

Demography of the alpine pioneer species *Saxifraga aizoides* in different successional stages at the glacier foreland of the Rotmoosferner (Obergurgl, Ötztal, Austria)

Demographie der alpinen Pionierart *Saxifraga aizoides* in verschiedenen Sukzessionsstadien im Gletschervorfeld des Rotmoosfernens (Obergurgl, Ötztal, Österreich)

Eckart Winkler^{1,*}, Silvia Marcante² & Brigitta Erschbamer²

¹Department of Ecological Modelling, UFZ Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318 Leipzig, Germany, eckart.winkler@ufz.de;

²Institute of Botany, University of Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria, brigitta.erschbamer@uibk.ac.at; silvia.marcante@uibk.ac.at

*Corresponding author

Abstract

The demography of the alpine pioneer species *Saxifraga aizoides* was investigated along a successional gradient at the Rotmoos glacier foreland (2,330–2,450 m a.s.l., Obergurgl, Ötztal, Austria) from recently deglaciated areas to advanced successional stages. A basic hypothesis of our study was that fecundity might play an essential role for population growth rate on the youngest site and become of minor importance at advanced successional stages. A matrix modelling approach was performed to calculate the main demographic parameters on 6, 33, and 81 year old moraines. Our results partly confirmed the prediction of the larger role of fecundity on the youngest sites. Here, seedling mortality was lower compared to the older sites, and the reproductive success was significantly higher. All in all, *Saxifraga aizoides* mainly follows a “persistence strategy” from the beginning, characterized by the fact that large individuals did not undergo mortality at the recently deglaciated site. However, in the long term a population decline will occur due to plant age and changes of environmental conditions along the successional gradient.

Keywords: colonization, demography, fecundity, matrix model, mortality, population growth rate, primary succession

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The retreating glaciers in the Alps offer excellent opportunities to study processes of primary succession. Immediately after retreat, colonization by different species starts (RAFFL et al. 2006, CANNONE et al. 2007, 2008), depending on seed availability (WOOD & DEL MORAL 1987, ERSCHBAMER et al. 2008, 2012, JONES & DEL MORAL 2009), the presence of safe sites (STÖCKLIN & ZOLLER 1991, STÖCKLIN & BÄUMLER 1996, JUMPPONEN et al. 1999, JONES & DEL MORAL 2005) and the prevailing abiotic site conditions (MARCANTE et al.

2012, 2014). Among the decisive initial processes, germination and establishment are the most sensitive ones (MARCANTE et al. 2009a), whereas all other demographic effects on the life cycle seem to be less vulnerable (JUMPPONEN et al. 1999).

From a demographic point of view the general process of succession is often described as a sequence of species with contrasting traits (e.g. TSUYUZAKI & DEL MORAL 1995, CACCIANIGA et al. 2006, GOBBI et al. 2010). Pioneer species with tiny, light and wind-dispersed seeds (STÖCKLIN 1990, STÖCKLIN & BÄUMLER 1996) are the first colonizers in Alpine glacier forelands. However, also clonal growth may be significant already at the beginning of primary succession (STÖCKLIN 1990). Also in the course of secondary succession (SILVERTOWN & FRANCO 1993), pioneer species with anemochorous dispersal arrive first, exhibiting high fecundity. They are replaced by species with high growth rates, and finally species with high survival rates prevail in late successional stages. For primary succession on glacier forelands MARCANTE et al. (2009a) and WINKLER et al. (2010) demonstrated for *Anthyllis vulneraria* ssp. *alpicola*, *Artemisia genipi*, *Poa alpina* and *Saxifraga aizoides* that they are characterized by long individual survival and low fecundity, and that this strategy holds irrespective of the stage at which a species is entering the succession. The relative importance of fecundity was found to be generally low also on the pioneer site, i.e. a moraine being ice-free for 33 years (MARCANTE et al. 2009a), but it remained open whether the strategy of the initially arriving species will differ from this basic pattern on areas deglaciated only very few years ago.

In the present study we assumed that an inclusion of such “youngest” habitats may change the overall picture towards the common model for successions, i.e. that at the beginning of colonization fecundity will play a greater role than in later successional stages because only by establishment of new individuals the succession can start. As a seed bank is lacking (CHAPIN et al. 1994), an external input of seeds must be taken into account, and seedling recruitment should be the most important initial driver of population growth.

In order to test the hypothesis on a shift towards a greater role of fecundity in the initial stage of population establishment, *Saxifraga aizoides* was selected as model species shaping initial colonization in a central Alpine glacier foreland in a dominant manner. The species disappears on advanced successional stages and reappears at later successional stages only after disturbance. The species was already studied at 33 and 81 year old moraines by MARCANTE et al. (2009a) from 2004 to 2006 showing that survival of adult individuals was crucial for this species already at the 33 year old moraine. These studies were continued to get a better knowledge on year-to-year fluctuations, and a new study was initiated at a moraine being ice-free for only 6 years. The present paper will give an overview on the methods applied, and it reports on species demography along the successional gradient. We aimed to answer the following questions: (1) How do populations develop in size and structure from their first establishment up to older successional stages? (2) How do demographic processes and population growth rates vary along successional stages and between years? (3) Which is the predicted fate of populations of different successional stages?

2. Methods

2.1 Study sites

The research area lies at 2330–2450 m a.s.l. in the glacier foreland of the Rotmoos Valley (Obergrugl, Ötztal, Tyrol, Austria; 46°49'N 11°02'E), being an Austrian LTER site (Long-Term Ecological Research, Tyrolean Alps) and a Natura 2000 area (KOCH & ERSCHBAMER 2010, 2013, MAYER &

ERSCHBAMER 2014). The three study sites followed a primary succession gradient from A₀, a site deglaciated since 2001 at 2,450 m a.s.l. (being 6 years ice-free in 2007), a pioneer site A₁ at the glacier stage of 1971 (2,390 m a.s.l., 33 years ice-free) to B, an early successional stage at the glacier stage 1923 (2,330 m a.s.l., 81 years ice-free, MARCANTE et al. 2009a, b). In 2007, A₀ was mainly characterized by a low cover of *Linaria alpina*, *Saxifraga aizoides*, *Saxifraga oppositifolia*; at A₁ *Artemisia genipi*, *Linaria alpina*, *Saxifraga aizoides* and *S. oppositifolia*, dominated. At stage B, early successional species prevailed such as *Poa alpina*, *Racomitrium canescens*, *Saxifraga bryoides*, *Silene acaulis* s.l. and *Trifolium pallescens* (Table 1). The nomenclature follows FISCHER et al. (2008). For further site description see RAFFL & ERSCHBAMER (2004) and RAFFL et al. (2006).

