Genet longevity and population age structure of the clonal pioneer species *Geum reptans* based on demographic field data and projection matrix modelling

Stáří genet a populační věková struktura pionýrského klonálního druhu *Geum reptans*, zjištěné pomocí demografických terénních dat a projekčních maticových modelů

Lucienne C. d e W i t t e, Daniel S c h e r r e r & Jürg S t ö c k l i n

D e d i c a t e d t o t h e m e m o r y o f L e o š K l i m e š

Section of Plant Ecology, Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland, email: lucienne.dewitte@unibas.ch, daniel.scherrer@unibas.ch, juerg.stoecklin@unibas.ch

de Witte L. C., Scherrer D. & Stöcklin J. (2011): Genet longevity and population age structure of the clonal pioneer species *Geum reptans* based on demographic field data and projection matrix modelling. – Preslia 83: 371–386.

Genet life span is a key demographic trait for understanding life history of plants. However, the longevity of clonal plants is hard to determine, especially when inter-ramet connections are short-lived and plants subsequently move independently of one another in space by means of an expansive growth strategy. In this study we estimated genet life span in the clonal pioneer species *Geum reptans*, living on glacier forelands, by using a projection matrix model based on demographic field data of ramets collected at two sites and in three subsequent years. We then calculated genet age structure at different population ages using multiple simulations, including a maximum carrying capacity and density-dependent mortality. Additionally, we estimated the age of the two field populations by comparing results from simulations with population structure recorded in the field. According to our simulations, more than half of the genets die within the first three decades. However, a considerable proportion survived more than 50 years and some genets even became immortal as they produced so many ramets that the risk of the entire genet becoming extinct was zero. Simulated genet age structures were strongly left skewed with many young and a few very old genets. The rather low carrying capacity was reached only after 350 years, after which density-dependent mortality started to influence genet age structure considerably. The age of the two field populations was estimated to be 250 and 450 years, respectively. Results indicate that in clonal plants, genet immortality can potentially lead to unlimited persistence of established populations. In the case of *G. reptans*, old populations may experience competition and increased mortality due to the ongoing succession in older parts of the glacier foreland that will prevent populations reaching their maximum carrying capacity. But due to the ability of this plant to colonize new sites and follow retreating ice on glacier forelands, populations of *G. reptans* can be very old as recorded here for the two field populations in the Swiss Alps.

K e y w o r d s: alpine vegetation, clonal reproduction, demography, genet age, glacier foreland, mortality risk, population persistence, recruitment, Swiss Alps

Introduction

Clonal life cycles and slow growth of individuals are among the most noticeable adaptations of plants in alpine habitats characterized by severe climatic conditions, strong natural fragmentation, sharp boundaries and a high frequency of disturbance (Hartmann 1957, Billings & Mooney 1968, Bliss 1971, Callaghan 1988, Klimeš et al. 1997). Clonality com-

pensates for the loss of parts of plants due to disturbance, and can thereby considerably enhance genet longevity and prolong population persistence over long periods of time (Cook 1979, Eriksson & Jerling 1990). In general, clonal plants strongly benefit from their capability to reproduce asexually as well as sexually, because the product of a single zygote can persist almost indefinitely as the mortality risk of genets is spread among their ramets (Eriksson & Jerling 1990), while sexual reproduction occurs only occasionally (Aarssen 2008).

Age structure and genet turnover in plant populations are determined by genet life span, a key demographic trait for understanding life history (Weiher et al. 1999), population dynamics (Harper 1977, Silvertown & Lovett Doust 1993) and evolutionary fitness (Silvertown 1991). Extended longevity of genets is known to slow down turnover rates of individuals and extend the persistence of populations, especially of clonal plants (Helm et al. 2006), and could play an important role in determining community stability and the vegetation responses to present and future climate change (Steinger et al. 1996, Eriksson 2000, Körner 2003, García et al. 2008, Morris et al. 2008). Even populations that have a negative population growth rate are able to persist for long periods of time due to the longevity and high survival rates of established genets. For example, Eriksson (1994) predicted, based on stochastic matrix models, that populations of *Potentilla anserina*, *Rubus saxatilis* and *Linnaea borealis* consisting of more than 250 ramets are able to persist much longer than 50 years despite a negative population growth rate, just by continuous vegetative reproduction and high adult survival. Often, clonal plants are even considered to be potentially immortal and the several extremely long life spans reported seem to confirm this (Thomas 2002, de Witte & Stöcklin 2010).

Unfortunately, there is little reliable data on genet life span and population age structure for clonal plants, because, in contrast to ramet age, genet age is difficult to measure (Dietz & Schweingruber 2002, de Witte & Stöcklin 2010). Due to the longevity of many clonal species, it is impractical to follow cohorts of ramets from birth until death of the genet. Moreover, there are two different types of clonal growth strategies in herbaceous plant species, for which the application of a common method for estimating age is not appropriate (de Witte & Stöcklin 2010). In clonal plants that form clearly delimited and dense patches and have long-lasting inter-ramet connections, genet age can be estimated using indirect methods based on genet size and increase in size over time. However, in spreading clonal plants with decaying inter-ramet connections, these methods cannot be used because genets become fragmented and genet size is poorly correlated with genet age. Currently for such plants, the only feasible alternative approach is a demographic analysis based on population growth models.

