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Germination and establishment of snowbed plants of the North-Eastern Calcareous Alps (Austria)

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A b s t r a c t : Climate change induced habitat loss and fragmentation. This will increase the importance of migration disproportionately for species restricted to small and well-defined habitat patches. This study focuses on the impact of vegetation cover along a snow melt gradient on germination and establishment of *Achillea atrata, A. clusiana, Arabis caerulea* and *Gnaphalium hoppeanum*. Additionally, we also quantified the effect of above- and below-ground allocation patterns on the probability of seedling recruitment. Seeds were sown, and seedlings pre-grown in a climate chamber were transplanted to a snowbed-complex on mt. Rax (Lower Austria/Styria).

Germination from sown seeds was higher in plots with open vegetation. Neither biomass allocation nor site conditions had a statistically significant impact on seedling survival, but trends could be detected. Seedlings with reduced root growth showed lower survival rates for three species, *Achillea atrata, A. clusiana*, and *Arabis caerulea.* Seedlings transplanted to intermediate positions showed the lowest mortality, and dense vegetation led to a higher seedling survival than open vegetation.

Our results indicate that competitive and facilitative effects of the surrounding vegetation on snowbed species may change along different phases of their life cycles. An increase in vegetation cover of alpine snowbeds will thus threaten the viability of these populations mostly by reducing the open sites necessary for their germination.

K e y w o r d s : Alpine vegetation; Calcareous Alps; establishment; germination; snowbed; transplantation

Z u s a m m e n f a s s u n g : **Keimung und Etablierung von Schneeboden-Pflanzen in den nordöstlichen Kalkalpen (Österreich)**
Klimawandel verursacht Habitatverluste und -fragmentierung. Die Bedeutung der Ausbreitung für ökologisch eng eingenischte Arten nimmt dadurch stark zu. Die vorliegende Untersuchung konzentriert sich auf Einflüsse der Dichte von Schneebodenvegetation auf Keimung und Etablierung von *Achillea atrata, A. clusiana, Arabis caerulea* und *Gnaphalium hoppeanum*. Die Erhebung erfolgte entlang eines Gradienten von zunehmend früherer Schneeschmelze bzw. längerer Vegetationsdauer. Zusätzlich wurde die Wirkung von unterschiedlichem ober- bzw. unterirdischen Wachstum auf die Wahrscheinlichkeit des Überlebens von Keimpflanzen untersucht. Samen wurden im Gelände ausgesät, Keimlinge in Klimakammern vorkultiviert und in einen Schneeboden-Komplex auf der Rax-Alpe (Niederösterreich/Steiermark) verpflanzt.

An Stellen offener Vegetation war die Keimrate der ausgesäten Samen höher. Weder die anfänglich unterschiedliche Biomasseverteilung der Keimlinge noch die Standortsbedingungen hatten

einen statistisch signifikanten Einfluss auf das Überleben der Keimlinge, es zeigten sich jedoch Tendenzen: Keimlinge mit verringertem Wurzelwachstum zeigten bei drei Arten, *Achillea atrata, A. clusiana* bzw. *Arabis caerulea*, tendenziell geringere Überlebensraten. Jene Keimlinge, die in mittlere Standortsbereiche verpflanzt worden waren, zeigten die geringste Sterblichkeit, dichte Standortsvegetation führte zu höherer Überlebensrate als offene Schneebodenflächen.

Unsere Ergebnisse zeigen, dass sich Effekte von Konkurrenz und Förderung durch die umgebende Vegetation auf Schneeboden-Arten während der verschiedenen Phasen des Lebenszyklus ändern. Eine dichtere Vegetationsdecke der alpinen Schneeböden bedroht die Überlebensfähigkeit der Populationen vor allem dadurch, dass diese die für die Keimung nötigen offenen Stellen verringert.

Schlagworte: alpine Vegetation; Etablierung; Kalkalpen; Keimung; Schneeboden; Transplantation

Introduction

Alpine areas are likely to be particularly sensitive to the impacts of global warming (Grabherr & al. 1994, Theurillat & Guisan 2001, Walther & al. 2002). As a result of climate change, the template of suitable habitats for alpine species will shift upwards (Grabherr & al. 1994, Theurillat & Guisan 2001, Walther & al. 2002). Thus, rapid invasions of more competitive species from lower elevations may displace alpine species with lower migration capacities. This shift will most likely lead to a reduction and isolation of habitats, and may result in at least local extinction of species (Gottfried & al. 1998). In particular, plant species thriving in already patchily distributed habitats are likely to be severely affected by further habitat fragmentation.

Snowbeds in the northeasternmost Calcareous Alps in Austria are confined to the uppermost regions (Dullinger & al. 2000, Grabherr & al. 1995). In this area snowbed vegetation is patchily distributed within a matrix of alpine swards. Due to different times of snowmelt within a snowbed, a complex site-gradient develops from the rim to the centre, which represents the effect of the duration of snow cover on nutrient availability and soil moisture. Long lasting snow cover constrains the length of the growth period resulting in a very self-contained flora of highly adapted species. These snowbed specialists are commonly thought to be weak competitors and may therefore be especially prone to competitive displacement by invading grassland species under climate warming (Englisch 1999, Grabherr & al. 1995, Pauli & al. 2003). Further reduction of, or even complete loss of this habitat type threatens to drive a number of plant species to complete extinction as a high proportion of snowbed plant species are endemics of the North Eastern Calcareous Alps (e.g. *Achillea clusiana, Campanula pulla).* To explain these patterns of change due to shifting habitats, investigations of the outcome of competitive interactions are needed (Heegaard & Vandvik 2004).