Mean annual soil temperatures at A₁ in 3 cm soil depth were 2.2 °C and 7.6 °C during the snow-free season, respectively (June–September, means of 14 years; ERSCHBAMER 2013). Permanent snow cover lasts from October to late May, June or even to the beginning of July (A₀), with differences in snow melt of 10 to more than 25 days between the oldest and the youngest study site.

2.2 The species

The study species, *Saxifraga aizoides* (Saxifragaceae), is a long-lived perennial arctic-alpine herb with an altitudinal range of 800–3,000 m. It has small, halfsucculent leaves forming multi-ramet mats or cushions (KAPLAN 1995). Each flower raceme comprises, at a maximum, ten yellow or orange flowers (WEBB & GORNALL 1989). Each capsule has 103–687 seeds (MARCANTE et al. 2013); seed mass amounts to 0.04 ± 0.01 mg (SCHWIENBACHER & ERSCHBAMER 2002). *Saxifraga aizoides* is characterized by a mixed mating system, i.e. the species is self-compatible as well as outcrossing.

Table 1. Species composition and cover abundance of the species (extended Braun-Blanquet scale according to REICHELT & WILMANN 1973) at the three study sites A₀, A₁ and B in the glacier foreland of the Rotmoosferner. A₀ = glacier stage 2001, A₁ = glacier stage 1971, B = glacier stage 1923.

Tabelle 1. Artengarnitur und Artmächtigkeit (erweiterte BRAUN-BLANQUET-Skala nach REICHELT & WILMANN 1973) auf den drei Untersuchungsflächen A₀, A₁ und B im Gletschervorfeld des Rotmoosferners. A₀ = Gletscherstand 2001, A₁ = Gletscherstand 1971, B = Gletscherstand 1923.

| Species | A ₀ | A ₁ | B |
|--------------------------------|----------------|----------------|----|
| <i>Saxifraga aizoides</i> | + | 2a | + |
| <i>Saxifraga oppositifolia</i> | + | 2a | 1 |
| <i>Linaria alpina</i> | + | 1 | + |
| <i>Artemisia genipi</i> | | 1 | 1 |
| <i>Poa alpina</i> | | 1 | 2a |
| <i>Cerastium uniflorum</i> | | + | + |
| <i>Sedum atratum</i> | | + | + |
| <i>Saxifraga bryoides</i> | | + | 2a |
| <i>Campanula scheuchzeri</i> | | + | 1 |
| <i>Trifolium pallescens</i> | | | 2a |
| <i>Racomitrium canescens</i> | | | 2a |
| <i>Arabis caerulea</i> | | | 1 |
| <i>Erigeron uniflorus</i> | | | 1 |
| <i>Silene acaulis</i> s.l. | | | 1 |
| <i>Stereocaulon alpinum</i> | | | 1 |
| <i>Artemisia mutellina</i> | | | + |
| <i>Minuartia gerardii</i> | | | + |

This was interpreted as an ideal strategy to cope with the pollinator limitation in the recently deglaciated open areas (RAFFL et al. 2007). The seeds are usually dispersed by wind and they form long-term persistent seed banks (MARCANTE et al. 2009b, SCHWIENBACHER et al. 2011).

The species occurs on moist and calcareous habitats, such as glacier forelands, screes, snow beds, fens and brook banks. At the study sites it is a characteristic pioneer species immediately after deglaciation (ERSCHBAMER et al. 1999, NIEDERFRINIGER SCHLAG & ERSCHBAMER 2000; RAFFL et al. 2006).

2.3 Population sampling

In July 2004, three plots of 1 m² were established randomly-stratified at site A₁ and eight plots at site B; at site A₀ eleven plots were established in 2007. All plots were distributed in approximately homogeneous areas and fenced off against grazers (sheep, horses) and tourists. The relatively large number of plots at B and A₀ was intended to give sufficient numbers of established individuals of different size classes for estimating reliable transition rates. Individual data were collected over a period of 5 years (2004–2008; A₁, B; see also MARCANTE et al. 2009a) or 2 years (2007–2008, A₀). In each plot, one main census per year was conducted. In order to record exactly the same individuals, each 1 m² plot was permanently marked and fixed by metal nails. On these nails a frequency frame of 1 m² could be fixed, subdivided into 100 1 dm² subplots; each plant (established individuals and seedlings) was marked with a coloured wire. As we used a size-based analysis, vegetative and generative shoots for each established individual were counted. We pooled together raw data from all plots in order to get a representative distribution of individual sizes.

2.4 Matrix model analysis

For the evaluation of individual data we distinguished six life-cycle stages, seedlings and five size classes of ‘adult’ individuals, in the following manner:

- Seedlings with cotyledons and generally one pair of leaves; only newly recruited individuals were counted as seedlings; small individuals that already had one shoot belonged to size class 1.
- Size class 1, individuals with one shoot.
- Size class 2, individuals with 2–5 shoots.
- Size classes 3, 4, and 5, i.e. large individuals with 6–10, 11–50 and >50 shoots, respectively.

We performed a matrix analysis of population demography (CASWELL 2001) on the basis of this stage classification; calculation of transition rates and mortalities was described in detail by MARCANTE et al. (2009a). Fecundities f_i of individuals of size class i (i.e. the entries 2 ... 6 of the first row of the matrices) were determined by a partition of all generative shoots of the population on these classes. The fecundity f_i of an individual of class i was given by $f_i = S g_i / x_i$, with S representing the total number of newly emerged seedlings, g_i the proportion of generative shoots belonging to the individuals of class i , and x_i the number of these individuals. This calculation relied on the assumption that all generative shoots contributed approximately in an equal manner to reproduction, irrespective of the size class to which they belonged. For a comparison of reproduction between different successional stages two additional measures were calculated under the assumption that average seed numbers per generative shoot did not markedly differ between these stages: a) reproductive potential P_{Ri} , the average number of generative shoots per individual of size class i (an approximation of seed number per individual), and b) reproductive success S_R , the average number of seedlings per generative shoot.

Dispersal was implicitly included by the assumption that there was an equilibrium between propagule inflow and outflow. As we analyzed the establishment of a population on bare substrate, we neglected any contribution of a seed bank to the generation of new seedlings; hence the building up of the seed bank is included in the net fecundities.

Transition matrices were constructed for each site from the pooled set of plots for each annual transition: four transitions for A₁ and for B, one transition for A₀. For each of these nine transition matrices, population growth rates λ_{matrix} were calculated. To account for stochasticity introduced through sampling, standard deviations of population growth rates λ were estimated by a bootstrapping procedure (CASWELL 2001).

2.5 Projection of population development

Stochastic simulations projecting population development accounted for individual demographic and for environmental stochasticity, as described by MARCANTE et al. (2009a). The simulations started with the individual numbers in the different life-cycle stages in year 2004 or 2007, respectively. To account for environmental stochasticity, in each simulation step one of the four transition matrices in question was drawn at random with equal probability in an uncorrelated manner (MÜNZBERGOVÁ 2005; only possible for A₁ and B). Population development was studied with 100 runs per case over 20 years, and from these simulation runs stochastic growth rates λ_{stoch} was calculated (see MARCANTE et al. 2009a). Survival probabilities p_s of populations were given by the proportion of populations surviving after a projection time T of 25 or 50 years, where ‘survival’ was defined by the existence of at least one established individual (individuals in stages 2 ... 6, irrespective of its size class).

