Demographic Consequences of the Two Reproductive Modes in Poa alpina L. along a Primary Succession Gradient in the Central Alps

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Abstract

Poa alpina grass plays a predominant role across the entire range of primary succession on alpine glacier forelands. One demographic factor that reacts clearly to changing environmental conditions is reproduction. Using permanent plot data, the complete life cycle of *Poa alpina* was studied along a successional gradient of the Rotmoos glacier foreland (2300–2400 m a.s.l., Central Alps, Austria) over a period of three years. We used matrix modeling to study the importance of the generation of plantlets and seedlings along the successional gradient and their ability to form adult individuals, and we hypothesized that plantlets develop faster to adults than seedlings because they start already with 3–4 developed leaves.

The study showed that plantlet and seedling fecundities of *Poa alpina* changed differently in the course of succession: seedling establishment was observed over the entire range of the successional stages, whereas plantlet establishment almost vanished with ongoing succession. In the pioneer stage, plantlets were more important than reproduction by seedlings. But we found neither a higher survival rate nor a significant advantage in development to adults for plantlets compared to seedlings. Opportunistic reproduction—plantlets under harsh abiotic conditions, seeds under increasing density—may therefore explain the fact that the species is ubiquitous along the whole glacier foreland.

Introduction

In the alpine zone, primary succession on barren land resulting from glacier retreat has attracted the interest of ecologists for more than a century (Coaz, 1887, *in* Matthews, 1992, and review there). Initial colonization in glacier forelands of the Alps requires the input of seeds, plant fragments or vegetative propagules from outside the area because a seed bank has to be developed from zero (Stöcklin and Bäumler, 1996; Erschbamer et al., 2001; Marcante et al., 2009a). Thus, dispersal is the first major filter for primary succession (Walker and del Moral, 2003). After the arrival of propagules (Matthews, 1992; Stöcklin and Bäumler, 1996), life history traits (Stöcklin, 1990; Stöcklin and Favre, 1994; Stöcklin and Bäumler, 1996), physiological traits (Chapin, 1993), reproduction (Stöcklin, 1992; Pluess and Stöcklin, 2005; Weppler et al., 2006), or plant population dynamics (Stöcklin, 1990; Niederfriniger Schlag and Erschbamer, 2000; Weppler et al., 2006; Marcante et al., 2009b) govern the colonization and the development of plant communities along the primary succession gradient.

Poa alpina plays a predominant role among the few species that occur across the whole range of a successional gradient on glacier forelands in the central Austrian Alps (Raffl et al., 2006). Using permanent plot data and matrix analysis, Marcante et al. (2009b) investigated the life cycles of *Poa alpina* and three other species along this gradient. This demographic study showed that in the pioneer stage *Poa alpina* strongly increases in population size. With ongoing succession population growth rate decreases, but this species is able to maintain its population even in the late successional stage with rates of population increase of $\lambda \approx 1$. Probably due to a high degree of vegetative and reproductive

variability, the species is able to cope with the changing environmental conditions along the successional gradient as well as with different degrees of intra- and interspecific interactions. *Poa alpina* exhibits sexual reproduction via seeds (seedlings) and asexual reproduction via plantlets. The asexual reproduction mode is called "pseudoviviparous" (Pierce et al., 2003) or "viviparous" (Körner 1999). Plantlets are developed by maternal tissues and not by zygotes and consist of 3–4 leaves when released from the maternal plant. Along the successional gradient in the Central Alps it was shown that reproduction via plantlets played a predominant role in the pioneer stage but that reproduction shifted strongly towards seed production in older successional stages (Marcante et al., 2009b).

Compared to seedlings, plantlets are able to root and establish quickly after dispersal (Lee and Harmer 1980). Adults arising from plantlets were reported to be reproductive plants after only one year (Elven, 1974, 1980, *in* Matthews, 1992). In contrast, the seedlings of *Poa alpina* require at least three years of growth before they start to reproduce (Matthews, 1992). These differences in the rate of development of adult plants would give plantlet reproduction a clear advantage over seedling reproduction. But the demographic matrix analyses of Marcante et al. (2009b) were based on the common assumption that the fate of an individual in a transition step depends only on the stage that an individual has just reached but not on its past history (Caswell, 2001). Thus, the analyses did not differentiate between adults of different origin.

Poa alpina plants that arise either from plantlets or from seedlings cannot be distinguished, once established, on a morphological basis. However, when the field work underpinning a demographic analysis comprises more than one time step it is

possible by "individual tracing" to include past effects in the calculation of demographic rates (Tanner et al., 1996; Ehrlén, 2000). With respect to the demography of *Poa alpina*, such a tracing would allow us to study the impact of a new individual's mode of origin on its future development.

We used the data provided by Marcante et al. (2009b) to decompose reproduction of *Poa alpina* into its asexual and sexual components along a gradient of primary succession. As this data set comprised two annual steps it allowed following the impact of their origin on the fate of plants. This demographic analysis was accompanied by a survey on the occurrence and the fecundities of asexual and sexual inflorescences as well as on resulting offspring numbers along the successional stages. Finally the life-cycle analyses of Marcante et al. (2009b) were discussed with a focus on reproductive mode. We aimed to answer the following questions:

(1) Does the production of plantlets and seeds of *Poa alpina* depend on the successional stage?
(2) Does "net fecundity," i.e. the reproductive success of *Poa alpina* plantlets or seeds, vary along the successional gradient?
(3) Do seedlings and plantlets differ in their ability to form established adult individuals?
(4) Does population growth rely on both modes of reproduction over the whole range of succession?