Some researchers have used population transition-matrix models to understand life history and investigate population dynamics and individual longevity in plants (Callaghan 1976, Hamilton et al. 1987, Cochran & Ellner 1992, Erschbamer 1994, Erschbamer & Winkler 1995, Molau 1997, Erschbamer et al. 1998, Barot et al. 2002, Diemer 2002, Ehrlén & Lehtilä 2002, Nicolè et al. 2005, Weppler et al. 2006). These models have increased the understanding of the structural and demographic properties of plant populations, especially for clonal species. For example, they allow us to study long-term population demography based on short periods of observation (Watkinson & Powell 1993). Moreover, they can be used to determine the age structure of populations rather than estimating the age of individuals, a crucial issue for understanding population demography

and viability. An example is the investigation of the life history of *Silene acaulis* inferred from size-based population projection matrices (Morris & Doak 1998). This study revealed a life expectancy of more than 300 years for 1.8% of the newborn of this herbaceous alpine plant, while 8.0% survived at least 50 years. Demographic data on long-lived clonal plants at the genet level is still scarce (Menges 2000) and there is a need for studies that use population models to investigate individual longevity and population persistence.

Here we present a study of genet longevity and population age structure of the herbaceus *Geum reptans* based on demographic modelling. Because of its well-known morphology (Conert et al. 1995, Pluess & Stöcklin 2005, Weppler & Stöcklin 2005, 2006), demography (Weppler et al. 2006), genetic constitution (Pluess & Stöcklin 2004) and dispersal ability (Pluess & Stöcklin 2004, Tackenberg & Stöcklin 2008) the alpine clonal pioneer species *G. reptans* is ideal for such a study. The projection-matrix models are based on empirical data collected on two glacier forelands in the Swiss Alps. Our particular objectives are (i) to assess genet longevity of *G. reptans*, (ii) to investigate the genet age structure in established populations and (iii) to estimate the age of the two field populations by comparing results from simulations with the genet stage structures recorded in the field. Finally, this study provides an opportunity to discuss the effect of clonality on life span, genet turnover and persistence of a plant during primary succession on glacier forelands.

Materials and methods

Study species

Geum reptans L. (*Rosaceae*) is a perennial clonal rosette plant widely distributed from the Central European Alps eastwards to the Carpathian Mountains. It is one of the first pioneer species to colonize protosoils left by retreating glaciers (Braun-Blanquet 1948) and occurs preferentially on moist moraines and alluvial soils of glacier forelands, screes and mountain ridges between 1950 and 3800 m a.s.l. (Conert et al. 1995). With ongoing succession the pioneer species is outcompeted by grasses and dwarf shrubs (Lüdi 1921). *Geum reptans* is hardly ever found in alpine grasslands (Rusterholz et al. 1993).

As a hemicryptophyte, *G. reptans* produces clusters of rosettes sprouting from a monopodially and vertically growing rhizome (epigeogenous rhizome; Klimešová et al. 2011) in spring. Vegetative growth of a plant results in an increase in the number of side rosettes sprouting from the rhizome. The age at first reproduction is several years and depends on environmental conditions (Weppler et al. 2006). *Geum reptans* reproduces clonally by producing new rosettes at the end of above-ground stolons and sexually by seeds as an outbreeder via predominantly fly-pollinated flowers (Conert et al. 1995, Hess 2001). Both flower heads and stolons develop from axial leaf buds that were initiated in the previous year. Connections (stolons) between mother plant and daughter rosettes can be at least 1 m in length and decay within a year. Therefore, the size of genetic individuals (genets) cannot be distinguished by eye. Herbchronology revealed that single plants (ramets = cluster of rosettes attached to a single rhizome) are never older than about 40 years (J. Stöcklin, unpublished). Molecular analysis indicates that ramets that are > 4 m apart usually belong to different genets (Pluess & Stöcklin 2004). The seeds are adapted to wind dispersal (Tackenberg & Stöcklin 2008). Mechanistic modelling showed that seed

dispersal is limited, with only a small fraction being dispersed further than 10 m (0.03%; Tackenberg & Stöcklin 2008). *Geum reptans* does not have a persistent seed bank (Schwienbacher & Erschbamer 2002, Schwienbacher et al. 2010).

