation depending on environmental conditions and individual variation in reproduction (chapter 2). While high seed production can rapidly increase population growth,

low seed availability does not necessarily lead to a negative population growth since continuous clonal reproduction can balance potential seed losses. Accordingly, population growth rate would only decrease as a result of a general lack of reproduction. However, since elasticity analysis revealed that λ is most sensitive to survival of adults, limitation in sexual reproduction by seed predation is not expected to have more than only slight effects on population growth. Thus, the local abundance of *G. reptans* does not critically depend on seed supply suggesting that population dynamics is probably not limited by pre-dispersal seed predation which has also been shown for other perennial species (Andersen 1989; Fröberg & Eriksson 2003). Nevertheless, predation could be an important factor generating differences in the reproduction of individuals, thereby decreasing effective population size, and thus facilitating genetic change, particularly genetic drift (Crawford 1984; Heywood 1986).

Surprisingly, seed predation resulted in an increase in stolon dry-weight in predated plants suggesting a change in resource allocation due to less resources used for seed ripening after pre-dispersal seed predation favouring clonal reproduction. However, as leafy stolons of *G. reptans* are expected to mainly support themselves, it seems unlikely that a higher stolon mass may increase clonal establishment and therefore directly compensate for reduced sexual establishment due to seed loss.

Although pre-dispersal seed predation by host-specific gall midge larvae did not limit population growth of *G. reptans*, the production of viable seeds was substantially reduced. Therefore, infested populations may have reduced amounts of seeds available for dispersal and colonisation of new sites which may be of particular relevance in the naturally fragmented alpine landscape.

Conclusions

In summary, my results demonstrate that sexual and clonal reproduction both have an equally important role for population dynamics of the high alpine plant *Geum reptans*. Reproduction by seeds acts as mechanism promoting not only genetic diversity and dispersal but also rapid population growth in favourable years. Clonal reproduction serves to ensure population increase by slow but continuous growth even under distinct environmental variability and unfavourable weather conditions. The relative importance of sexual and clonal reproduction is highly variable among populations of *G. reptans*. However, the observed variation could only be explained to a small degree by contrasting habitats. A higher frequency of clonal reproduction occurred in populations from high and low altitudes in comparison with intermediate populations. Taken together, my results suggest that variation in reproduction could either be attributed to individual

plasticity in response to different habitat conditions or resulted from genetic differentiation among populations, probably partly random in nature. Plant size is suggested to be an additional factor influencing the relationship between sexual and clonal reproduction demonstrating a higher threshold size for investment in sexual reproduction.

The outstanding importance of adult survival for the life-history of *G. reptans* highly exceeding the impact of reproduction demonstrates the significance of longevity and persistence for this pioneer species of glacier-forelands. In long-lived *G. reptans*, adult survivorship is expected to serve as a buffer against temporal variation in reproduction that may be particularly important in frequently disturbed alpine habitats.

The importance of persistence and the ability for clonal growth balancing reduced seedling recruitment explain why, despite substantial seed losses, population growth of *G. reptans* might not be limited by pre-dispersal seed predation. In *G. reptans* as a long-lived perennial clonal plant being most vulnerable to adult mortality, seed supply is of minor importance for population dynamics. In unpredictable habitats where successful recruitment by seeds may not occur every year, this might be an important adaptation. However, seed predation by reducing the proportion of viable seeds restricts successful colonisation of new sites, thereby contributing to the not very high frequency of this species

in the alpine landscape and reducing gene-flow among populations.

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