Materials and Methods

RESEARCH AREA

The research area lies in the Central Alps of Austria on the glacier foreland of the Rotmoos Valley (Obergurgl, Oetztal, Tyrol, 46°49′N, 11°02′E) at 2300–2400 m a.s.l. The U-shaped valley is almost level, ascending only slightly near the glacier tongue. Over the last 150 years the glacier has retreated by more than 2 km. The largely well preserved chronosequence exhibits a series of glacier moraines. The main moraines of 1971, 1923, and 1858 (Gernot Patzelt, University of Innsbruck, unpublished, 1995) represent the pioneer (A), early (B), and late (C) successional stages of a primary successional gradient. Mean annual precipitation is approximately 1460 mm (Kaufmann, 2001), and soil temperatures at 10 cm depth along the successional gradient are shown in Figure 1 (Rüdiger Kaufmann, personal communication). The lowest winter temperatures were recorded at the early successional site, and the highest summer temperatures were clearly observed at the late successional site. The annual mean temperatures for the three study years were 2.3 °C at the pioneer site, 2.8 °C at the early successional site, and 3.2 °C at the late successional site. Snow cover lasts from October to late May or early June, with differences in snow melt of 10–17 days between the oldest and the youngest moraine.

The pioneer stage is characterized by pioneer assemblages mainly composed of *Saxifraga aizoides*, *S. oppositifolia*, *Linaria alpina*, and *Artemisia genipi* (Raffl and Erschbamer, 2004; Raffl et al., 2006). The pioneers are then replaced by early successional species such as *Trifolium pallescens* and *Poa alpina*. Additionally, *Festuca* spp., *Silene acaulis*, and *Salix* spp. occur. The late successional sites were dominated by species such as *Agrostis alpina*, *Anthyllis vulneraria* ssp. *alpicola*, *Kobresia myosuroides*, *Leotondon hispidus* ssp. *alpinus*, and *T. pratense* ssp. *nivale* (Raffl and Erschbamer, 2004). The nomenclature follows Fischer et al. (2005).
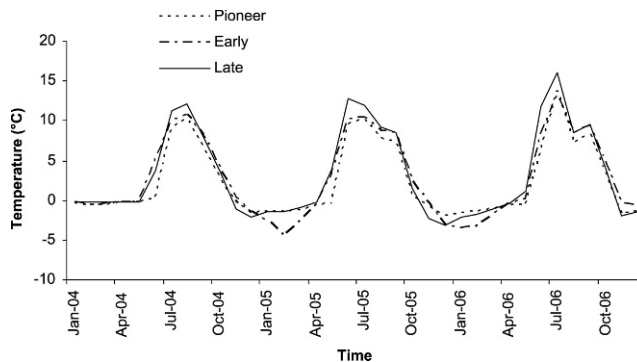

FIGURE 1.   Mean monthly soil temperatures at a depth of 10 cm for the three successional stages (pioneer, early, late) of the Rotmoos glacier foreland from 2004 to 2006 (data: Rüdiger Kaufmann).

Soil development along the glacier foreland is rather slow, from a Syrozem on the youngest moraines to Pararendzinas of 3–4 cm depth on the oldest moraine (Erschbamer et al., 1999).

THE SPECIES

Poa alpina (Poaceae) is a very common arctic-alpine grass that reproduces asexually by plantlets or sexually by seeds. It is a tussock-building grass with the new shoots appearing almost intravaginally (Wilhalm, 1996). Each shoot is potentially capable of producing one inflorescence. The reproduction mode depends on photoperiod and temperature (Heide, 1989). In phytotrons sexual reproduction is induced by short days at temperatures of up to 18 °C or long days and temperatures between 3 and 6 °C. Given short days and marginally low temperatures the species can also produce mixed inflorescences with plantlets, mainly at the terminal parts of the inflorescence (Heide, 1989, and personal communication), and seeds. In the field pseudoviviparous and seminiferous forms were, however, always strictly separated (Marcante et al., 2009a, b).

The plantlets are capable of photosynthesis (Lee and Harmer, 1980; Pierce, 1998; Pierce et al., 2000, 2003) and they produce adventitious roots, becoming rapidly established after wind or water dispersal. This speed of establishment may give them an advantage over seeds in short arctic/alpine growing seasons (Lee and Harmer, 1980).

In the study area *P. alpina* is a ubiquitous species along the whole glacier foreland, occurring from the pioneer stage to the late successional stage (Erschbamer et al., 1999; Tscherko et al., 2004; Raffl and Erschbamer, 2004; Raffl et al., 2006), with highest abundances on the early successional stage (ice free since 40–70 years; Raffl et al., 2006).

POPULATION SAMPLING

Poa alpina was studied in three successional stages: pioneer, early-, and late successional stage. In July 2004, three permanent plots of 1 m² were established randomly on homogeneous areas of each stage; these were fenced in to protect against large domestic grazers and tourist trampling. Data on individual plants were collected over a period of 3 years, from 2004 to 2006. In each plot, one main census per year was conducted during the growing season (July–September). In order to record exactly the same individuals in every census, each 1 m² plot was fixed by metal nails and subdivided into dm². Each individual (adults and seedlings) was marked with a colored wire. For each adult individual vegetative and reproductive

shoots were counted. Individuals exhibiting either asexual or sexual reproduction (n_P and n_S) in the permanent plots of the pioneer stage were recorded in 2006 and 2009.

The number of plantlets or seeds per inflorescence (inflorescence fecundities f_{IP} and f_{IS}) and the number of inflorescences per adult individual (inflorescence frequencies n_{IP} and n_{IS}) were determined in August 2004 at all three successional stages. As the determination of inflorescence fecundities was destructive, plants were analyzed from samples collected in an area around the permanent plots ("fecundity samples"). For each stage approximately 20 small (≤ 5 vegetative shoots and inflorescences) and 20 large (>5 vegetative shoots and inflorescences) individuals were sampled.

LIFE CYCLE STAGES

Following field observations and previous studies (Schwienbacher, 2004), we distinguished life cycle stages on the basis of "size." The categories used were as follows:

Seedlings (with coleoptile and generally one pair of leaves): Seeds germinate soon after snowmelt in early summer following production in the previous year or, possibly, from a permanent seed bank (Marcante et al., 2009a). Only newly recruited individuals were considered as seedlings; small individuals already displaying one shoot were assigned to the adult stage 1 category.

Plantlets: Individuals with first adventitious roots and about three leaves, already established.

Adult stage 1: Small individuals with one (mostly vegetative) shoot.

Adult stage 2: Individuals with 2 shoots. Some individuals of this stage already had one reproductive shoot.