Empirical data for the simulation of demographic properties

The demographic data for *G. reptans* was collected over three years (two transitions) on two rocky glacier forelands in the Swiss Alps: Vadret da Porchabella and Furkapass (Weppler et al. 2006). The ramets were divided into five different life-cycle stages according to Weppler et al. (2006; Fig. 1): seedlings; juveniles; small adults; medium-sized adults; and large adults. Seeds germinate soon after snowmelt in the year following their production. Juveniles are young ramets that originate from sexual reproduction and are older than one year but not yet reproducing. Small, medium and large adults have increasing numbers of leaf rosettes and form three stages of reproducing ramets. The population growth rates (λ) of *G. reptans*, obtained from matrix modelling, varied between 0.999 and 1.074, and the variation among years was greater (up to 7%) than among populations (0.2%). The estimated population size was between 5000 and 20,000 plants on the glacier foreland where the study populations occurred (Weppler et al. 2006).
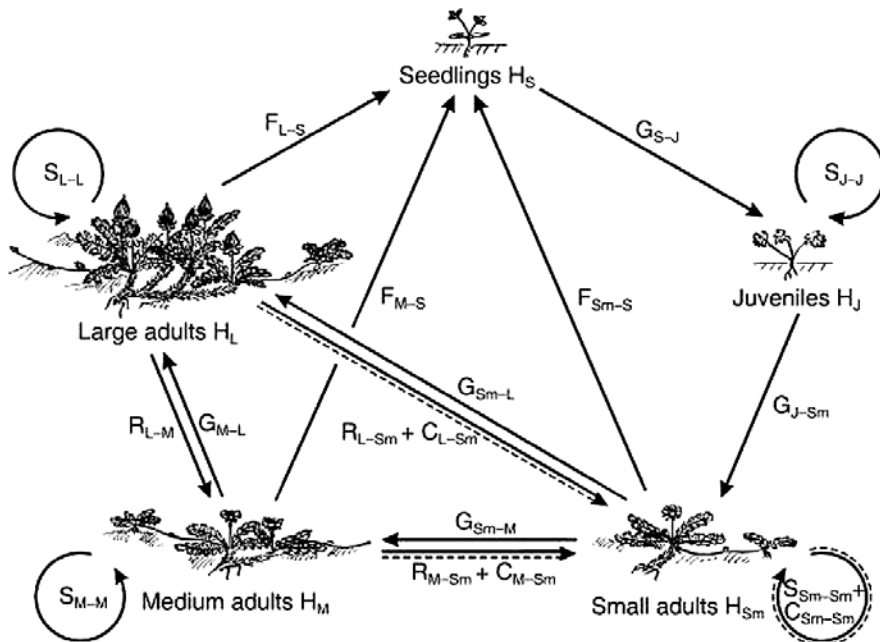
Modelling assumptions and simulation methods

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 (taken from Weppler et al. 2006, published with permission).

The small differences among populations allowed us to pool all the data from different years and the two sites (Table 1), resulting in a data set consisting of 1827 transitions of ramets. The model used for demographic simulations was a linear stage-classified population projection matrix model (Caswell 2011) of the form:

$$n_{t+1} = An_t,$$

where n_t is a vector of k stage classes and A is a square matrix of dimension k. The elements of A are stage-specific fecundities and/or transition probabilities that describe the generation of ramets in each class by ramets in all other classes from one year to the next. The geometric growth rate of the population when the population has reached a stable distribution of stages is the dominant eigenvalue of A, λ. The right eigenvector of A, w_m, describes the stage distribution of the population

$$Aw_m = \lambda_m w_m$$

and is the proportional representation of each stage class once the population has reached the equilibrium growth rate (Caswell 2001).

Table 1. – Average transition matrices of two populations of *Geum reptans* (Vadret da Porchabella, Furkapass) during a study period of 3 years. Transition matrices for each population contain the life-cycle stages (seedlings; juveniles; small, medium and large adults) and the probabilities of ramets remaining in the same stage or changing to another stage, respectively, within one year. Transition probabilities reflecting sexual reproduction (new genets) are given in italics. Probabilities of transitions to the stage of a small adult are based on values for survival of small adults or retrogression of medium or large adults from the previous year or production of new small adults via clonal reproduction (new ramets, second value in bold type). After Weppler et al. (2006).

	Seedlings	Juveniles	Small adults	Medium adults	Large adults
Vadret da Porchabella, 2000–2002 (λ=1.051)					
Seedlings	–	–	*0.02*	*0.08*	*0.22*
Juveniles	0.95	0.57	–	–	–
Small adults	–	0.32	0.89+**0.03**	0.2+**0.08**	0+**0.14**
Medium adults	–	–	0.08	0.67	0.07
Large adults	–	–	0.01	0.12	0.92
Furkapass, 2001–2003 (λ=1.038)					
Seedlings	–	–	*0.14*	*0.33*	*0.31*
Juveniles	0.90	0.60	–	–	–
Small adults	–	0.21	0.85+**0.02**	0.21+**0.22**	0.05+**0.05**
Medium adults	–	–	0.06	0.71	0.18
Large adults	–	–	0.01	0.08	0.73

The demographic parameters of a population used in the simulations are influenced by several factors. Demographic stochasticity (inherent variation in individual time of death and reproductive rates that are not due to differences in ecological condition; Goodman 1987) will introduce variation into the demography of a population in a given time period. Variation in environmental conditions influences the whole population, and the microclimatic changes and differences alter the survival probabilities and fecundities of single

ramets (environmental stochasticity; Tuljapurkar 1989). Additionally, it is possible that several elements of the transition matrix are not independent and covary (Gani 1987). Ideally, all these factors should be incorporated into the design of empirical studies and simulations of population demography. However, this is often impossible, and especially the covariation between different elements of the transition matrix is difficult to measure in long-lived plants.