Most alpine plant species and particularly snowbed species are slowly growing perennials with long generation times (Chambers 1995, Nagy & al. 2003). Survival in the harsh environmental conditions is facilitated by adaptations such as clonal growth and asexual reproduction (Bernhardt 1996, Körner 1999). Even if alpine plants flower regularly, seedling mortality is very high (Erschbamer & al. 2001, Niederfriniger-

Schlag & Erschbamer 2000) and successful seedling recruitment is consequently rare (Bliss 1971, Körner 1999). In contrast, adults have a marked ability to persist, even under changing environmental conditions (Fenner 2000). Thus, germination and establishment are the most critical phases in alpine plant life.

Safe sites – small differences in micro-environmental parameters, including biotic interactions with neighbour plants – are important for the fate of a seedling in extreme alpine areas (Urbanska & Schütz 1986). Higher vegetation cover leads to a reduction of solifluction and lowers wind speed (Körner 1999), and strongly affects soil-forming processes by ameliorating abiotic micro-climatic conditions (Gobat & al. 2004). Recruitment and survival of seedlings are strongly influenced by substrate properties like depth, chemistry, or particle-size (Chambers 1995) because of their balancing effect on water and nutrient supply (Körner 1999). Seedling establishment is also highly dependent on the soil surface stabilization provided by established plants, which acts to prevent deleterious soil movements (Chambers & al. 1990).

However, in addition to their beneficial effects, adults also put competitive pressure on germinating seedlings in close proximity. The growth of seedlings is affected by root and shoot competition, which strongly interact (Cahill 2002, Dillenburg & al. 1993). Although Aerts & al. (1991) showed that there is not necessarily a trade-off between the abilities to compete for above- and below-ground resources – as stated by Tilman (1988) – a change in allocation patterns to root and shoot biomass of a seedling can strongly affect its total competitive ability. Calcareous alpine snowbed habitats are usually characterised by a rather open vegetation cover over a substrate that frequently has a high fraction of coarse scree. This should enlarge the below-ground zone of influence of plants (Casper & al. 2003) and therefore potentially increase root competition – even when vegetation cover is sparse.

Although previous research has examined germination and seedling establishment in alpine areas (Körner 1999), we are not aware of any studies of calcareous alpine snowbed species. This study was conducted to analyse the impact of environmental conditions on the early phases in the life-cycles of some model species of the calcareous snowbed flora of the northeasternmost Alps in Austria. In detail, the following questions were addressed:

(1) What are the effects of position along a complex gradient of site conditions and variation in resident vegetation cover on germination and seedling establishment rates?

(2) How are resource allocation patterns in seedlings influencing seedling establishment?

Materials and Methods

Study area

The study was conducted on mt. Rax (15°42′E, 47°41′N), a table mountain in the North-Eastern Calcareous Alps of Austria – at the boundary between the states Niederösterreich (Lower Austria) and Steiermark (Styria) – at an altitude of 1820–1880 m a.s.l.

(Fig. 1) The rugged surface of the mountain was shaped by Pleistocene glaciations and karst landform development. The cold temperate, humid climate on the plateau is characterized by a mean annual temperature of approximately 2°C and an annual precipitation of about 2100 mm, with a distinct peak during the summer season. Following Solar (1963), soils are mainly different types of terra-fusca (chromic cambisols) and rendzina (rendzic leptosols).

Due to the fine-scaled variation in topography a rich mosaic of vegetation types has developed. Calcareous snowbed communities (Arabidetalia caeruleae) are located in dolines, trenches, and on eroded slopes on debris with poorly developed soils (Englisch & al. 1993). Within the study area various types of snowbed communities have established, namely the Salicetum retusae-reticulatae, the Campanulo pullae – Achilleetum atratae and the Campanulo pullae – Achilleetum clusianae (Dirnböck & Greimler 1997). The surrounding grasslands were syntaxonomically classified mainly as Seslerio-Caricetum sempervirentis and different Caricion firmae associations (Dirnböck & Greimler 1997). Syntaxonomic nomenclature follows Grabherr & Mucina (1993).

Study species

All species restricted to snowbed vegetation in the study area were screened for their germination ability in a preliminary study, and the four species with the highest germination rates – *Achillea atrata, A. clusiana, Arabis caerulea*, and *Gnaphalium hoppeanum* – were chosen so that a sufficient number of seedlings would be available for transplantation. All of the selected species are subalpine to subnival, and widespread on calcareous bedrock in the Alps, except for the endemic *Ach. clusiana* (Staudinger & al.