Adult stages 3 and 4: Individuals with 3…5 and with more than 5 shoots.

The numbers of vegetative and reproductive shoots were added up to assign individuals to stages.

DEMOGRAPHY: TRANSITION RATES AND REPRODUCTION

Transition rates a_{ij} from life cycle stage j to stage i were calculated for each stage as the proportion of individuals in the permanent plots remaining in that stage or having changed to a given other stage within an interval of 1 year (Caswell, 2001):

$$a_{ij} = \frac{x_{ij}}{x_j} \qquad (1)$$

with x_j being the number of individuals in stage j at time t, and x_{ij} the number of individuals making a transition in time step $t…t+1$ from stage j to stage i (including stage j itself). Mortality m_j in stage j was given by

$$m_j = 1 - \sum_i a_{ij} \qquad (2)$$

where a_{ij} are the transition rates as given above.

Transition rates which take into account the history of individuals were calculated in the same manner as given by Equation (1), but only considered those individuals that were in stage k at time step $t - 1$:

$$a_{ijk} = \frac{x_{ijk}}{x_{jk}} \qquad (3)$$

Transition rates were calculated separately for each plot of a successional stage. Rates that followed Equation (1) were obtained

TABLE 1

Inflorescence fecundities f_{IP} and f_{IS} (number of plantlets or seeds per inflorescence) in dependence on successional stage. The numbers in parentheses give sample sizes. Small individuals: 2–5 shoots, large individuals: >5 shoots.

		Successional stage		
		Pioneer	Early	Late
Plantlets	Small indiv.	16.1 ± 7.5 (16)	24.9 ± 12.0 (11)	14.9 ± 5.2 (12)
	Large indiv.	15.4 ± 8.4 (103)	24.1 ± 8.4 (10)	15.6 ± 8.5 (28)
Seeds	Small indiv.	15.6 ± 11.6 (13)	45.8 ± 27.1 (11)	22.7 ± 19.3 (12)
	Large indiv.	29.6 ± 25.7 (64)	42.1 ± 32.0 (42)	19.3 ± 16.1 (48)

for the time steps 2004…2005 and 2005…2006 (Marcante et al., 2009b), whereas rates including individual history [Equation (3)] were calculated for time step 2005…2006 under consideration of the state k of these individuals in 2004. This evaluation considered 1-shoot individuals that originated either from seedlings or from plantlets: in the third year of the study (2006), all states of individuals were registered that were 1-shoot adults in the second year (2005) and either plantlets or seedlings in the first year (2004).

Net fecundities f_{NP} and f_{NS}, numbers of plantlets and seedlings newly established at time step $t + 1$ in the permanent plots related to the number of adult individuals in the same plot in the preceding time step t, were calculated for each plot per successional stage and for two transitions (2004–2005 and 2005–2006). Seed or plantlet exchange with the surroundings of the plots or with a permanent seed bank was only implicitly considered (Marcante et al., 2009b).

The construction of complete demographic matrices from the transition rates and the calculation of rates of population increase λ followed Marcante et al. (2009b).

STATISTICAL ANALYSES

All statistical tests were performed with the statistical analysis package Statistica 7.0. Plantlet and seedling inflorescence frequencies and net fecundities were compared with each other in dependence on successional stage using a two-factor ANOVA as well as a Scheirer-Ray-Hare test (performed because the condition of homogeneous variances was not fulfilled even after log transformation of data). Differences between plantlet and seedling fecundities for each individual stage were also evaluated by U test. To evaluate the dependence of reproduction on shoot density Spearman's rank correlation coefficients R were calculated instead of Pearson's coefficient r, because the condition of equal variance was not fulfilled. Seed or plantlet numbers per inflorescence were evaluated by two-factor ANOVA. For the evaluation of transition rates for plantlets, seedlings, and small adults, a log-linear analysis of contingency tables was performed.

Results

ASEXUAL AND SEXUAL FECUNDITIES

Inflorescence fecundities f_{IP} and f_{IS} are given in Table 1 for small and for large individuals of the outside-plot "fecundity samples." They were highest at the early successional stage and did not differ between size classes. When values for small and large individuals were averaged, a two-factor ANOVA resulted in significant differences for both successional stages and reproduction modes ($p < 0.001$), but not for interactions of the two factors. For plantlet as well as for seed inflorescence fecundities, the
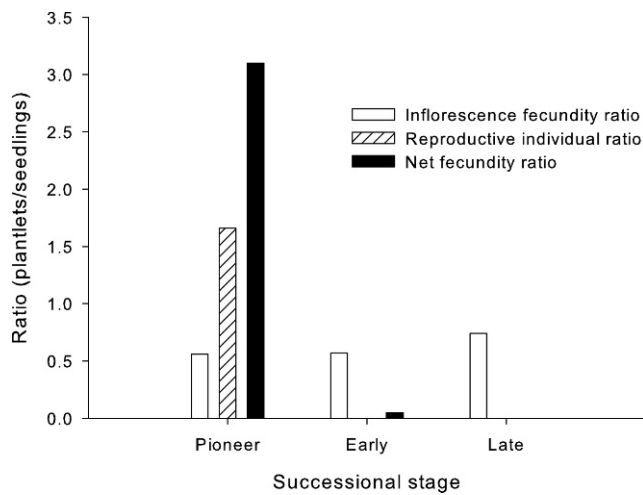
E. WINKLER ET AL. / 229

FIGURE 2. Ratios of plantlet and seedling fecundities as a function of successional stage. White bars—inflorescence fecundity ratio f_{IP}/f_{IS} averaged over small and large individuals; hatched bars—ratio between reproducing individuals with either plantlets or seeds (n_P/n_S); black bars—net fecundity ratio f_{NP}/f_{NS}.

differences between pioneer and late successional stage were non-significant. The same held in the late successional stage for the difference between seed and plantlet formation. The inflorescence fecundity ratio increased during the course of succession (Fig. 2).

Inflorescence frequencies n_{IP} and n_{IS} in the "fecundity samples" decreased from the pioneer to the late successional stage for large pseudoviviparous as well as for large seminiferous individuals (Table 2). A two-factorial ANOVA gave a highly significant ($p < 0.001$) dependence on stage, but no dependence on reproductive mode, and no interaction between stage and mode.