In our models we accounted for demographic and environmental stochasticity. The demographic stochasticity was implemented by a multinomial distribution for transitions and a Poisson distribution for fecundities according to Akcakaya (1991). The environmental stochasticity was simulated by bootstrapping 50% of all ramets in each stage class in our dataset to parameterize a transition matrix for each year of a simulation. These transition matrices include both spatial and temporal variance, because we pooled data from different sites and years. To produce a realistic yearly dynamic for *G. reptans*, every time step (year) in the simulation included survival taking into account mortality during winter and growth by clonal reproduction in spring. This was followed by sexual reproduction in summer. Possible effects of intra- and interspecific competition were not simulated here because the influence of competition in open and nutrient-rich habitats such as glacier forelands is likely to be low. Nevertheless, the influence of competition is implicitly incorporated in our model by the fact that the demographic parameters were based on a study of the field populations where natural competition is assumed to occur.

Life span of genets

To estimate the life span of a genet under natural conditions we simulated the survival and clonal growth of genets based on the demography recorded in well-established populations (Weppler et al. 2006). Sexual reproduction was not included in these simulations, as this would produce new genets. We ran 1,000,000 simulations starting from either a 'seedling' (stage 1), a 'juvenile' (stage 2) or a 'small adult' (stage 3). Each genet was modelled separately assuming no restrictions on space, resources or competition, because the possible influences of these factors were already incorporated in the field data. Therefore these simulations considered genet development in an established population. At each time step each ramet of a genet either survived/grew or died based on a multinomial distribution. Additionally, at each time step, new ramets are produced by clonal growth based on a Poisson distribution. Simulations of a genet were run for a maximum of 2500 years or until all ramets of the genet were dead. Results are presented as a frequency distribution of modelled genet age from all simulations performed.

Genet age structure in established populations

To determine the theoretical age distribution of genets after 100, 250, 500, 1000 and 2500 years, we ran another type of simulation starting with a 'newly established' population of 10 'seedlings' (10 different genets). These scenarios were based on the demographic parameters recorded by Weppler et al. (2006) and growth conditions in established populations as no data on "virgin" habitats were available. These simulations included sexual and clonal reproduction. To prevent unrealistic population sizes we set a maximum carrying capacity of 10,000 ramets and applied a density function of the type 'ceiling' for ramets (Caswell 2001). Most observed populations had between 5000 and 20,000 ramets

depending on the size of the glacier foreland and therefore 10,000 ramets seemed reasonable since the field data suggest that natural populations rarely reach the carrying capacity because of the high dynamics of the habitat (glacial retreat and succession).

While we made no distinction between clonally and sexually produced plants for the total population size of ramets and the ramet carrying capacity, sexual reproduction created new genets every year. Based on the above simulations of genet life span we calculated the life span for each newly emerged genet and the resulting residence time in the population. But as the genet life span simulations were density-independent (no maximal carrying capacity) the number of genets was still increasing, even when the number of ramets in these simulations was already at the carrying capacity. To prevent the number of genets exceeding the number of ramets (which is impossible in nature) the carrying capacity for genets was defined separately. The carrying capacity for genets was set at 7500, which is 75% of the ramets carrying capacity. Therefore, at the carrying capacity of ramets at least 25% of the ramets need to be clones. We chose 75% as the data of Weppler et al. (2006) showed that clonal and sexual reproduction are almost similarly important for the population dynamics and therefore a rather large proportion of clonal offspring must be assumed.

To regulate the number of genets we tested two types of density-dependent mortality. The first type assumes age-independent mortality of genets ('random') with all genets having the same density-dependent mortality independent of their actual size when the threshold for genets was reached. The second type assumes older genets have a lower density-dependent mortality than younger ones ('age-dependent'), as genets with a large number of ramets are less likely to disappear. In our model, age-dependent mortality of genets means that if the carrying capacity is reached, no new genets (seedlings) can establish until genets disappear by density-independent mortality. We applied these two different density-dependent mortalities to determine whether and how strongly the models are affected by our assumptions. All models were implemented and evaluated with R 2.10.1 (R Development Core Team 2009).

Age estimation of field populations

Based on the average transition matrix of Weppler et al. (2006) we calculated the mean time spent in subadult classes ('seedlings' and 'juveniles') according to the simplified formula of Barot et al. (2002):

$$E\left(\tau_{seed}, s\right) = 1 + \sum_{i=1}^{s-1} \frac{1}{1 - p_i}$$

where τ_{seed} is the first stage, s the first adult stage and p is the survival probability in stage i. This formula was used to calculate the proportion of subadults among all ramets in our modelling results.

The comparison of the modelled subadult proportion with the proportion observed in field populations allowed us to roughly estimate their age. This is possible because subadult individuals must be "new" single-ramet genets, as subadult ramets cannot be produced by clonal growth or retrogression. Based on the assumption, that the proportion of "old" genets increases with time, the proportion of subadult ramets is a rough indicator of the age of a population.