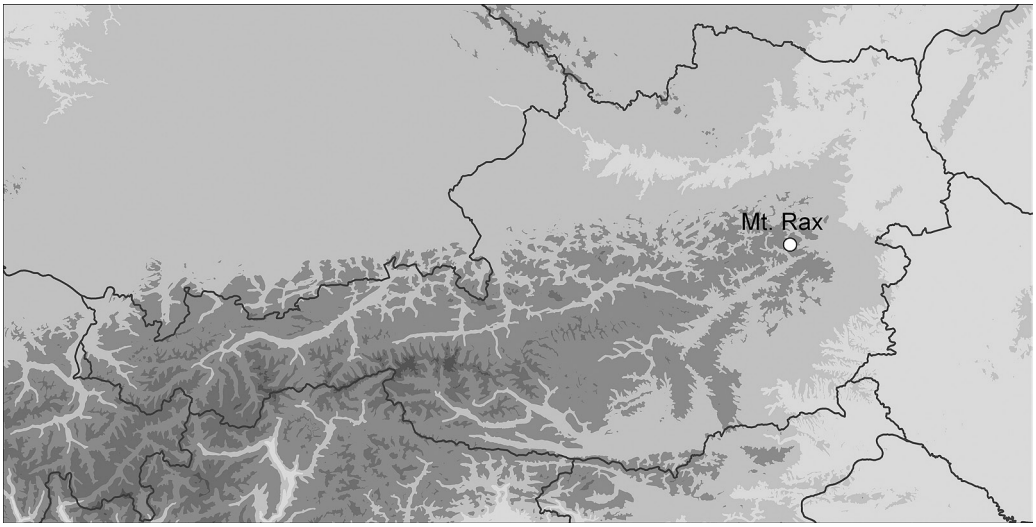

Fig. 1: Map of Austria; the study area mt. Rax in the North-Eastern Calcareous Alps of Austria. — **Abb. 1:** Untersuchungsgebiet Rax-Alpe in den nordöstlichen österreichischen Kalkalpen.

2009). The species are insect-pollinated and predominantly long-living, perennial herbs, except for the short-lived perennial *Ar. caerulea*. All species are adapted to anemochorous dispersal to some degree. *Arabis caerulea* seeds show a skinny fringe, while seeds of *Asteraceae* species are generally characterised by a hairy pappus facilitating wind dispersal which is the case for *G. hoppeanum*. The pappus, however, is reduced in *Ach. atrata* and *Ach. clusiana*. – Taxonomy and nomenclature of the taxa mentioned follow Fischer & al. (2008).

Study design

Matured seeds were collected in September 2003 from populations on mt. Rax and surrounding mountain ranges and stored under dry conditions at 4°C to 6°C. The germination experiment was conducted from February to May 2004. Seeds were cold-wet stratified by storing them at +4°C (Schuetz & Rave 1999, Cavieres & Arroyo 2000) for two weeks in moist plastic bags. To promote a higher ratio of shoot growth in a group of individuals, half of the seeds were treated with gibberellic acid (compare Ruge 1966), the rest was left untreated as control group. Gibberellic acid-treated seeds were moistened with a 4 mmol/l Auxillin-solution, wrapped in aluminium foil, and stored for four days at 4°C (Sayers & Ward 1966, Urbanska & Schütz 1986, Baskin & al. 2002).

Seeds were placed on a double layer of filter paper in petri dishes and moistened with distilled water (Schuetz & Rave 1999, Baskin & al. 2000). Germination was conducted in a climate chamber with a 15 h photoperiod, 90% humidity and a 23/15°C day-night cycle. After germinating, seedlings were transferred to multi-pot-plates filled with two parts mineral soil, one part sand and one part 4-year-old leaves compost and cultivated in the University of Vienna's common garden until ready for transplantation to the study site. Seedlings were protected from excessive radiation for several days after transfer to the garden.

Five transects were established within a large snowbed site of the study area. Each transect consisted of three pairs of plots, with each pair having one plot within open vegetation (cover: 34±15%, estimated in September) and one within dense vegetation (cover: 85±9%, estimated in September). The three plot pairs of each transect were established just upside the actual snow line at three consecutive dates of transplantation, separated by two and a half weeks: 25 June (further referred as early snowmelt), 13 July (intermediate snowmelt) and 30 July (late snowmelt). Hence, the plot pairs of each transect were located along a snowmelt gradient from the rim to the centre of the snowbed (see Fig. 2). This gradient should represent the complex effects of the length of snow cover on soil, soil movements, moisture, light, temperature and nutrient availability. Edges of the 1×1 m plots were permanently marked with aluminium tubes for repositioning of the grid (see below).