In the plots of the pioneer stage, individuals were found reproducing either asexually or sexually (Table 3). Their numbers and ratios were highly variable, and when averaged over three plots and two years, the number of asexually reproducing individuals was higher than that of sexually reproducing individuals by a factor of 1.66 (Fig. 2). A subset of the individuals had inflorescences in both years (2006 and 2009), and these plants always retained their reproductive mode. No individuals with changing mode were observed. In the early and late successional stages there were only sexually reproducing individuals inside the plots. However, some plantlet-producing plants could be found in the surroundings, with decreasing abundance from the early to the late successional stage.

TABLE 2

Inflorescence frequencies n_{IP} and n_{IS} (numbers of pseudoviviparous and seminiferous inflorescences) per individual in dependence on successional stage (mean values and standard deviations). The numbers in parentheses give individual sample sizes. For the definition of small and large individuals see Table 1.

		Successional stage		
		Pioneer	Early	Late
Pseudoviviparous inflorescences	Small indiv.	1 (16)	1 (11)	1 (12)
	Large indiv.	4.9 ± 0.8 (21)	3.3 ± 0.6 (3)	2.8 ± 0.9 (10)
Seminiferous inflorescences	Small indiv.	1 (12)	1 (11)	1 (10)
	Large indiv.	4.9 ± 0.5 (13)	3.2 ± 0.6 (13)	2.8 ± 0.6 (17)

TABLE 3

Numbers of individuals with generative shoots producing either plantlets (n_P) or seeds (n_S) in the three permanent plots of the pioneer stage A. The numbers in parentheses give the numbers of individuals being present in 2006 as well as in 2009 showing the same reproductive mode.

	Plot (pioneer stage)							
	1		2		3		Total	
	2006	2009	2006	2009	2006	2009	2006	2009
Plantlets	5	5 (2)	7	3 (2)	10	18 (7)	22	26 (11)
Seeds	3	5 (2)	14	3 (2)	2	2 (0)	19	10 (3)

Net fecundities for plantlets and seedlings (f_{NP} and f_{NS}), determined from the permanent-plot data for each stage and plot separately, are included in Figure 3, and the ratio of net fecundities is given in Figure 2. In the pioneer stage, net fecundity ratio was higher than the ratio of the numbers of reproducing individuals with plantlets or seedlings, n_P/n_S, and much higher than that of inflorescence fecundities, f_{IP}/f_{IS}. But already at the early successional stage net fecundity ratio was very small, and at the late successional stage we had a net fecundity ratio of zero: no newly established plantlets were found. In spite of this striking feature in the dependence of net fecundities on the mode of reproduction and on the successional stage, statistical tests (two-factor ANOVA and Scheirer-Ray-Hare test) only revealed a significant dependence of net fecundity on successional stage ($p < 0.01$) and not on reproductive mode. A U-test evaluation of differences between reproduction modes for each individual successional stage resulted in significant differences for all stages ($p = 0.025$, 0.0064, and 0.0074). In the pioneer stage plantlet net fecundity per adult was higher than seedling net fecundity, but the reverse holds for the older successional stages.

Density of *P. alpina*, given by the number of shoots per permanent plot, increased with the progress of succession (one-factor ANOVA, $p = 0.008$), and net fecundities of both reproductive modes decreased with increasing shoot density. Net fecundities of both modes were significantly correlated with density (Fig. 3; Spearman's rank correlation coefficients $R = -0.47$ and -0.60 for the two modes; $p < 0.05$), with regression coefficients $b = -0.0007 \pm 0.0003$ ($p = 0.04$) and $b = -0.0003 \pm 0.0001$ ($p = 0.03$) for asexual and sexual reproduction.

DEVELOPMENT OF ESTABLISHED PLANTLETS AND SEEDLINGS

The fate of established plantlets or seedlings ("juveniles") is shown in Figure 4. In accordance with the matrices of Marcante et al. (2009b) in the time step after establishment they can either die or remain in the juvenile stage (stasis), or they can develop into adults having one or more shoots [Equations (1) and (2)].

Contingency analysis showed significant dependence of juvenile fate on successional stage but not on the mode of origin ($p < 0.01$ and $p = 0.33$). Also two-factor ANOVA showed a significant dependence of juvenile development on successional stage, but only marginal dependence on reproductive mode. Mortality of juveniles decreased with ongoing succession ($p = 0.002$) and was somewhat lower for plantlets than for seedlings (difference almost significant: $p = 0.07$, with no significant interaction term). On the other hand the stasis rate increased with succession and was partially higher for plantlets than for seedlings (differences not significant). Transition rates into adult stage 1 for plantlets and for seedlings did not differ significantly.
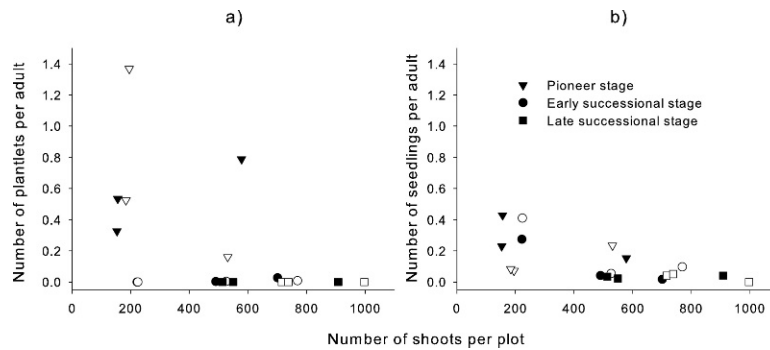
Transitions to adult stages 2 and 3 were rather low, but showed (non-significantly) an increase with succession ($p = 0.09$). They were somewhat higher for plantlets than for seedlings, but the differences were non-significant. Especially for the late-successional stage the very small number of plantlets has to be taken into account, giving rise to non-homogeneous variances. Hence, at this stage, any differences between the fate of seedlings and plantlets can only be considered as trends.