Results

Life span of genets

The simulations of the life span of genets starting with 'seedlings' showed that 56% of the genets died before they reached reproductive age, which is on average 3.46 years (Fig. 2). The simulations starting with 'juveniles' gave similar results as 51% of the genets died before reproducing. When the models were started with 'small adults' (reproductive stage 3) they predicted a weaker peak in mortality in the first years, with more than 80% of the genets dying in the first 30 years, which is approximately the life span of large ramets (Weppler et al. 2006). In all simulations, however, a considerable proportion of genets survived for more than 50 years (6.6–13.2%), 100 years (4.3–8.7%), 500 years (3.0–6.1%) and even 2500 years (2.9–5.9%; Fig. 2). It is important to bear in mind that the model predicts the age of genets and not the age of ramets, which is rarely more than 50 years.
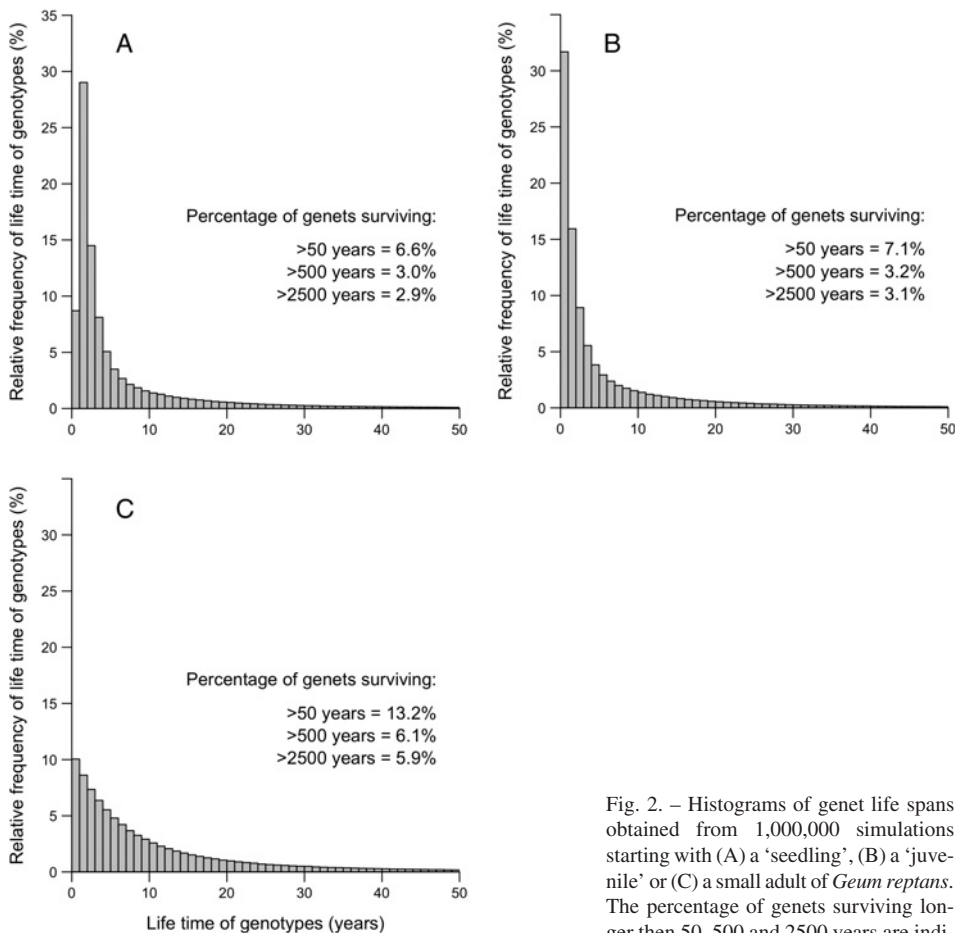

Fig. 2. – Histograms of genet life spans obtained from 1,000,000 simulations starting with (A) a 'seedling', (B) a 'juvenile' or (C) a small adult of *Geum reptans*. The percentage of genets surviving longer then 50, 500 and 2500 years are indicated within each panel.
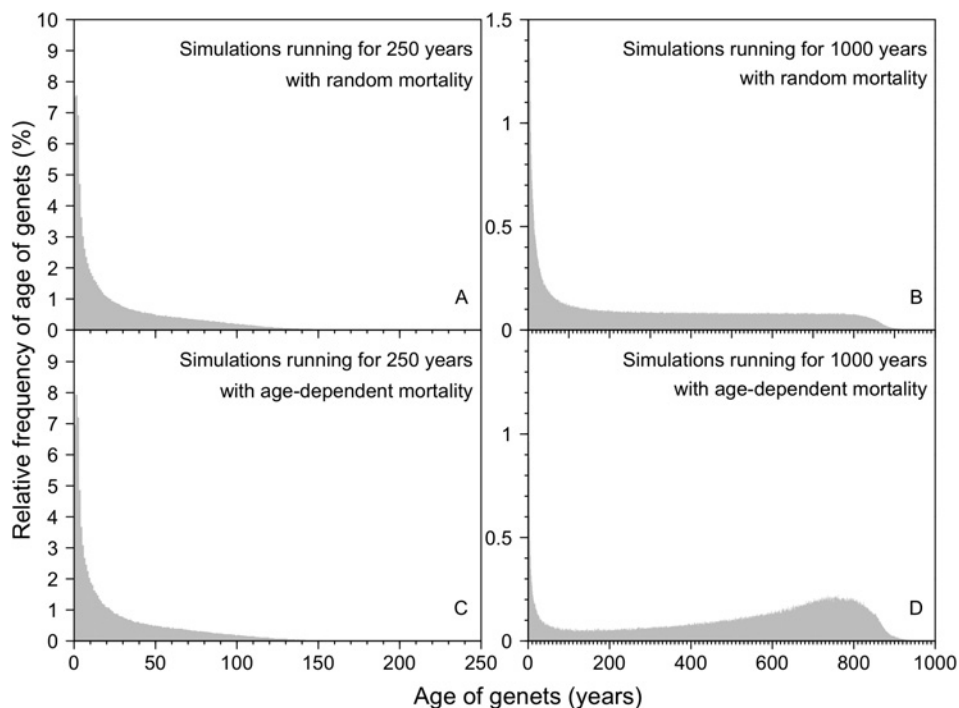
Fig. 3. – Genet age structure of *Geum reptans* populations emerged from 10 'seedlings' after 250 and 1000 years. A – genet age structure after 250 years assuming random mortality of genets due to density; B – same population as A after 1000 years; C – genet age structure after 250 years assuming strong age-dependent mortality of genets due to density; D – same population as C after 1000 years.