Each plot was subdivided by a removable grid, consisting of 100 cells (0.1×0.1 m). Ten seedlings of each of the four study species were planted into each plot (one per cell with cells randomly selected). The individual seedlings were marked with brightly col-

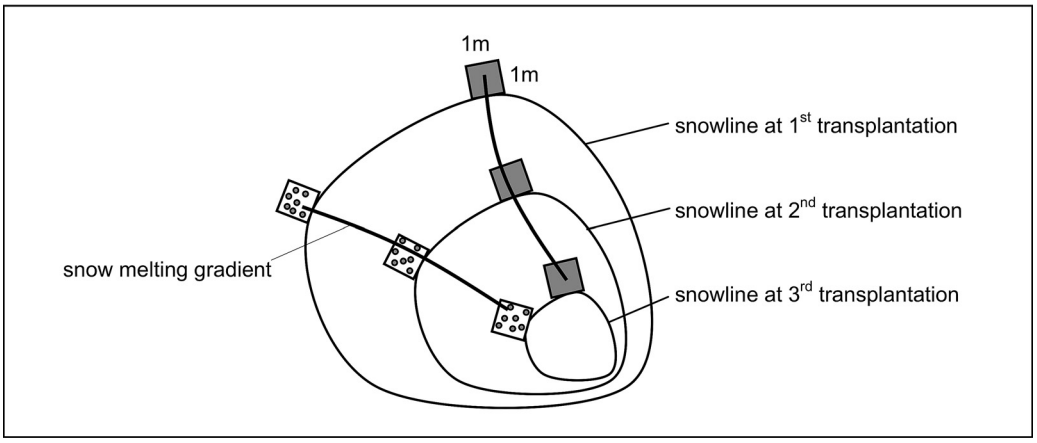

Fig. 2: Overview of experimental layout. Outlines represent the actual snow limit at transplantation time. The 1×1 m plots are depicted as dotted quadrats for open vegetation (cover <60%) and grey-filled quadrats represent plots with dense vegetation (cover ≥60%). — **Abb. 2:** Skizze der Versuchsanordnung. Die Umrisslinien entsprechen der aktuellen Schneegrenze zur Zeit der Transplantation. Die 1×1 m Flächen mit offener Vegetation (Deckung <60%) werden als gepunktete Quadrate abgebildet, jene mit geschlossener Vegetation (Deckung >60%) als graue Quadrate.

oured threads for identification in consecutive observations. Additionally, we randomly chose six cells (without a transplanted seedling) for each species to observe germinability. Three of these cells were sown-in with 100 seeds (50 for *G. hoppeanum*) each, the remaining three were used as control cells to examine natural germination.

Observations were recorded at 2½, 5 and 7½ weeks after transplantation. Transplanted seedlings were recorded as living or dead. Germinated seeds were counted in the sown-in and control cells. Due to the morphological similarity of seedlings from *Ach. atrata* and *Ach. clusiana* they could not be distinguished in the control cells.

To estimate the growth of transplanted seedlings in a non-destructive way, we counted the number of rosettes for the *Achillea*-species and the length of the longest vital leaf for *Arabis caerulea* and *G. hoppeanum*. These size measurements were done shortly before the transplantation and at the end of the vegetation period.

Statistical Analyses

We analysed the impact of germination treatment (gibberellic acid) and plot conditions (time of snowmelt, vegetation cover) – all hereafter referred to as predictors – on seedling survival across the three times of measurement. States of predictors (e. g. with or without gibberellic acid) are referred to as predictor levels. The number of predictor levels (n) is three for time of snowmelt and two otherwise. Four-dimensional contingency tables of sample proportions, one dimension for each observation and one for the predictor, were built, resulting in $3n$ marginal distributions, one for each predictor level

at each observation. We note that the three marginal distributions of a predictor level across time are not independent.

To compare the probability distributions of being alive at each of the three observations among predictor levels, i. e. to compare the first-order marginal distributions, a Maximum Likelihood approach for Marginal Logit Models was used. The model was defined as

$$\text{logit}\,[P(y_t = 1)] = \alpha + \beta_1 x + \beta_2 t + \beta_3 xt,$$

where y defines the status of the seedling (dead/alive), t represents the observation time and x represents the predictor. Time t was included as a linear effect and therefore coded as 0, 1, and 2 to account for equal differences between observations. Predictors were interpreted as nominally scaled and coded 0 and 1 (or 0, 1, and 2). Predictor levels 0 (without gibberellic acid, early snowmelt, and open vegetation) were used as a reference. The models were fitted for each predictor separately.

Marginal homogeneity corresponds to three identical response distributions among predictor levels across the three observations ($P(y_1 = 1) = P(y_2 = 1) = P(y_3 = 1)$). A likelihood ratio test compares the likelihood maximized under marginal homogeneity – maximum likelihood estimations of the marginal probabilities are the sample probabilities in that case – to the maximum likelihood fit constrained by the defined model (Agresti 2002).

The model was fitted with the MPH.fit function for Multinomial-Poisson Homogeneous models (Lang 2002), which gives consistent estimates of regression coefficients regardless of the form of the joint distribution, because marginal and joint parameters are orthogonal.

Time effects and odds ratios were derived from that function. The time effect represents the mortality rate (i. e. negative survival rate) across observations of each predictor level and was calculated as $\exp(\beta_2 + \beta_3)$. High absolute values of the time effect indicate high mortality. The odds ratio represents the estimated odds of being alive for a predictor level compared to the respective reference level at time t. Values below 1 denote that the probability of being alive is lower for an individual of a certain predictor level as compared to an individual belonging to the respective reference level. Odds ratios were computed as $\exp(\beta_{1d} + \beta_3 t)$, where β_{1d} is the regression coefficient of the dummy variable coding the respective predictor level. For these statistical analyses we used R 2.0.1 (R-Development-Core-Team 2004).