DEVELOPMENT OF ADULTS EMERGING FROM PLANTLETS OR SEEDLINGS

Differences in the development of small adults (1 shoot) that were formed in the preceding time step either from established plantlets or from seedlings are analyzed in Figure 5. With respect to the mode of origin the results of the "individual tracing" [Equation (3)] could only be evaluated for the pioneer and the early successional stage since in the oldest stage individuals formed from plantlets were missing. Two-factor main-effect ANOVA

showed that mortality of 1-shoot adults was significantly lower in the early successional stage than in the pioneer stage ($p = 0.037$), but with no effect of the origin of the individuals from seedlings or plantlets. Also for transition to larger individuals no significant differences could be detected, either in dependence on successional stage or on the mode of origin. An absence of any significant interaction between the fate of individuals and successional stage or mode of origin was also demonstrated by contingency analysis ($p = 0.15$ and 0.47).

EFFECT OF ASEXUAL AND SEXUAL REPRODUCTION ON POPULATION GROWTH

Asexual and sexual net fecundities, broken down into the contributions of the individuals of each life cycle class, entered into population-dynamic matrices (Marcante et al., 2009b) and thus influenced the rates of population increase λ. In Figure 6 these λ-values are compared with the population growth rates that would result if one or both modes of reproduction (plantlets and/
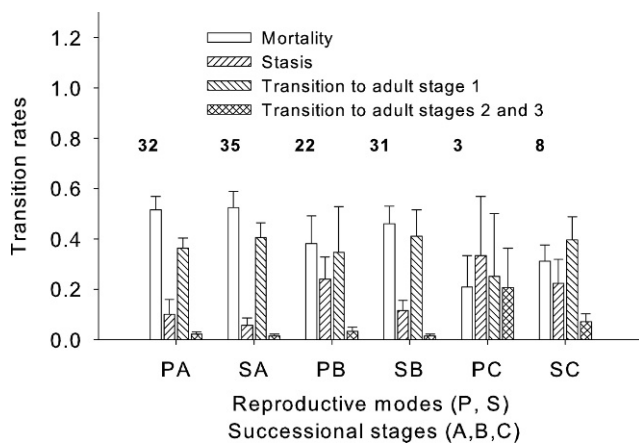

FIGURE 4. Transition rates (mean values and standard errors) for plantlets P and seedlings S in dependence on successional stage (pioneer stage A, early successional stage B, late successional stage C). The rates in each group average over 3 plots per stage and two transitions. The numbers on the bars denote the average number of seedlings or plantlets per plot entering into the calculation of rates.
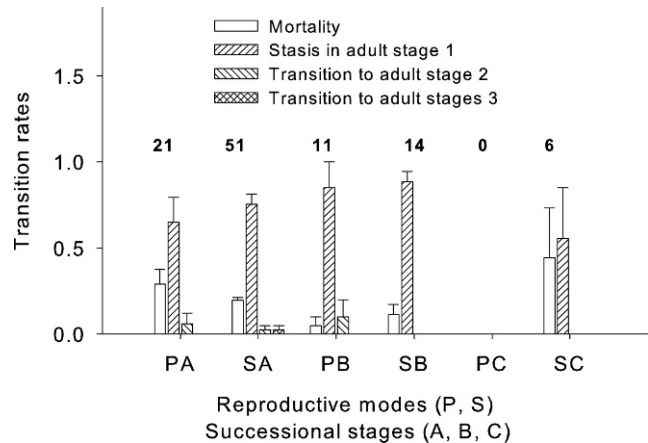

FIGURE 5. Transition rates (mean values and standard errors) for one-shoot adults originating in the preceding step from plantlets P or seedlings S, respectively, as a function of successional stage (see legend to Fig. 4). The rates in each group are averaged over three plots per stage. The numbers on the bars denote the number of individuals per stage entering into the calculation of rates.
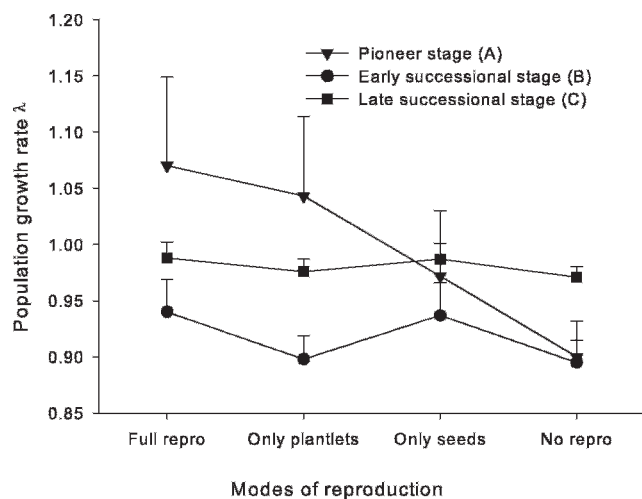
FIGURE 6. Rates of population increase, λ, for different combinations of reproductive modes as a function of successional stage (triangle: pioneer stage; circle: early successional stage; square: late successional stage). Given are averages (mean ± s.e.) over both time steps and all plots per stage.

or seedlings) were missing. Population increase ($\lambda > 1$) was found only at the pioneer stage, and this population growth required plantlet reproduction. All other scenarios resulted in populations of decreasing size ($\lambda < 1$). Seed reproduction alone was unable to maintain population growth in all successional stages. At the older stages differences between λ-values under different assumptions for reproduction were smaller than in the pioneer stage. Inclusion of reproduction by either seedlings or plantlets only slightly increased the λ-values (Fig. 6). But even in the absence of any reproduction, λ-values were still rather high, corresponding to the low impact of fecundity on growth rate λ; the contribution of fecundity to total elasticity was only 0.03 (Marcante et al., 2009b).

Discussion

FECUNDITY PARAMETERS AND SUCCESSIONAL STAGES

In the study area, *P. alpina* showed inflorescences that produced either plantlets or seeds over all three successional stages comprising around 150 years of primary succession. Plantlet and seed inflorescence fecundity values did not differ anywhere and were highest in the early successional stage. Individuals that produced either plantlets or seeds did also not differ in the number of inflorescences per plant (inflorescence frequency), which was steadily decreasing from the pioneer to the late successional stage.