Genet age structure in established populations

The simulations predict no difference in the genet age structure of established populations with random or age-dependent mortality due to density effects in populations younger than 250 years (Fig. 3). In these "young" populations the age structure was always strongly left skewed, reflecting a large proportion of genets in subadult stage classes. This left-skewed age distribution is typical for the exponential growth phase of populations that have not yet reached carrying capacity, which took approximately 350 years in the simulations.

Density-dependent mortality started to influence population age structure only in populations older than 500 years. In simulations with 'random' density-dependent mortality a small but stable proportion of very old genets were predicted after 500 years, though the young genets still dominated the population (Fig. 3). Assuming 'age-dependent' mortality led to an increasing proportion of very old genets in populations older than 500 years, because after reaching the carrying capacity few new genets were able to establish.

Estimated age of field populations

Based on the average projection matrix the mean time spent in non-reproductive classes (stage 1 and stage 2) in the simulations was about 3.46 years (formula of Barot). By using this threshold in the simulations the proportion of subadult ramets (stage 1–2) among all

ramets (stage 1–5) in populations of different ages were obtained (Table 2). As there were two different types of density dependent mortality of genets (random mortality and age-dependent mortality) a (broad) range of proportions of subadults were obtained, especially if the model ran for long periods of time. However, in simulations that ran for less than 500 years all scenarios showed similar proportions of subadults. The two populations studied by Weppler et al. (2006) showed the subadult proportions of 20% at the Furkapass and 10% at Vadret da Porchabella. By comparing this field data with the simulation results (Table 2) a predicted age of a little more than 250 years for the population at Furkapass and 450 years for that at Vadret da Porchabella were obtained.

Table 2. – Simulation-based proportion of subadult ramets (stage 1–2) among all ramets (stage 1–5) in populations emerged from 10 seedlings after 100, 250, 500, 1000 and 2500 years, presented for two scenarios with regard to the type of mortality. Population age represents time since establishment. Means ± standard deviations of subadult proportions (%) are shown.

Population age (years)	Mortality type	
	Random	Age-dependent
100	44.8±6.7	45.3±4.9
250	24.2±3.0	24.4±5.6
500	15.2±1.0	7.9±0.9
1000	8.9±0.6	2.1±0.2
2500	4.1±0.2	0.1±0.1

Discussion

The results indicate that most genets of *Geum reptans*, despite their marked ability to reproduce clonally, die at young ages. But a small percentage of genets are very old and achieve immortality by producing many ramets and spreading the risk (Eriksson & Jerling 1990). The left-skewed frequency distribution of genet age in populations will only change when the carrying capacity is reached and density-dependent mortality becomes strong, which affects predominantly young and small genets. This is probably rare in many natural populations of pioneer plants living at high altitudes and growing slowly.

When discussing these results, it should be kept in mind, that there are a few caveats about the way the projection-matrix models were constructed and the simulations run. First, there may be some variation in transitions that were not detected with the sample sizes used to parameterize the model. Second, our estimated rates of population growth and genet or ramet survival are based on only four annual transitions, and it was assumed that the year-to-year variation is not higher than between these transitions. Thereby we might have excluded extreme events affecting germination rate, mortality and growth. Finally, we did not include any spatial structure in our simulations and assumed unlimited dispersal. This could have influenced the results by affecting parameters such as population growth rate and the mortality risks of genets. However, it is unlikely that these caveats affected the overall pattern of the results and had little effect on the quantitative predictions.

Life span of genets

Our results indicate that the initial mortality of *G. reptans* is rather high and decreases markedly with increasing age, implying that most genets die within the first three decades of their life. Some genets even seem to become immortal, probably because with increasing age the genets also increase in number of ramets. Thereby, the risk of mortality of a genet is reduced as it is spread among all the ramets produced during the genet's lifetime. Tanner (2001) reports an increasing 'expected remaining life span' (ERL), based on risk spreading, for other clonal species like *Potentilla anserina*, which has a similar growth strategy to *G. reptans*.