To compare the germination rates in the sown-in and in the control cells a one-factorial ANOVA was carried out. We used the number of seedlings at the third observation in this analysis, because seedling density was highest at that time. The probability of being alive at the third observation in dependence on the number of rosettes (for *Ach. atrata* and *Ach. clusiana*) or the length of longest leaf (*Ar. caerulea*, *G. hoppeanum*) before transplantation was estimated using logistic regression models. These analyses were performed using S-Plus 2000 (Mathsoft 1999).

Results

Seedling transplantations

The mortality of transplanted seedlings was low for all species and predictor levels and ranged from 0% to 14% (see Table 1). Seedling mortality rates during the growing period and model fit derived from marginal logit models are given in Table 2. A comparison between predictor levels at each observation is illustrated in Fig. 3. Differences

Table 1: Comparison of percentage of dead seedlings at the third observation (7½ weeks after transplantation) with respect to seed treatment (with and without gibberellic acid), location along the snowmelt gradient (early: near the rim of the snowbed; late: near the centre of the snowbed), and density of vegetation cover. — **Tab. 1:** Vergleich der Prozentsätze toter Keimlinge bei der dritten Beobachtung (7½ Wochen nach der Transplantation) abhängig von der Behandlung der Samen mit (with) bzw. ohne (without) Gibberellinsäure, von der Position im Aperungs-Gradient (früh = early: nahe des Schneebodenrandes; spät = late: nahe des Schneebodenzentrums; mittel = intermediate) und von der Vegetationsdichte (offen = open bzw. geschlossen = dense).

		Achillea atrata	*Achillea clusiana*	*Arabis caerulea*	*Gnaphalium hoppeanum*
Gibberellic acid	Without	3.3	3.2	7.6	5.7
	With	3.5	7.1	9.7	4.2
Snowmelt	Early	3.0	1.0	14.0	11.0
	Intermediate	0.0	0.0	5.0	1.0
	Late	7.0	12.0	9.0	4.0
Vegetation cover	Open	4.7	6.0	12.7	4.0
	Dense	2.0	2.7	6.0	6.7

Table 2: Model fit, *p*-value and time effect for Multinomial-Poisson Homogeneous models. G^2-values are given for a likelihood ratio test comparing the likelihood maximized under marginal homogeneity with the maximum likelihood estimate under the defined model. High G^2-values (here for vegetation cover for *Arabis caerulea* and *Gnaphalium hoppeanum*) indicate significant differences to the saturated model and therefore an inadequate model fit. The *p*-values indicate probabilities for the differences among predictor levels. The time effect represents a measure of the increasing mortality (the decrease in the number of surviving seedlings) among observations. It was derived from model coefficients β_2 and β_3. A large absolute time effect refers to a large increase in mortality between observations. — **Tab. 2:** Modelltauglichkeit (model fit), *P*-Wert (*p*-value) und Zeiteffekt (time effect) eines *Multinomial-Poisson* homogenen Modells. G^2-Werte für einen Test der Wahrscheinlichkeitsrate (likelihood ratio), der die maximierte Wahrscheinlichkeit (likelihood) unter marginaler Homogenität (marginal homogeneity) mit der maximalen Wahrscheinlichkeit für ein definiertes Modell vergleicht. Hohe G^2-Werte (hier für Vegetationsdichte bei *Arabis caerulea* und *Gnaphalium hoppeanum*) indizieren signifikante Unterschiede zum saturierten Modell und daher eine ungenügende Modelltauglichkeit. Die *P*-Werte indizieren Wahrscheinlichkeiten für die Unterschiede zwischen den Prädiktorenniveaus. Der Zeiteffekt repräsentiert ein Maß für die steigende Sterberate (die Abnahme der Zahl der überlebenden Keimlinge) zwischen den Beobachtungszeitpunkten; er wurde von den Modellkoeffizienten β_2 und β_3 abgeleitet. Ein großer absoluter Zeiteffekt bezieht sich auf eine große Zunahme der Sterblichkeit zwischen den Beobachtungen.

a) ***Achillea atrata***

Predictor	Predictor group	G^2 (model)	*p*-value (predictors)	Time effect
Gibberellic acid	Without	0.18		−0.62
	With		0.82	−0.52
Snowmelt	Early	1.80		−0.25
	Intermediate		0.79	−0.81
	Late		0.34	−0.51
Vegetation cover	Open	0.18		−0.63
	Dense		0.57	−0.52

b) ***Arabis caerulea***

Predictor	Predictor group	G^2 (model)	*p*-value (predictors)	Time effect
Gibberellic acid	Without	2.18		−0.43
	With		0.80	−0.46
Snowmelt	Early	1.09		−0.55
	Intermediate		0.61	−0.47
	Late		0.45	−0.26
Vegetation cover	Open	5.90		−0.45
	Dense		0.14	−0.50

c) ***Achillea clusiana***

Predictor	Predictor group	G^2 (model)	*p*-value (predictors)	Time effect
Gibberellic acid	Without	3.30		−0.71
	With		0.11	−0.38
Snowmelt	Early	1.52		−0.08
	Intermediate		0.25	−0.64
	Late		0.46	−0.51
Vegetation cover	Open	3.72		−0.72
	Dense		0.99	−0.30

d) ***Gnaphalium hoppeanum***

Predictor	Predictor group	G^2 (model)	*p*-value (predictors)	Time effect
Gibberellic acid	Without	0.30		−0.26
	With		0.18	−2.50
Snowmelt	Early	1.66		−0.47
	Intermediate		0.32	−0.35
	Late		0.16	−0.00
Vegetation cover	Open	6.67		−0.42
	Dense		0.40	−0.25

between predictor levels were not statistically significant throughout, although some trends could be detected.