In contrast to this correspondence between plantlets and seeds, there were large differences in the number of plantlet or seed-producing individuals per plot as well as in the number of establishing plantlets or seedlings (net fecundity), and both differences reversed their sign with ongoing succession. At the pioneer stage, plantlet net fecundity was much higher than seedling net fecundity. But already at the early successional stage only a few plantlets were produced and established, and at the oldest stage plantlet establishment was practically absent during the study period. This observation is in line with studies on *P. alpina* along altitudinal gradients (Weyand, 2005, *in* Rudmann-Maurer et al., 2007) and on viviparous species in general (Bauert, 1993; Pluess and Stöcklin, 2005). Nevertheless, plantlets do establish during the late successional stage, as indicated by the occurrence of a very small number in the study plots. They were probably introduced by dispersal from younger moraines or from

the few pseudoviviparous individuals occurring close to the study plots.

The decrease of the number of inflorescences per individual in the course of succession denotes the existence of factors that negatively affect reproduction during succession. Earlier studies related changes in reproduction with changes in temperatures (see Fig. 1), soil quality (Tscherko et al., 2004), or above- and belowground community development (Bardgett et al., 2005; Raffl et al., 2006). At the pioneer stage the mean annual temperature is lower than at the older stages and the duration of snow cover is longer, thus harsher conditions prevail close to the glacier tongue. In general asexual reproduction in alpine species is associated with such stressful conditions (Lee and Harmer, 1980; Stöcklin, 1992; Pluess and Stöcklin, 2005; Weppler et al., 2006).

Also in our study the stressful conditions of the pioneer stage obviously favor the production of plantlets. The two reproductive modes of *Poa alpina* were found to be related to photoperiod, temperature (Bachmann, 1980, *in* Wilhalm, 1996; Heide, 1989), and humidity (Bachmann, 1980, *in* Wilhalm, 1996). Under controlled conditions in growth chambers, long photoperiods and increasing temperatures caused a switch from the pseudoviviparous to the seminiferous form (Heide, 1989; Keller and Körner, 2003). The increase in temperature may be a factor switching reproduction from plantlet to seed production also under field conditions.

One environmental factor that readily can be observed is density. Vegetation density in general (Raffl et al., 2006) and shoot density (Marcante et al., 2009b) of *P. alpina* in particular increase with ongoing succession. We found by regression analysis that plantlet establishment decreased with increasing density much more than seedling establishment. But regression analysis did not fully reflect a qualitative feature of the dependence: reproduction by plantlets completely ceased with ongoing succession (and increasing density), whereas there was some seedling establishment also in the latest stage. The observed general reduction of net fecundity and especially the shift of reproduction from asexual to sexual mode as a reaction to vegetation density correspond with model analyses by Winkler and Stöcklin (2002). These authors studied the contrast between asexual reproduction with low dispersal distances and sexual reproduction with high dispersal ability for *Hieracium pilosella* (a species with short aboveground stolons) in a grass sward of increasing density, and they showed that with increasing intra- and interspecific competition, reproduction by seeds became more and more advantageous. Also for *P. alpina* there are strong differences in dispersal abilities of plantlets and seeds. Both are probably barochorous and only secondarily dispersed by wind. But seeds are relatively lightweight (0.30–0.32 mg; Erich Schwienbacher, unpublished) whereas plantlets are many times heavier (3–11 mg; Brigitta Erschbamer, unpublished). Therefore, seed dispersal in glacier forelands occurs around the mother plant at distances of 0–10 m (Stöcklin and Bäumler, 1996). Plantlets will be dispersed very closely around the mother plant (if not transported further away by post-release movement, e.g. by water flow or strong winds), with the inflorescences sometimes simply hanging down to the ground. In denser swards such as the late successional stage, plantlet establishment is therefore almost impossible.

Our findings suggest the existence of changes in cost-benefit ratio for asexual and sexual reproduction. Though there is a large literature on arctic-alpine clonal plants (review in Jónsdóttir et al., 1996) and on the benefits of asexual reproduction in experimental settings (Stuefer et al., 1994), cost-benefit analyses either on plantlet or on seed production of *P. alpina* or other alpine species are lacking. Additionally, any cost-benefit analyses of reproduc-

tion modes must also take into account dispersal and establishment processes (Winkler and Fischer, 1999), making any detailed considerations practically impossible.

SURVIVAL AND DEVELOPMENT OF INDIVIDUALS EMERGING FROM PLANTLETS OR SEEDLINGS

Plantlet and seedling mortality was remarkably high on the younger successional stages and decreased on the oldest one, but there were almost no differences between plantlets and seedlings. Weppler et al. (2006) concluded that vegetative offspring of *Geum reptans* had no advantage over seedlings for surviving winter. According to our results, plantlets of *Poa alpina* seem to be subjected to the same establishment risks as seedlings (Chambers et al., 1991; Tsuyuzaki et al., 1997; Mong and Vetaas, 2006; Erschbamer et al., 2008), i.e. desiccation of the upper soil stratum, needle ice, soil temperature, nutrient supply (review in Niederfriniger Schlag and Erschbamer, 2000), microtopography (Mong and Vetaas, 2006), and the lack of safe sites (Erschbamer et al., 2008). In the pioneer stage, where population growth highly depended on plantlets, no differences in the transition rates of plantlets and seedlings to small adults with one or two shoots were detected.

Elven (1980, *in* Matthews, 1992) found, without giving details, that *P. alpina* individuals arising from plantlets were already reproductive after only 1 year—much more rapidly than individuals arising from seedlings. We could not confirm these results in our study. Adult plants with one shoot did not differ in their fate with respect to their mode of origin. At our site *P. alpina* individuals were long-lived, and their development was not affected by any small starting advantage that "plantlet individuals" may have.

REPRODUCTION AND POPULATION GROWTH

The matrix models presented by Marcante et al. (2009b) included two reproductive modes, production and establishment of plantlets and of seedlings, but they did not differentiate for adults between their origins. Our present analysis of individual-tracing data confirmed the validity of this approach, in contrast to other findings in the literature.