3. Results

3.1 Population size and structure

Highest densities of individuals were recorded at site A₁ (Fig. 1). However, the population declined over the study period of 5 years by 25%. At site B the number of established individuals was much lower than at A₁, and seedling density was lower even by an order of magnitude. Unlike A₁ and B, site A₀ showed an increase of established individuals and seedling density in the period 2007–2008.

The population structures markedly changed over the successional stages (Fig. 2a). The proportion of seedlings decreased with ongoing succession, mainly between the sites A₁ and B, as did the proportion of small individuals of size class 1. On the other hand, the proportion of large and very large individuals increased with ongoing succession.

Whereas at site A₁ and B population structure was rather even over the plots (details not shown), the 11 plots in A₀ differed in their patterns (Fig. 2b). Seedlings were largely dominating, whereas a few plots included already large and very large individuals (size classes 4 and 5), and seedlings were missing there.

3.2 Population matrices and species demography

The transition matrices calculated from individual transitions are presented in the Supplement E1. Rates of population growth (λ) from matrix analysis are given in Table 2 for all successional stages, differentiated for the four transition steps 2004–2008, together with standard deviations from bootstrapping analysis and the averages over the four transitions at A₁ and B. At these two sites, growth rates were smaller than 1, with only one exception (2004–2005 at A₁). At site A₁ the λ -values were steadily decreasing from year to year. This held also for site B, but the population recovered to some degree in the last time step. Site A₀ showed a remarkable contrast: Whereas in the last annual transition 2007–2008 the A₁ population was decreasing in size by almost 25%, the A₀ population in the same period was nearly doubling.

Within all successional stages mortality was decreasing with the size of individuals (Fig. 3), and at A₀ it was even zero for very large individuals with more than 50 shoots (size class 5). Mortalities of seedlings and of very small individuals (size class 1) were lower in the initial phase of colonization (A₀) as compared to the subsequent stages; other differences along the successional gradient were negligible.

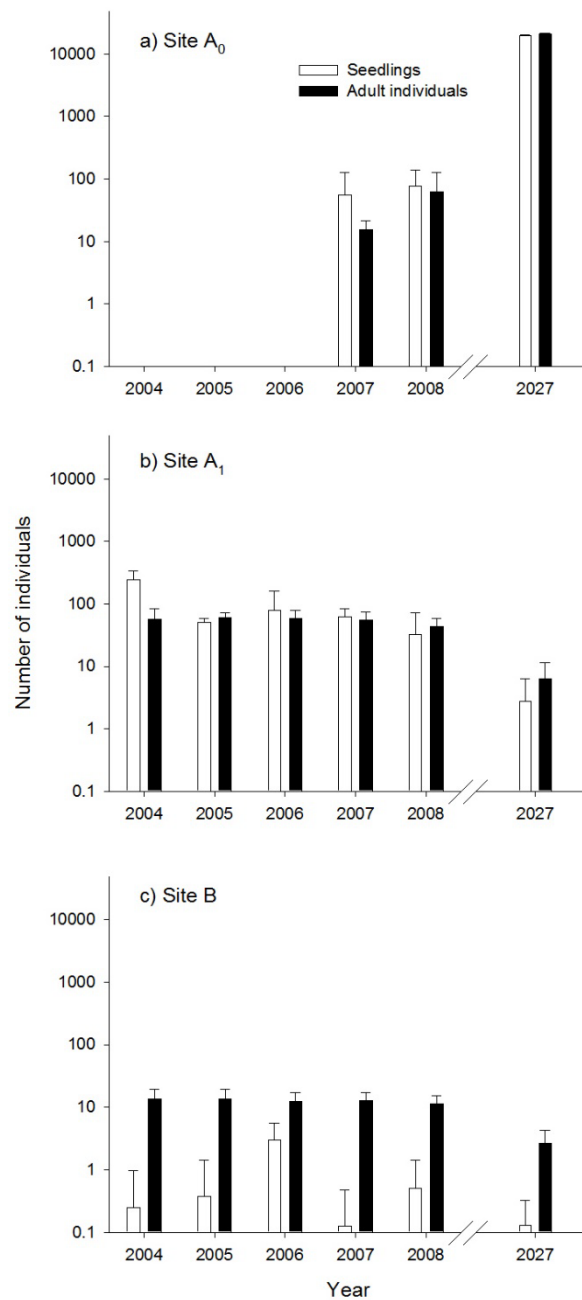


Fig. 1. Population sizes of *Saxifraga aizoides* (numbers of seedlings and of established individuals per m²) recorded per site (A₀, A₁, B) during the study period 2004–2008 (averages over all plots of a site, with standard deviations) and projected for 2027 by stochastic matrix simulation.

Abb. 1. Populationsgrößen von *Saxifraga aizoides* (Zahl der adulten Individuen und der Keimlinge pro m²), registriert je Sukzessionsstadium (A₀, A₁, B) im Untersuchungszeitraum 2004–2008 (Werte gemittelt über alle Plots eines Standorts, mit Standardabweichung) sowie die durch stochastische Simulation vorhergesagte Populationsgröße für 2027.