Seedlings emerged from seeds stratified with gibberellic acid showed slightly lower to equal survival compared to their control group for *Ach. atrata*, *Ach. clusiana* and

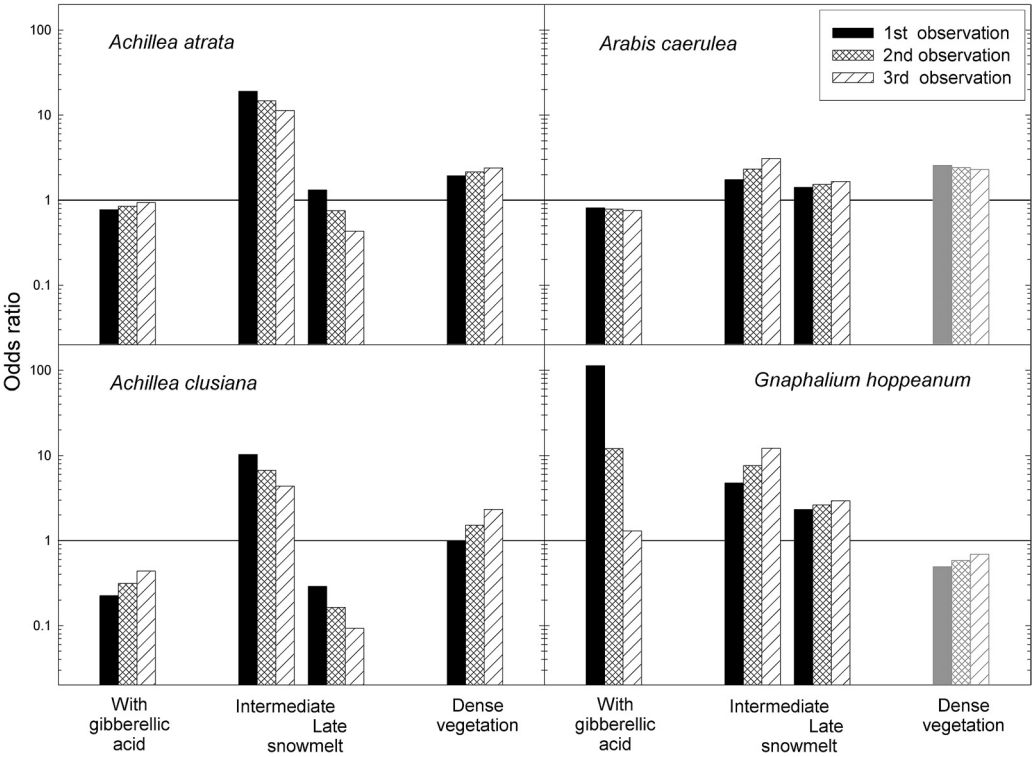

Fig. 3: Impacts of predictors on seedlings survival. One group of each predictor (without gibberellic acid, early snowmelt and open vegetation) was used as reference (represented by the horizontal line at 1 on the y-axis). Bars illustrate the odds ratio of predictor levels compared to the reference group for each observation. Ratios above ca. 10 are caused by mortality rates of (nearly) zero. Observations were made 2½, 5, and 7½ weeks after transplantation. Grey bars indicate a non-significant likelihood ratio test (compare G^2 in Table 2), i. e. an inadequate model fit. These models were thus not interpreted, but are illustrated for completeness. — **Abb. 3:** Einfluss der Prädiktoren auf das Überleben der Keimlinge. Eine Gruppe jedes Prädiktors (ohne Gibberellinsäure, früher Zeitpunkt der Schneeschmelze und offene Vegetation) wurde als Referenz verwendet (repräsentiert durch die horizontale Linie bei 1 auf der y-Achse). Die Balken bilden die *Odds Ratio* (Verhältniszahl) der Prädiktorenniveaus im Vergleich zu Referenzgruppe jedes Prädiktors ab; mit Gibberellinsäure = with gibberellic acid; mittlerer/später Zeitpunkt der Schneeschmelze = intermediate/late snowmelt; geschlossene Vegetation = dense vegetation. Verhältniszahlen (ratio) über ca. 10 werden durch Mortalitätsraten (nahe) von Null verursacht. Die Beobachtungen wurden 2½ (erste Beobachtung = 1st observation), 5 (zweite Beobachtung = 2nd observation) und 7½ (dritte Beobachtung = 3rd observation) Wochen nach der Transplantation gemacht. Graue Balken deuten einen nicht signifikanten *Likelihood ratio test* an (vergleiche G^2 in Tab. 2) und daher eine ungenügende Modelltauglichkeit. Diese Modelle wurden daher nicht interpretiert und werden nur der Vollständigkeit halber dargestellt.