The analysis of whole life-cycle dynamics presented in this study focused on the role of reproduction for population development. In general, the importance of reproduction for population dynamics of alpine species under highly variable and unfavorable conditions is low as was revealed by elasticity analysis (Morris and Doak, 1998; Forbis and Doak, 2004). For *P. alpina* this general feature is supplemented by changes along the successional stage in the relative importance of the two forms of reproduction for population increase rates λ. Only at the pioneer stage was reproduction by plantlets essential, ensuring an average increase of population size by 5…10% per year. With ongoing succession the importance of reproduction and especially of plantlet reproduction decreased monotonically, almost vanishing in the late successional stage. Here, population behavior is largely determined by stasis and mortality.

Several authors have considered recruitment by seedlings to be of low importance for local population dynamics of alpine species due to their capacity for clonal propagation (Hartmann, 1957; Billings and Mooney, 1968; Bliss, 1971; Chambers et al., 1990; Stöcklin, 1992). Alpine seedlings have been observed in nature only rarely (Bell and Bliss, 1980; Cooper et al., 2004). However, several recent studies have highlighted the occurrence of

seedlings also in alpine environments (Niederfriniger Schlag and Erschbamer, 2000; Welling and Laine, 2000; Erschbamer et al., 2001; Forbis, 2003; Forbis and Doak, 2004; Marcante et al., 2009b) and their importance for population growth (Weppler et al., 2006). We found successful establishment of *P. alpina* seedlings, but their contribution to population growth remained limited, as seed reproduction alone was not able to ensure population growth. At the pioneer stage the ability of populations to increase in size was exclusively due to plantlet reproduction, whereas at the early and late successional stages neither reproduction by seedlings nor by plantlets had any marked effect on the λ-values. Only large-scale studies in heterogeneous areas such as glacier forelands, taking into account also genetic aspects, may reveal the existence of source-sink populations and the role of seed dispersal in such surroundings.

CONCLUSIONS

Seedling and plantlet net fecundities developed during primary succession in a contrasting manner: seedling establishment was observed over the whole range of stages, whereas plantlet establishment was dominant in the pioneer stage but almost vanished with ongoing succession.

In the pioneer and early successional stages the production of plantlets made a significant contribution to population increase, whereas in the older successional stages population behavior was largely determined by stasis and mortality. Seedling establishment did not contribute to population growth in any decisive way.

We found neither a higher survival rate nor a significant advantage in development for plantlets compared to seedlings. Development of adults was not affected by the mode of origin.

The opportunistic reproduction, by plantlets under harsh conditions and seeds under favorable conditions, contributes to the fact that the species is ubiquitous over the whole successional range.

References Cited

Bardgett, R. D., Bowman, W. D., Kaufmann, R., and Schmidt, S. K., 2005: A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution*, 20: 634–641.

Bauert, M. R., 1993: Vivipary in *Polygonum viviparum*—An adaptation to cold climate? *Nordic Journal of Botany*, 13: 473–480.

Bell, K. L., and Bliss, L. C., 1980: Plant reproduction in a high arctic environment. *Arctic and Alpine Research*, 12: 1–10.

Billings, W. D., and Mooney, H. A., 1968: The ecology of arctic and alpine plants. *Biological Review*, 43: 481–529.

Bliss, L. C., 1971: Arctic and alpine life cycles. *Annual Review of Ecology and Systematics*, 2: 405–438.

Caswell, H., 2001: *Matrix Population Models*. Sunderland, Massachusetts: Sinauer.

Chambers, J. C., MacMahon, J. A., and Brown, R. W., 1990: Alpine seedling establishment: the influence of disturbance type. *Ecology*, 71: 1323–1341.

Chambers, J. C., MacMahon, J. A., and Haefner, J. H., 1991: Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology*, 72: 1668–1677.

Chapin, F. S., III, 1993: Physiological controls over plant establishment in primary succession. *In* Miles, J., and Walton, D. W. H. (eds.), *Primary Succession on Land*. Oxford: Blackwell Scientific Publications.

Cooper, E. J., Alsos, I. G., Hagen, D., Smith, F. M., Coulson, S. J., and Hodkinson, I. D., 2004: Plant recruitment in the High Arctic: seed bank and seedling emergence on Svalbard. *Journal of Vegetation Science*, 15: 115–224.

Ehrlén, J., 2000: The dynamics of plant populations: does the history of individuals matter? *Ecology*, 81: 1675–1684.

Erschbamer, B., Bitterlich, W., and Raffl, C., 1999: Die Vegetation als Indikator für die Bodenbildung im Gletschervorfeld des Rotmoosferners (Obergurgl, Ötztal, Tirol). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck*, 86: 107–122.

Erschbamer, B., Kneringer, E., and Niederfriniger Schlag, R., 2001: Seed rain, soil seed bank, seedling recruitment, and survival of seedlings on a glacier foreland in the Central Alps. *Flora*, 196: 304–312.

Erschbamer, B., Niederfriniger Schlag, R., and Winkler, E., 2008: Colonization processes on a central alpine glacier foreland. *Journal of Vegetation Science*, 19: 855–862.

Fischer, M. A., Adler, W., and Oswald, K., 2005: *Exkursionsflora für Österreich, Liechtenstein und Südtirol,* 2. Aufl., Linz: Land Oberösterreich, Biologiezentrum der OÖ Landesmuseen.

Forbis, T. A., 2003: Seedling demography in an alpine ecosystem. *American Journal of Botany*, 90: 1197–1206.

Forbis, T. A., and Doak, D. F., 2004: Seedling establishment and life history trade-offs in alpine plants. *American Journal of Botany*, 91: 1147–1153.

Hartmann, H., 1957: Studien über die vegetative Fortpflanzung in den Hochalpen. *Jahresbericht der Naturforschenden Gesellschaft Graubündens*, 86: 3–168.

Heide, O., 1989: Environmental control of flowering and viviparous proliferation in seminiferous and viviparous arctic populations of two *Poa* species. *Arctic and Alpine Research*, 21: 305–315.