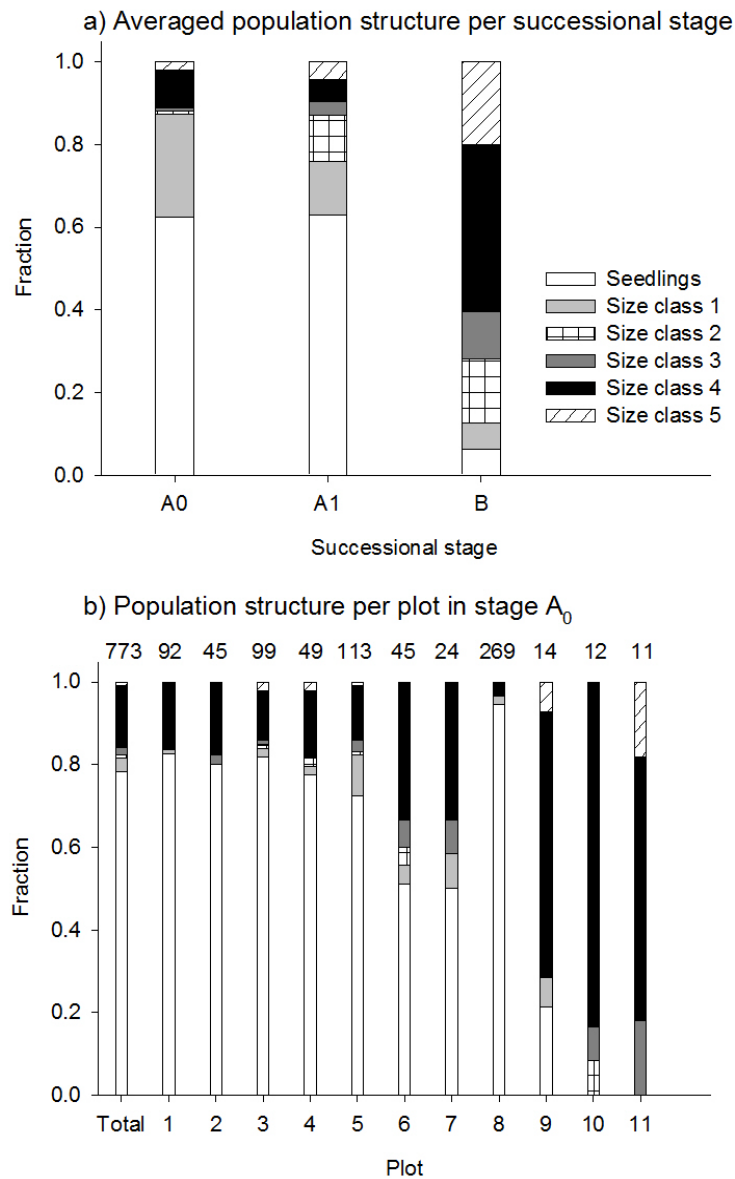


Fig. 2. Population structure (fractions of seedlings and adult individuals of different size classes) of *Saxifraga aizoides* recorded at the three sites A₀, A₁, and B. **a)** Average values over five years (2004–2008) or two years (2007–2008; stage A₀) for the pooled plots per site, **b)** Values for the 11 study plots and the total plot area at site A₀ in 2007. The total number of individuals per plot or in the total plot area is indicated above each bar.

Abb. 2. Populationsstruktur (Anteile der Keimlinge und der adulten Individuen in den verschiedenen Größenklassen) von *Saxifraga aizoides*, registriert an den Standorten der drei Sukzessionsstadien A₀, A₁ und B. **a)** Mittelwerte aus 5 Jahren (2004–2008) bzw. 2 Jahren (2007–2008; Stadium A₀) für die zusammengefassten Plots je Stadium, und **b)** Werte für die 11 einzelnen Plots und für den Gesamtplot in Stadium A₀ für 2007. Die Zahl der Individuen je Plot und auf dem Gesamtplot wird über jeder Säule angegeben.

Table 2. Population growth rates λ of *Saxifraga aizoides* along the successional gradient (A₀-A₁-B) of the Rotmoos glacier foreland. Given are a) λ_{matrix} -values for annual transitions (2004–2008) obtained from matrix analysis, standard deviations calculated by bootstrapping analysis, and averages over the annual transition for these values, b) λ_{stoch} -values obtained from stochastic matrix simulations with random drawing of a transition matrix, and c) projected population survival probabilities p_s within periods of 25 or 50 years.

Tabelle 2. Populationswachstumsraten λ der *Saxifraga aizoides*-Populationen (A₀-A₁-B) entlang des Rotmoosferner-Gletschervorfeldes. Angegeben werden a) λ_{matrix} -Werte für die Jahresübergänge (2004–2008), ermittelt aus Matrixanalysen, die zugehörigen Standardabweichungen, ermittelt durch Bootstrapping-Analysen, sowie Mittelwerte über alle Jahresschritte je Sukzessionsstadium, b) λ_{stoch} -Werte, ermittelt aus stochastischen Matrixsimulationen mit Zufallsziehung einer Übergangsmatrix je Zeitschritt, c) durch Projektionsrechnungen ermittelte Überlebenswahrscheinlichkeiten der Populationen für Zeitintervallen von 25 bzw. 50 Jahren.

| Site | Transition | λ_{matrix} | λ_{stoch} | p_s (25/50 years) |
|----------------|------------|---------------------------|--------------------------|------------------------|
| A ₀ | 2007–2008 | 1.364 ± 0.094 | | 1.0 / 1.0 |
| A ₁ | 2004–2005 | 1.014 ± 0.008 | | |
| | 2005–2006 | 0.967 ± 0.035 | | |
| | 2006–2007 | 0.874 ± 0.045 | | |
| | 2007–2008 | 0.745 ± 0.058 | | |
| | Average | 0.900 ± 0.120 | 0.898 ± 0.230 | 1.0 / 0.7 |
| B | 2004–2005 | 0.984 ± 0.015 | | |
| | 2005–2006 | 0.908 ± 0.049 | | |
| | 2006–2007 | 0.794 ± 0.098 | | |
| | 2007–2008 | 0.933 ± 0.030 | | |
| | Average | 0.905 ± 0.080 | 0.912 ± 0.085 | 1.0 / 0.7 |

Reproduction was characterized by two components: the reproductive potential P_{Ri} of individuals of size class i , and the reproductive success S_R . The reproductive potential of large and very large individuals (size classes 4–5) did not differ along the successional gradient (Fig. 4a). With ongoing succession the ability of smaller individuals to contribute to reproduction increased: at site B even size class 1 could consist of just one generative shoot. However, reproductive success markedly decreased over the course of succession: the values for the three successional stages differed by an order of magnitude (Fig. 4b).

3.3 Projection of population development

Projections of population development through stochastic simulations based on the transition matrices (Supplement E1) are included in Figure 1 for comparison with the population sizes found in the study period. The corresponding stochastic λ -values are also shown in Table 2, being in close agreement with the averaged deterministic λ -values.

For the population at A₀, the λ -value as well as the stochastic simulations indicated a strong increase in population size, with individual numbers more than two orders of magnitude higher than the field values of 2007–2008. At A₁ and B population sizes are expected to decrease: at A₁ by an order of magnitude, whereas at B, with already small populations, the decline will be somewhat slower. At these sites there is a danger of population extinction over the long run (after 50 years), as given by population survival probabilities p_s of Table 2.