Ar. caerulea, but possessed higher survival in *G. hoppeanum* for the stratified group. However, the differences between levels decreased over time. This decrease was very strong in *G. hoppeanum*. The seedlings transplanted to sites with intermediate snowmelt dates showed the lowest mortality rates for all species. Dense vegetation led to a higher seedling survival than open vegetation for both *Achillea* species (*Ar. caerulea* and *G. hoppeanum* showed an inadequate fit of the models and were thus not interpreted).

Seed sowing

Results from the seed-sowing experiment are shown in Table 3. Seedling emergence in sown-in plots was significantly higher than in the control plots for all species. Cells with open vegetation showed consistently higher seedling emergence than cells with dense vegetation, but differences were significant only for *Ar. caerulea* and *Ach. clusiana*.

Size measurements

Seedlings grown in the lowlands and transplanted to the alpine area reacted in a species-specific way during the first vegetation period. *Arabis caerulea* showed an average reduction in leaf length of 5 mm and *Ach. atrata* a loss of one rosette in every eighth plant. In contrast, every third *Ach. clusiana* seedling gained one rosette; leaf length of *G. hoppeanum* did not differ at all. However, observed reductions in above-ground biomass had negligible effects on survival rates. For *Ach. clusiana* small plants even showed higher survival than big ones.

Table 3: Number of germinated seeds per cell (10 × 10 cm; mean±SE) compared between sown-in and control cells, and between open and dense vegetation of sown-in cells. $n = 90$ for sown-in and control plots, $n = 45$ for open and dense vegetation of sown-in plots. 100 seeds were sown in each cell – except for *Gnaphalium hoppeanum* were only 50 seeds were used. Seedlings were counted at the beginning of September. Seedlings from *Achillea* species in the control cells could not be differentiated. —
Tab. 3: Anzahl gekeimter Samen pro Zelle (10 × 10 cm; Mittelwert±Standardfehler); Vergleich zwischen Zellen mit zusätzlich eingesäten Samen (sown-in) und Kontrollzellen (control) beziehungsweise zwischen offener (open) und geschlossener (dense) Vegetation der eingesäten Zellen. $n = 90$ für eingesäte und Kontroll-Zellen, $n = 45$ für offene und geschlossene Vegetation der eingesäten Zellen. Es wurden 100 Samen pro Zelle eingesät – mit Ausnahme von *Gnaphalium hoppeanum,* hier wurden nur 50 Samen pro Zelle gesät. Keimlinge wurden Anfang September gezählt. Keimlinge der beiden *Achillea*-Arten in den Kontrollzellen konnten nicht unterschieden werden.

	Achillea atrata	*Achillea clusiana*	*Arabis caerulea*	*Gnaphalium hoppeanum*
Sown-in cells	1.97±0.42	5.42±0.72	1.98±0.37	2.69±0.51
Control cells	0.14±0.05		0.08±0.04	0.06±0.04
ANOVA	$F = 35.9$; $p < 0.001$		$F = 26.4$; $p < 0.001$	$F = 26.5$; $p < 0.001$
Open vegetation	2.13±0.66	8.11±1.20	2.78±0.58	3.58±0.68
Dense vegetation	1.80±0.53	2.73±0.59	1.18±0.43	1.80±0.74
ANOVA	n.s.	$F = 11.6$; $p < 0.001$	$F = 4.3$; $p = 0.04$	n.s.

The probabilities for being alive at the third observation showed only weak dependencies on the size of transplanted seedlings (number of rosettes or longest leaf). Generally, plants with more rosettes (*Ach. atrata*) or longer leaves (*Ar. caerulea* or *G. hoppeanum*) had a higher chance to survive their first vegetation period, only *Ach. clusiana* showed the opposite trend.

Discussion

High survival rates for all transplanted seedlings were observed during the first vegetation period. This is in line with previous transplantation studies (May & al. 1982, Bruelheide 2000) which also concluded that high proportions of transplanted seedlings are able to establish in montane and alpine regions. The success of our transplanted seedlings could also have been enhanced by their comparatively large size at the time of transplantation. At the end of the growing period, transplanted seedlings were usually much larger than those germinated in the field. Whatever the reason, the low mortality rates considerably decreased the power of the statistical tests aimed to analyse the impact of predictors on seedling establishment. This lack of power brought about statistically non-significant results despite some visible trends. We hence interpret the most pronounced of these trends even if statistical tests delivered probability values below 95%.

Survival rates shortly after a stressful event such as transplantation from a common garden to an alpine habitat can be expected to strongly depend on plant size. However, our data did not support this expectation. We suggest that there are two possible reasons for this result. First, for a short interval after transplanting, changes in size measurements are likely to represent the recovery from the transplantation rather than site-dependent growth. For example, relatively large and long leaves of individuals in the common garden face an especially high risk of dying after the transplantation. This could result in observations of negative growth. However, the tiny proportion of biomass represented by that leaf is likely compensated by the growth of new but smaller leaves, leading to the discrepancy between the individuals, measured size and survival (pers. obs.). Second, the decline of rosette size varies strongly following linear to strongly exponential distributions, thus rosette number is a poor measure for the short-time growth of study species.