The frequency distributions of genet life spans obtained from simulations starting with three different stages are very similar (Fig. 2), except the initial mortality is low when the simulation started with already well-established ramets (small adults). But even in this case, only a fifth of the genets survived more than 30 years. The reason for this high initial mortality is the fact that only a small proportion of genets produce clonal offspring and many of them die before they reproduce vegetatively for the first time. The extreme longevity of a few genets, together with a strongly left-skewed genet age structure, are also found in other alpine clonal plants such as the tussock grass *Carex curvula* and the dwarf shrubs *Rhododendron ferrugineum*, *Vaccinium uliginosum*, *Salix herbacea* and *Dryas octopetala* (Steinger et al. 1996, Pornon et al. 2000, L. C. de Witte et al., unpublished). Comparison with these species should, however, be treated with care, as these species have a completely different growth strategy and usually form large and dense patches that dominate late-successional vegetation. In addition, the genet age of such species is estimated based on growth-ring analysis or indirect methods using size and growth-rate measurements (de Witte & Stöcklin 2010). This method of ageing genets cannot be used for species like *G. reptans*, because its genets consist of independent ramets and do not form clearly delimited dense patches of which the size and yearly expansion can be measured. In *G. reptans*, new daughter ramets can easily grow one metre away from the mother plant and the inter-ramet connections (stolons) are lost within one year. Therefore, the only possible method of estimating genet age in *G. reptans* is to simulate genet longevity based on demographic data and a matrix model, as in this study. Nevertheless, it is noteworthy that the pattern of a left-skewed frequency distribution of genet age in a clonal plant with a growth strategy consisting of short-lived above ground stolons, is similar to distributions of genet age in clonal plants that grow in large and dense homogeneous populations and other perennial plants measured in the field. This may indicate that the basic demographic properties of slow-growing clonal plants are very similar, irrespective of their growth strategies. A similar left-skewed frequency distribution of genet age is also recorded for the clonal species *Carex curvula*, *Dryas octopetala*, *Salix herbacea* and *Vaccinium uliginosum* (L. C. de Witte et al., unpublished). Also the study of Colling & Matthies (2006) on the non-clonal perennial *Scorzonera humilis* revealed a low mortality of adults, a life expectancy of several decades and a left-skewed frequency distribution of genet age at nutrient-poor sites where populations had a positive growth rate. In contrast for populations at nutrient-rich sites with low recruitment rates and negative population growth they record a right-skewed frequency distribution.

Despite the low frequency of old genets, our simulations indicate that in clonal plants with the capacity to potentially increase genet size indefinitely by producing new ramets, a small proportion of genets are practically immortal. To our knowledge, this is the first

time that the potential immortality of a clonal plant has been demonstrated based on field measurements and matrix modelling. An important consequence of such immortality is the practically unlimited persistence of a once established population of a clonal plant, when no extrinsic factors are destroying the population. In the case of *G. reptans*, populations are therefore likely to persist forever, if the ongoing succession does not displace pioneer stages on the glacier foreland resulting in alpine grasslands or dwarf shrub heaths. It is noteworthy that *G. reptans* occurs at altitudes where succession progresses very slowly or sometimes not at all.

Genet age structure in established populations

Genet age structure is not influenced by density- or age-dependent mortality, as long as the population does not reach carrying capacity. The carrying capacity used in our model was based on measurements of population size at field sites. As the vegetation on glacier forelands where *G. reptans* occurs is usually still open and at an early stage of succession, the carrying capacity we used may be considered as too low. Nevertheless, in the simulation, the carrying capacity of genets is first reached after 350 years. Only then does density-dependent mortality start to have a considerable affect on genet age structure, depending on the type of mortality (Fig. 3C, D). Random mortality, in which genets die independent of their age, results in the high mortality of young genets and more genets with a high ERL, which remains constant over the whole simulation period. However, age-dependent mortality results in an increase in the number of older genets each represented by many ramets, which reduces the risk of genets becoming extinct and results in a strong increase in genets with a high ERL. This implies that young genets are unlikely to survive in populations approaching the carrying capacity. Clearly, in natural populations approaching the carrying capacity, age-dependent mortality of genets is more realistic than random mortality, as old genets consist of more ramets and survive even when some ramets die. The simulations predict that very old populations of *G. reptans* are likely to be composed of mostly old genets and the establishment of new ones is prevented as long as density-dependent mortality or other disturbances do not create new open spaces for seedlings. Interestingly, however, the carrying capacity is reached only when the population is several hundred years old. Such old populations of *G. reptans* will probably occur only in older parts of glacier forelands where they are already exposed to competition and a high risk of mortality due to ongoing succession. The results thus indicate that populations of *G. reptans* on glacier forelands are usually not subjected to strong density-dependent mortality and exhibit left-skewed genet age distributions with a few very old and potentially immortal genets. This conclusion is consistent with the observation that *G. reptans* mostly occurs at pioneer sites where there is little vegetation cover and hence little competition.