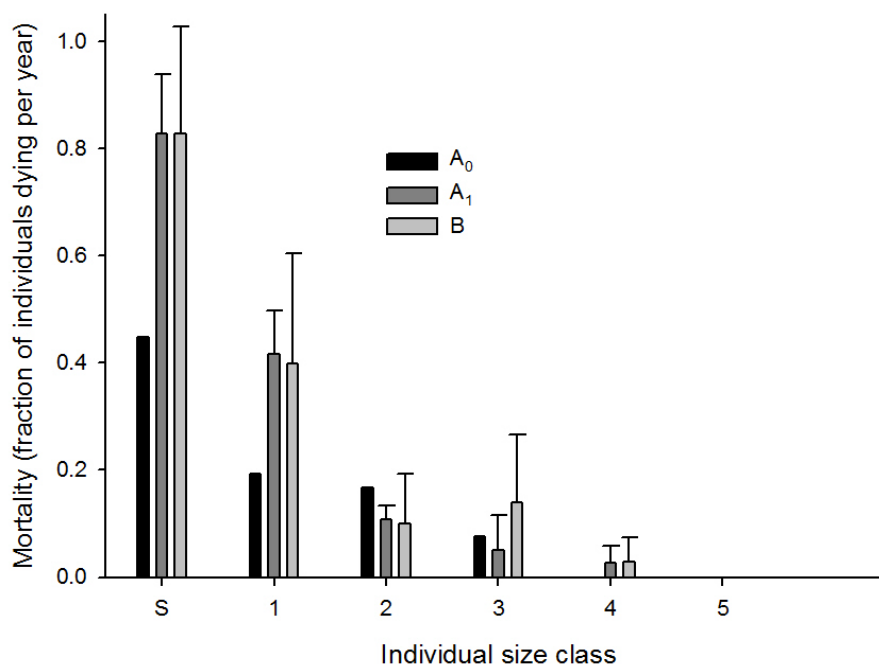


Fig. 3. Mortality (fraction of individuals dying per year) of *Saxifraga aizoides* seedlings and of individuals in the five size classes along the successional gradient derived from the transition matrices of the pooled plots per site. Given are averages over all transitions per site, with standard deviations.

Abb. 3. Mortalität (Anteil der je Jahr absterbenden Individuen) von *Saxifraga aizoides*-Keimlingen und von Individuen in den fünf Größenklassen entlang des Sukzessionsgradienten, abgeleitet aus den Übergangsmatrizen für die zusammengefassten Plots je Standort. Dargestellt werden Mittelwerte über alle Übergänge, zusammen mit Standardabweichungen.

4. Discussion

4.1 Population size and structure

A comparative analysis of population densities and life-cycle stage distributions from the very first period of primary succession, only a few years after deglaciation, until successional stages with population recession revealed essential features of population development. Densities of established individuals were of comparable size at the sites A₀ and A₁, but with a decrease at site B, reflecting the fact that *S. aizoides* is a species characterizing the initial period of primary succession. This decrease of density at site B is much more significant for seedlings. At the recently deglaciated site the distribution of individuals over the study plots and over size classes exhibited large spatial heterogeneity, reflecting the spatio-temporally fluctuating conditions on the new alpine habitat (RUSTERHOLZ et al. 1993) and the obvious irregularity of colonization events (BURGA 1999, WALKER & DEL MORAL 2003). As to be expected, most plots at this stage showed a population structure of young, progressive populations exhibiting a high number of seedlings and individuals in small size classes. A high allocation to sexual reproduction, early reproduction and fast growth are essential traits of

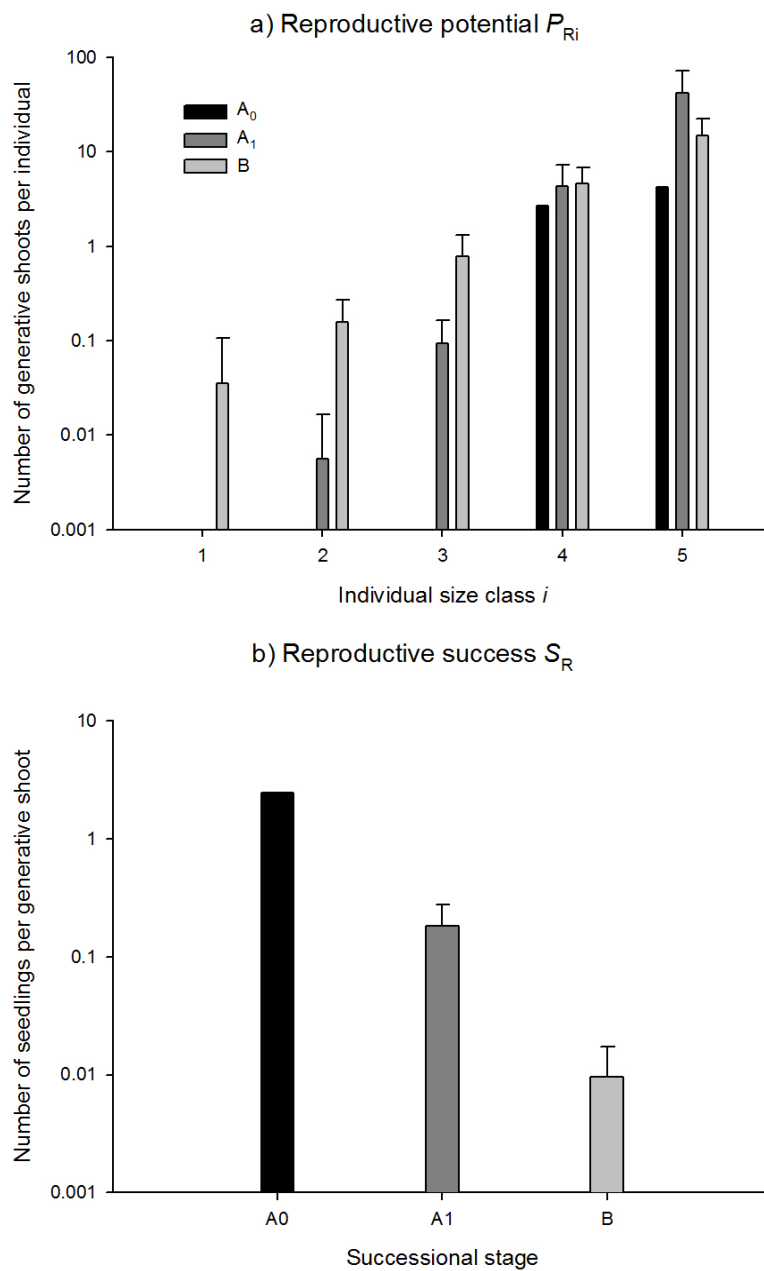


Fig. 4. Reproduction components depending on size class of *Saxifraga aizoides* individuals and on successional stage. **a)** Reproductive potential P_{Ri} (average number of generative shoots per individual), **b)** reproductive success S_R (number of established seedlings at time $t+1$ per generative shoot at time t). For details see legend Figure 3.