Jónsdóttir, I. S., Callaghan, T. V., and Headley, A. D., 1996: Resource dynamics within arctic clonal plants. *Ecological Bulletins*, 45: 53–64.

Kaufmann, R., 2001: Invertebrate succession on an alpine glacier foreland. *Ecology*, 82: 2261–2278.

Keller, F., and Körner, C., 2003: The role of photoperiodism in alpine plant development. *Arctic, Antarctic, and Alpine Research*, 35: 361–368.

Körner, C., 1999: *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems*. Berlin: Springer.

Lee, J. A., and Harmer, R., 1980: Viviparity, a reproductive strategy in response to environmental stress? *Oikos*, 35: 254–265.

Marcante, S., Schwienbacher, E., and Erschbamer, B., 2009a: Genesis of a soil seed bank on a primary succession in the Central Alps (Ötztal, Austria). *Flora*, 204: 434–444.

Marcante, S., Winkler, E., and Erschbamer, B., 2009b: Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? *Annals of Botany*, 103: 1129–1143.

Matthews, J. A., 1992: *The Ecology of Recently-deglaciated Terrain. A Geoecological Approach to Glacier Forelands and Primary Succession*. Cambridge Studies in Ecology. Cambridge/ New York: Cambridge University Press.

Mong, C. E., and Vetaas, O. R., 2006: Establishment of *Pinus wallichiana* on a Himalayan glacier foreland: stochastic distribution or safe sites? *Arctic, Antarctic, and Alpine Research*, 38: 584–592.

Morris, W., and Doak, D., 1998: Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany*, 85: 784–793.

Niederfriniger Schlag, R., and Erschbamer, B., 2000: Germination and establishment of seedlings on a glacier foreland in the Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 32: 270–277.

Pierce, S., 1998: Resource allocation in the pseudoviviparous alpine meadow grass (*Poa alpina* L.). PhD thesis. University of Durham, U.K.

Pierce, S., Stirling, C. M., and Baxter, R., 2000: Architectural and physiological heterogeneity within the synflorescence of the pseudoviviparous grass *Poa alpina* var. *vivipara* L. *Journal of Experimental Botany*, 51: 1705–1712.

Pierce, S., Stirling, C., and Baxter, R., 2003: Pseudoviviparous reproduction of *Poa alpina* var. *vivipara* L. (Poaceae) during long-term exposure to elevated atmospheric CO_2. *Annals of Botany*, 91: 613–622.

Pluess, A. R., and Stöcklin, J., 2005: The importance of population origin and environment on clonal and sexual reproduction in the alpine plant *Geum reptans*. *Functional Ecology*, 19: 228–237.

Raffl, C., and Erschbamer, B., 2004: Comparative vegetation analyses of two transects crossing a characteristic glacier valley in the Central Alps. *Phytocoenologia*, 34: 225–240.

Raffl, C., Mallaun, M., Mayer, R., and Erschbamer, B., 2006: Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 38: 421–428.

Rudmann-Maurer, K., Weyand, A., Fischer, M., and Stöcklin, J., 2007: Microsatellite diversity of the agriculturally important alpine grass *Poa alpina* in relation to land use and natural environment. *Annals of Botany*, 100: 1249–1258.

Schwienbacher, E., 2004: Populationsbiologische Studien an frühen Sukzessionsarten im Gletschervorfeld des Rotmoosferners (Ötztal, Tirol). Verbreitung und Standortsansprüche von *Artemisia genipi* und *A. mutellina*. Populationsstruktur von *A. genipi*. Master thesis. University of Innsbruck, Austria.

Stöcklin, J., 1990: Populationsstruktur des Rohbodenpioniers *Epilobium fleischeri* HOCHST. (Onagraceae) auf dem Morteratsch-Gletschervorfeld. *Verhandlungen der Gesellschaft für Ökologie*, 19: 30–43.

Stöcklin, J., 1992: Umwelt, Morphologie und Wachstumsmuster klonaler Pflanzen—Eine Übersicht. *Botanica Helvetica*, 102: 3–21.

Stöcklin, J., and Bäumler, E., 1996: Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*, 7: 45–56.

Stöcklin, J., and Favre, P., 1994: Effects of plant size and morphological constraints on variation in reproductive components in two related species of *Epilobium*. *Journal of Ecology*, 82: 735–746.

Stuefer, J. F., During, H. J., and de Kroon, H., 1994: High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *Journal of Ecology*, 82: 511–518.

Tanner, J. E., Hughes, T. P., and Connell, J. H., 1996: The role of history in community dynamics: a modeling approach. *Ecology*, 77: 108–117.

Tscherko, D., Hammesfahr, U., Marx, M.-C., and Kandeler, E., 2004: Shifts in rhizosphere microbial communities and enzyme activity of *Poa alpina* across an alpine chronosequence. *Soil Biology and Biochemistry*, 36: 1685–1698.

Tsuyuzaki, S., Titus, J. H., and del Moral, R., 1997: Seedling establishment patterns on the Pumice Plain, Mount St. Helens, Washington. *Journal of Vegetation Science*, 8: 727–734.

Walker, L. R., and del Moral, R., 2003: *Primary Succession and Ecosystem Rehabilitation*. Cambridge: Cambridge Press Syndicate of the University of Cambridge.

Welling, P., and Laine, K., 2000: Characteristics of the seedling flora in alpine vegetation, subarctic Finland, II. Floristic similarity between seedling flora and mature vegetation. *Annales Botanici Fennici*, 37: 133–147.

Weppler, T., Stoll, P., and Stöcklin, J., 2006: The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*. *Journal of Ecology*, 94: 869–879.

Wilhalm, T., 1996: Clonal growth and fragmentation in the alpine tussock-forming grass *Poa alpina*. PhD thesis. Swiss Federal Institute of Technology, Zürich, Switzerland.

Winkler, E., and Fischer, M., 1999: Two fitness measures for clonal plants and the importance of spatial aspects. *Plant Ecology*, 141: 191–199.

Winkler, E., and Stöcklin, J., 2002: Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Annals of Botany*, 89: 525–536.