The effect of gibberellic acid on seedling survival rate of our study species was generally negative. Only for *G. hoppeanum* seedlings was survival higher for stratified seedlings, but this difference decreased strongly during the vegetation period. Gibberellic acid treatments trigger excessive reserve consumption in the early phases of germination and growth. Most of the energy is spent in above-ground growth at the expense of root growth (Ruge 1966), leading to reduced nutrient uptake. Hence, seedlings with enhanced shoot growth may be less resistant to (temporary) shortage of nutrients and water, resulting in lower growth and higher mortality under the low-nutrient conditions of open alpine vegetation types (Heer & Körner 2002).

Even small variations in root biomass can alter the below-ground competitive abilities of plants (Cahill & Casper 2000). Several studies on species representing a wide range of families (reviewed in Wilson 1988) suggest that below-ground competition has a stronger influence on the balance of competing species than above-ground competition. Larger shoot and smaller root systems confer weaker overall competitive ability (Aerts & al. 1991) of three out of four study species. Hence, our data provide some evidence that light may be less limiting for plant growth than nutrient or water supply in the observed snowbed habitats – a plausible scenario in these mostly open vegetation types. Allocation of biomass within a plant to roots or shoots (i. e. the root-shoot interaction) is flexible to some extent, depending on what is the most limiting resource (Casper & al. 1998, Cahill 2002, Song & al. 2006). However, allocation adjustment might be limited for seedlings, potentially explaining the strong effects of the initial resource allocation.

The influence of vegetation cover differs between seedling establishment and germination. Dense vegetation decreased the mortality rates of seedlings for three out of the four study species (*Ach. atrata*, *Ach. clusiana*, *Ar. caerulea*). Similarly Niederfriniger-Schlag & Erschbamer (2000) counted higher numbers of seedlings on vegetated plots. Protection by standing crop and plant litter may enhance seedling survival by improving micro-site conditions (Urbanska & Schütz 1986). Even very small differences in site conditions influence the fate of a seedling and safe sites are of great importance especially in harsh environments like alpine ones (Urbanska & Schütz 1986, Callaway & al. 2002). The reason for the higher survival of *G. hoppeanum* seedlings in open vegetation remains largely obscure. One possibility is that the dense indumentum of *G. hoppeanum* seedlings protects leaves from damages due to insolation when few neighbours are present and light levels are high (Körner 1999). However, this may also be an artefact of the transplantations from the lowlands to the alpine belt, as *G. hoppeanum* seedlings may adapt more rapidly to intensive radiation. Germination was significantly higher in plots with open vegetation for *Ach. clusiana* and *Ar. caerulea*, contrary to the findings of Erschbamer & al. (2001) who observed higher seedling emergence on vegetated plots than on bare ground. However, Erschbamer & al. (2001) compared vegetated plots with completely bare ground whereas we contrasted dense and sparse vegetation cover.

The highest survival rates of seedlings on plots with intermediate snowmelt may be explained by a trade-off between resource supply and disturbance. Frequency and intensity of deleterious disturbance due to debris fall or small land slides and the magnitude and regularity of water and nutrient supply both increase towards the centre of the snowbed (Björk & Molau 2007). Increased snow depth has a considerable influence on soil composition (Borner & al. 2008), thus having a severe influence on vegetation cover. Additionally, unobserved erratic factors like herbivory, which are strongest at one end of the gradient, could interfere with a pattern of otherwise favourable survival at the concerned end of the gradient.

It is likely that recruitment rates are highest at intermediate vegetation densities. Germinating seedlings may already profit from protection and soil stabilization by other plants (Chambers & al. 1990), whereas levels of competitive interference are still low.

At densely vegetated sites seedlings suffer from shortages in essential resources such as light, nutrients and water due to their low competitive abilities. With increasing size the competitiveness of seedlings increases and the optimal balance of competitive and facilitative interactions may thus shift towards denser vegetation. Taken together, a mosaic of open and dense vegetation might be optimal for generative recruitment, i.e. comprising both germination and seedling establishment. Small-scale disturbance regimes which are typical for alpine environments provide such a mosaic and may thus enhance colonization processes (Dirnböck & Dullinger 2004).

Predicted changes in climatic conditions with an increase in mean annual temperature of 1.4°C to 5.8°C until the end of this century (IPCC 2001) will significantly prolong the growing season. Summers will become warmer and drier on average (IPCC 2001). Species from surrounding communities will likely invade into the snowbeds and vegetation cover will probably increase towards the level of alpine grasslands. Snowbed specialists will hence face increased levels of biotic interactions. Our results indicate that competitive and facilitative effects of the surrounding vegetation on snowbed species may change along different phases of their life cycles. A dense neighbourhood obviously hampers seed germination but may well promote the survival of already established seedlings. A climate change driven increase in the vegetation cover of calcareous alpine snowbeds will thus threaten the viability of the populations of snowbed specialists, primarily by reducing the prevalence of open sites necessary for their germination.

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