Abb. 4. Reproduktionskomponenten in Abhängigkeit von der Größenklasse der *Saxifraga aizoides*-Individuen und dem Sukzessionsstadium. **a)** Reproduktionspotential P_{Ri} (durchschnittliche Anzahl an generativen Trieben je Individuum, **b)** Reproduktionserfolg S_R (Zahl der etablierten Keimlinge im Jahr $t+1$ je generativem Trieb im Jahr t). Details in Legende Abbildung 3.

r-strategists (GADGIL & SOLBRIG 1972). The first two traits can be confirmed for *S. aizoides*, being in line with traits of other early colonizers on glacier forelands, e.g. *Epilobium fleischeri* (STÖCKLIN 1990). However, similar to *E. fleischeri*, *S. aizoides* exhibits high seedling mortality, though being lower than in later successional stages. In order to compensate this disadvantage, alpine species frequently propagate additionally to seeds also by clonal reproduction (STÖCKLIN 1990, 1999; RUSTERHOLZ et al. 1993; PLUESS & STÖCKLIN 2005;

WINKLER et al. 2010, FISCHER et al. 2011). *Saxifraga aizoides* has no clonal propagation. However, shoots disconnect easily from the cushions, the fragments being transported by water or avalanches. We already found the structure of an aged population, characteristic for later successional stages, some plots at the recently deglaciated site. These plants most likely stem from plant fragments dispersed to the respective plots, because large individuals with more than 50 shoots can never develop within the 6 years elapsed since deglaciation. WALLINGER et al. (2008) investigated the input of plant fragments by avalanches and found that mainly late successional species were introduced to the glacier foreland in this way. According to personal observations (B. Erschbamer), *S. aizoides* can also be introduced by floods during summer time. Unfortunately, empirical investigations of this task are still missing. However, we know that introduced plant fragments may act as ‘patch nucleation’ (CUTLER et al. 2008) enhancing population development by providing a high quantity of seeds. In this context it is remarkable that in all plots of the three successional stages we found a small number of individuals with one or two shoots that could not be assigned to seedlings in the preceding year. They could not be included in the matrix calculations because of their uncertain origin. Nevertheless, they may denote a colonization potential by small fragments, which was decreasing from site to site by an order of magnitude.

Introduction of plant fragments may be important because seed limitation has to be assumed especially for the youngest sites, as proven by several experiments at the study area (NIEDERFRINIGER SCHLAG & ERSCHBAMER 2000, ERSCHBAMER et al. 2008, ERSCHBAMER 2014).

4.2 Species demography

Demographic processes and resulting growth rates of *S. aizoides* varied with time since deglaciation. At the pioneer and the early successional sites, population growth rates λ were, in most cases, somewhat smaller than 1, leading to gradually declining populations. A major reason for population decline, especially at the early successional site, may be the change of environmental conditions, when space becomes limiting, leading to intra- and interspecific competition (ERSCHBAMER et al. 2008). Compared to recently deglaciated sites, site B is much drier and has a much higher diversity (RAFFL et al. 2006). *Saxifraga aizoides* is adapted to open and especially moist environments such as scree, brook bank and snow bed areas (FISCHER et al. 2008). Generally, drought was identified as a major obstacle for germination and recruitment at site A₁ (ERSCHBAMER 2014). By means of experimental irrigation it could be shown that the seedling number of selected glacier foreland species increased significantly compared to control plots (ERSCHBAMER 2014).

Reproductive success decreased markedly over the course of succession, even under the observed increase of reproductive potential. Several authors (FORBIS 2003, PLUESS & STÖCKLIN 2005, WEPPLER et al. 2006) have documented similar effects for other alpine species. At the sites A₁ and B reduced seedling establishment was accompanied by high mortality of the seedlings in the subsequent time step (< 80%). At A₀, despite harsh conditions, seedlings had a high chance to be transformed into established individuals, probably

due to the moister substrate. Other demographic processes (individual growth, stasis, size reduction, and formation of generative shoots) differed much less between the successional stages, and thus do not markedly contribute to successional changes in population structure and performance (MARCANTE et al. 2009a).

4.3 Projection of population development

Projections by matrix models depend upon the assumption that environmental conditions will, on an average, not change over the projection period, as outlined by MARCANTE et al. (2009a). But in our primary succession system there are a lot of sources for environmental change: increase in intraspecific competition due to an increase in density, changes in interspecific interactions in the progress of succession, changes in habitat conditions, environmental stochasticity, catastrophes, and also drastic changes in alpine ecosystems as a consequence of the ongoing climatic change (ERSCHBAMER et al. 2008, 2011; PAULI et al. 2007). There are two obstacles to the inclusion of such factors into projection simulations: limited knowledge and insufficient simulation tool. Empirically, some of these impacts will only be incompletely covered, even by a 5-year study, but they become clearer when successional stages are compared. Increasing competition is manifested in the reduction of reproductive success as shown by *S. aizoides* at site B. An inclusion of any density-dependent demography into simulations would go beyond the range of simple matrix models. An extension of modelling towards flexible ‘individual-based simulation models’ (IBM) that may incorporate complex environmental features is not considered here.

Our stochastic projections assumed that matrices, which represent the situation in one annual transition step, can be randomly selected in the course of simulations over a longer time period for a given successional stage. This assumption means that conditions for population development in the four transitions 2004–2008 reflect a random sequence of events. However, especially the 5-year development of the λ -values at site A₁ gives the impression of a steady process towards a breakdown of the population, most likely due to the gradual changes of the environmental conditions in the progress of primary succession. Indeed, such a breakdown of population cannot be excluded. Permanent plot studies of ERSCHBAMER et al. (2008) showed a sudden strong reduction of cover of *S. aizoides* and of *S. oppositifolia* at the 1971 moraine (A₁). But after this breakdown the populations were recovering again to some extent, and this reversal justifies the random-selection assumption in the projection simulations of this study. Despite this methodical problem, all indicators, the λ -values, the population sizes and the simulations showed that populations were gradually declining at stages A₁ and B, i.e. beginning approximately 30 years after deglaciation.

For the recently deglaciated site A₀ a population behaving like the ‘simulation population’ would reach numbers of individuals per m² more than two orders of magnitude greater than those of the comparable field population at site A₁; it would reach densities beyond any reasonable limits. Additionally, an increasing backflow from the permanent seed bank must be taken into account. Therefore, our demographic parameters deduced at site A₀ can represent only a very short period, and damping effects must inevitably come into play. At first, we have to assume that the population enters a stage of density-dependent development rather soon after initialization (RUSTERHOLZ et al. 1993). Colonization of an area after deglaciation by a pioneer species such as *S. aizoides* may occur at a rather low number of suitable microsites (STÖCKLIN & ZOLLER 1991). All suitable sites will be rapidly occupied, thus preventing further spread of the species after just a few years (MARCANTE et al. 2009a, WINKLER et al. 2010). As a consequence, rate of population increase λ will decline rapidly,

at least until the steady-state value $\lambda \approx 1$, as was found for A₁ and B. Additionally, as the ice-free area is colonized within a short time period and further establishment of seedlings is prevented we have individuals of approximately uniform age in the first decades of population development. More or less a whole cohort will now become senescent about 30 years after the first colonization, as found by ERSCHBAMER et al. (2008) at site A₁, triggered by environmental stress (increasing drought) and probably by competition from other, later arriving species (RUSTERHOLZ et al. 1993, STÖCKLIN & BÄUMLER 1996).