Estimated ages of field populations

If the proportion of subadults predicted by simulations with age-dependent mortality are used to estimate the age of the field populations studied in the Swiss Alps by Weppler et al., then they are a few hundred years old. This seems quite realistic for a pioneer species on glacier forelands above 2000 m a.s.l. *Geum reptans* is able to colonize new soil, e.g. left by retreating glaciers, by means of wind-dispersed seeds or even by vegetative growth, as stolons easily grow up to 1 m in length. It is a reasonable assumption that the colonization

capacity of *G. reptans* is sufficient to escape competition resulting from primary succession and to colonize freshly deglaciated bedrock and soil, provided there is sufficient moisture. The field populations, the demographic measurements of which were used in the simulations, are according to the estimates, either the remains of a more widespread occurrence of *G. reptans* during the postglacial period when glaciers started to retreat, or from the Little Ice Age with several cooler periods and glacial expansions between 1350 and 1820 when temperatures in the Alps dropped considerably (maximal –4.5°C; Büntgen et al. 2006). From 1850 onwards, glaciers in the Alps were retreating steadily, creating new space for population expansion. Thus, today we see populations on glacier forelands that have expanded steadily for more than 150 years. Clearly, at this age, density-dependent mortality has an insignificant effect on the genet age structure, as revealed by the simulations.

Ramet and genet demography

Currently there are only a few studies explicitly on both ramet- and genet-level dynamics (e.g. Hartnett & Bazzaz 1985, Eriksson 1986, 1988, Karlson 1991, Eriksson 1994, Damman & Cain 1998). Most ecological studies do not consider the genet level but take ramets as the individual unit and look at the demographic properties of populations without regard to genetic identity. Consequently, matrix models or other types of models have hardly been used to investigate genet longevity and population age structure in long-lived clonal plants (Menges 2000). A notable exception is the matrix model study of the endangered herbaceous plant, *Scorzonera humilis*, by Colling & Matthies (2006). As in this study they also record a high ERL of adult genets. Ehrlén & Lehtilä (2002) review the use of population matrix models to determine the longevity of 71 species of herbaceous perennials. They report ramet life spans ranging from 4 to almost 1000 years, with more than half of the species studied having a ramet life expectancy of more than 35 years. But even in this study, genet life span was not investigated. The reason for this is the great difficulty in identifying genets, measuring genet sizes and estimating genet life spans of clonal plants.

A future task will be to use demographic techniques on genet data obtained by molecular genotyping studies to make more accurate predictions at the genet level. For example, a combined demographic-molecular approach is likely to reveal spatial and temporal patterns at the genet level and thus characteristics particularly relevant to clonal life histories and population viability (e.g. de Steven 1989, Torimaru & Tomaru 2005, Araki et al. 2009).

Conclusions

The results demonstrate that predicting life-history parameters, such as genet longevity or genet age structure of populations, using simulations based on projection matrix models is a promising way of reaching a better understanding of the dynamics of long-lived clonal plants such as *Geum reptans*. Especially for clonal plants with a growth strategy that includes a great spacing out of ramets and decaying connections, this demographic approach to longevity is a valuable achievement as other methods are not suitable for estimating genet age. Moreover, this approach enables the analysis of the age structure of whole populations and, therefore, to investigate population structure and demography. We hope that such an approach will be applied to other populations and species in the future, enabling comparisons between species and a better insight into the life history of clonal plants in general.

Acknowledgements

Souhrn

Délka života genety je klíčovým demografickým parametrem, u rostlin s klonálním růstem se však určuje obtížně, zejména když spojení mezi ramety přetrvává krátce a rostliny poté obsazují prostor nezávisle na sobě. V práci jsme pomocí projekčních maticových modelů, založených na demografických datech sbíraných na dvou stanovištích po dobu tří let, studovali délku života genety klonálního druhu *Geum reptans*, který je pionýrským druhem sukcese na předpolí ledovce ve Švýcarských Alpách. Pomocí počítačových simulací, zahrnujících maximální nosnou kapacitu prostředí a na hustotě závislou mortalitu, jsme spočítali věkovou strukturu genet v různě starých populacích a srovnáním těchto simulací s terénními daty jsme odhadli skutečné stáří dvou populací v terénu. Simulace ukázaly, že více než polovina genet uhyne během prvních tří desetiletí, značná část však přežívá více než 50 let a některé jsou v podstatě nesmrtelné, protože při akumulaci dostatečného počtu ramet je riziko úhynu nulové. Simulovaná věková struktura genet měla výrazně šikmé rozdělení, populaci tvořil velký počet mladých a několik málo velmi starých genet. Poměrně nízké nosné kapacity prostředí je dosaženo po pouhých 350 letech, poté začíná být věková struktura výrazně ovlivněna na hustotě závislou mortalitou. Populace *G. reptans* dosahují ve Švýcarských Alpách značného stáří, pro dvě v terénu studované populace bylo odhadnuto na 250 a 450 let. Naše výsledky ukazují, že populace klonálně rostoucích rostlin mohou díky prakticky nesmrtelným genetám přetrvávat v terénu bez omezení. V případě *G. reptans* dochází u starých populací ke kompetici a zvýšené mortalitě díky sukcesi probíhající ve starších částech předpolí ledovce, což populacím brání dosáhnout maximální nosné kapacity prostředí. Populace tohoto druhu jsou však schopny kolonizovat nová místa, a sledovat tak ustupující čelo ledovce.

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