4.4 Conclusions

To our knowledge this is the first demographic study to address species dynamics of an alpine plant from the very first period of primary succession, only a few years after deglaciation, until stages representing recessive populations and to follow species dynamics over several years.

According to the classical *r*-strategy concept for initial colonization, established seedlings should quickly develop into reproducing plants, with a high number of offspring and the building up of a seed bank. The pioneer species in glacier forelands were generally found to have a huge number of seeds but they also follow a persistence strategy whereby clonal growth and dispersal equally contribute to population growth. We have shown that this strategic concentration on persistence holds also for *S. aizoides*, even at the youngest, only recently deglaciated sites. A low degree of reproduction is outbalanced by low mortality for several decades, especially for large individuals until individuals are ageing and reproduction becomes almost impossible.

Erweiterte deutsche Zusammenfassung

Einleitung – Das Zurückweichen der alpinen Gletscher eröffnet eine ausgezeichnete Möglichkeit, Prozesse der primären Sukzession zu untersuchen. Pionierarten mit einer großen Anzahl kleiner, leichter und windverbreiteter Samen (STÖCKLIN 1990, STÖCKLIN & BÄUMLER 1996) und zudem klonaler Reproduktion (STÖCKLIN 1990) sind in der Regel die Erstsiedler. Ein entscheidendes Merkmal sollte dabei die hohe Fekundität sein. Ähnlich wie in Sekundärsukzessionen wird erwartet, dass sich auch im Verlauf der Primärsukzession nach den Pionierarten sogenannte Folgearten mit hoher Wachstumsrate und langer Lebensdauer einstellen, bei denen die Fekundität als Merkmal zurücktritt. Von MARCANTE et al. (2009a) wurde allerdings anhand von vier charakteristischen Arten gezeigt, dass während der Primärsukzession im Gletschervorfeld Arten mit hoher Überlebensfähigkeit, aber relativ geringer Fekundität häufig sind. Es blieb jedoch offen, ob diese Aussage wirklich auch für die Phase unmittelbar nach dem Gletscherrückzug gilt, denn eine Primärsukzession muss unabdingbar mit einer Kolonisation von außen beginnen, verbunden mit einer Ausbreitung der Pionierarten auf dem neuen Areal. Ziel des vorliegenden Projektes war es daher, die Demographie der Pionierart *Saxifraga aizoides* auf 6 Jahre alten eisfreien Flächen zu untersuchen und das Populationswachstum mit dem auf älteren Flächen (33 und 81 Jahre eisfrei) zu vergleichen. Folgende Fragen sollten beantwortet werden: (1) Unterscheiden sich die Populationen auf unterschiedlich alten Flächen hinsichtlich Größe und Struktur? (2) Wie stark variieren die demographischen Prozesse und Wachstumsraten der Populationen von Jahr zu Jahr? (3) Welche Entwicklung kann für die Populationen der unterschiedlich alten Flächen prognostiziert werden?

Methoden – Die Demographie von *Saxifraga aizoides* wurde entlang eines Sukzessionsgradienten im Gletschervorfeld des Rotmoosferners (2.330–2.450 m Meereshöhe, Obgurgl, Ötztal, Österreich) untersucht. Folgende Versuchsflächen wurden ausgewählt: A₀ - eine seit 6 Jahren eisfreie Fläche, A₁ – ein Pionierstadium (33 Jahre eisfrei) und B - ein Folgestadium (81 Jahre eisfrei). Die typische

Artengarnitur der drei Sukzessionsstadien ist in Tabelle 1 dargestellt. In 1-m²-Flächen wurden über den Zeitraum 2004 bis 2008 (A₁ und B) bzw. 2007 bis 2008 (A₀) alle Individuen (Keimlinge und adulte Pflanzen) der Art gezählt und in ihrer Entwicklung verfolgt, wobei die adulten Individuen durch die Größenklassen 2–6 (2 = Individuum mit einem Trieb, 3 = 2–5 Triebe, 4,5,6 = 6–10, 11–50 bzw. > 50 Triebe) charakterisiert waren. Mit Hilfe von Matrixmodellen wurden Fekundität und Mortalität ermittelt und die Populationswachstumsrate λ berechnet. Zusätzlich wurde die Entwicklung der Populationen für die kommenden 20 Jahre unter konstanten Umweltbedingungen vorhergesagt.

Ergebnisse – *Saxifraga aizoides* wies auf den Untersuchungsflächen A₀ eine geringe Individuendichte auf, mit sehr heterogener Verteilung und Populationsstruktur. Die höchste Individuendichte wurde in den Flächen A₁ beobachtet (Abb. 1). Im Sukzessionsstadium B war die Individuendichte, vor allem die der Keimlinge, deutlich geringer. In den Flächen A₀ fanden sich vor allem Keimlinge und kleine Individuen, aber auch bereits einige größere Individuen (Abb. 2).

In den Flächen A₀ wiesen die Populationen eine Wachstumsrate $\lambda > 1$ auf (Tab. 2), besaßen also ein Wachstumspotential. In den Untersuchungsflächen A₁ sanken die Wachstumsraten von Jahr zu Jahr. Dies gilt auch für die Untersuchungsflächen B. Während im letzten jährlichen Übergang 2007–2008 die A₁-Population um rund 25 % absank, hat sich die A₀-Population im selben Zeitraum nahezu verdoppelt. Die Mortalität sank auf allen Flächen mit zunehmender Größe der Individuen (Abb. 3). Für Keimlinge und kleine Individuen war die Mortalität in A₀ deutlich niedriger als in den älteren Sukzessionsstadien. Besonders auffallend war die Abnahme der Fekundität entlang des Sukzessionsgradienten: die Werte variierten jeweils um eine Größenordnung (Abb. 4). Die Ergebnisse, wie sie in den Übergangsmatrizen zusammengefasst sind (siehe Anhang E1), bestätigten teilweise die Vermutung einer bedeutenderen Rolle der Fekundität an den jüngsten, eben erst eisfrei gewordenen Flächen.

Führt man Simulationen des Populationswachstums für die kommenden 20 Jahre durch (Tab. 2), zeigt sich in A₀ eine sehr starke Zunahme der Individuenzahl im Ausmaß von mehr als zwei Größenordnungen im Vergleich zu 2007–2008. Die Populationsgröße in A₁ und B sinkt dagegen weiter ab.

Diskussion – Unserer Kenntnis nach ist dies die erste demographische Studie, die die Dynamik einer alpinen Pflanzenart unmittelbar vom Beginn der Besiedlung wenige Jahre nach dem Gletscherrückgang bis zu Stadien mit rezessiver Population bei einer Untersuchungsdauer von mehreren Jahren zum Inhalt hat.

Saxifraga aizoides folgt von Anfang an eher einer „Persistenz-Strategie“ (FORBIS & DOAK 2004, WEPLER et al. 2006, MARCANTE et al. 2009a), abzulesen an der Tatsache, dass an den jungen Standorten große Individuen noch keiner Mortalität unterlagen. Bei unveränderten Bedingungen würde die Population in wenigen Jahren daher in sehr starkem Maße anwachsen. Wie sich allerdings im Folgestadium B zeigte, geht das Populationswachstum mit der Zeit zurück. Die Hauptursache dürften hier die Änderungen der Umweltbedingungen, der Vegetationsdeckung und die Veränderung der Artengarnitur sein. Das Folgestadium B ist bereits wesentlich artenreicher (RAFFL et al. 2006) und trockener, was für *Saxifraga aizoides*, einer Charakterart offener, feuchter Pionierstandorte, sicherlich problematisch ist. Ein Mangel an Keimungsstellen sowie das Auftreten von intra- und interspezifischer Konkurrenz (ERSCHBAMER et al. 2008) dürften mit zunehmender Sukzession immer entscheidender werden. Die geringe Fekundität kann zwar einige Jahrzehnte durch die geringe Mortalität von großen Individuen ausgeglichen werden, allerdings nur so lange, bis die Population aus Altersgründen abstirbt.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Stage-based transition matrices of *Saxifraga aizoides* for the annual transition steps between 2004 and 2008 at the three sites A₀, A₁, and B derived from the data of the pooled plots per site.

Anhang E1. Übergangsmatrizen auf der Basis von Lebenszyklusstadien von *Saxifraga aizoides* für die Jahresschritte zwischen 2004 und 2008 und die drei Sukzessionsstandorte A₀, A₁, und B, konstruiert aus den Daten der zusammengefassten Plots je Standort.

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Supplement E1. Stage-based transition matrices of *S. aizoides* for the annual transition steps between 2004 and 2008 at the three sites A₀, A₁, and B derived from the data of the pooled plots per site. Transition matrix stages: stage 1 = seedlings, stages 2-6 = individuals of size classes 1-5.

Anhang E1. Übergangsmatrizen auf der Basis von Lebenszyklusstadien von *S. aizoides* für die Jahresschritte zwischen 2004 und 2008 und die drei Sukzessionsstandorte A₀, A₁, und B, konstruiert aus den Daten der zusammengefassten Plots je Standort. Stadien der Übergangsmatrix: Stadium 1 = Keimlinge, Stadien 2-6 = Individuen der Größenklassen 1 bis 5.

| Stage | Transition | Transition matrix | | | | | |
|----------------|------------|-------------------|--------|--------|--------|--------|---------|
| A ₀ | 2007-08 | 0.0050 | 0.0000 | 0.0000 | 0.0000 | 6.5553 | 10.5126 |
| | | 0.5438 | 0.6154 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0033 | 0.1538 | 0.3333 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.0385 | 0.3333 | 0.0769 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.1667 | 0.8462 | 0.6897 | 0.1429 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.3103 | 0.8571 |
| A ₁ | 2004-05 | 0.0416 | 0.0000 | 0.0000 | 0.0000 | 0.3348 | 4.8970 |
| | | 0.0444 | 0.3684 | 0.1525 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.1228 | 0.5763 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.1695 | 0.8750 | 0.0400 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0169 | 0.1250 | 0.8800 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0800 | 1.0000 |
| | 2005-06 | 0.0000 | 0.0000 | 0.0000 | 0.0187 | 0.6583 | 8.9146 |
| | | 0.1457 | 0.5147 | 0.1860 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0066 | 0.1176 | 0.6047 | 0.4444 | 0.0417 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.1163 | 0.4444 | 0.0417 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.1111 | 0.8333 | 0.0800 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0417 | 0.9200 |
| | 2006-07 | 0.2636 | 0.0000 | 0.0063 | 0.0201 | 0.7169 | 4.3013 |
| | | 0.0628 | 0.5224 | 0.1333 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0084 | 0.1493 | 0.6889 | 0.3571 | 0.0417 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0444 | 0.5714 | 0.1667 | 0.0417 |
| | | 0.0000 | 0.0000 | 0.0222 | 0.0000 | 0.7917 | 0.5000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.4583 |
| | 2007-08 | 0.1087 | 0.0000 | 0.0000 | 0.0123 | 0.7109 | 4.9151 |
| | | 0.0109 | 0.4386 | 0.2041 | 0.0000 | 0.0625 | 0.0000 |
| 0.0000 | | 0.1053 | 0.5918 | 0.4667 | 0.1250 | 0.0909 | |
| 0.0000 | | 0.0000 | 0.0612 | 0.4000 | 0.2813 | 0.0000 | |
| 0.0000 | | 0.0000 | 0.0000 | 0.0000 | 0.4375 | 0.2727 | |
| 0.0000 | | 0.0000 | 0.0000 | 0.0000 | 0.0313 | 0.6364 | |
| B | 2004-05 | 0.0000 | 0.0007 | 0.0000 | 0.0013 | 0.0179 | 0.0674 |
| | | 0.0000 | 0.2857 | 0.0714 | 0.1250 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.5714 | 0.7143 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.2143 | 0.6250 | 0.1000 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.1250 | 0.8000 | 0.0645 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.1000 | 0.9355 |
| | 2005-06 | 0.0000 | 0.0000 | 0.0030 | 0.0213 | 0.1458 | 0.5121 |
| | | 0.3333 | 0.1667 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.3333 | 0.7857 | 0.2308 | 0.0465 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0714 | 0.2308 | 0.1163 | 0.0588 |
| | | 0.0000 | 0.0000 | 0.0714 | 0.2308 | 0.7209 | 0.2941 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0233 | 0.6471 |
| | 2006-07 | 0.0000 | 0.0000 | 0.0010 | 0.0020 | 0.0090 | 0.0240 |
| | | 0.3600 | 0.6667 | 0.1111 | 0.0000 | 0.0000 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.6667 | 0.3636 | 0.0667 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.3636 | 0.2667 | 0.0000 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0909 | 0.6444 | 0.5217 |
| | | 0.0000 | 0.0000 | 0.0000 | 0.0556 | 0.0222 | 0.4783 |
| | 2007-08 | 0.0000 | 0.0000 | 0.0021 | 0.0114 | 0.0489 | 0.1325 |
| | | 0.0000 | 0.3077 | 0.1053 | 0.0000 | 0.0000 | 0.0000 |
| 0.0000 | | 0.0769 | 0.6316 | 0.1875 | 0.0952 | 0.0000 | |
| 0.0000 | | 0.0000 | 0.1053 | 0.5625 | 0.0952 | 0.0000 | |
| 0.0000 | | 0.0000 | 0.0526 | 0.2500 | 0.7381 | 0.4615 | |
| 0.0000 | | 0.0000 | 0.0000 | 0.0000 | 0.0476 | 0.5385 | |