

Alpine seed rain: comparing snowbeds with surrounding terrain



Nicklas Albertsson

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Supervisor: Johan Uddling and Lasse Tarvainen, Department of biological & environmental sciences

Examiner: Åslög Dahl, Department of biological & environmental sciences

Cover photo: Nicklas Albertsson. Some of the species classified from the seed samples.
Species from left to right: *Betula pubescens* ssp. *czerepanowii*, *Betula nana*, *Empetrum nigrum*, *Bistorta vivipara*, *Phleum alpinum*, *Dryas octopetala*.

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Abstract

Seed dispersal is a fundamental process for plants in general and snowbeds constitute a unique and important alpine habitat, exhibiting specialized plant communities and providing important ecosystem effects. The knowledge of how seed rain in snowbeds differs from surrounding terrain provides important insight to understand future vegetation shifts and can help pinpoint possible restoration efforts. Also, it could be a part of understanding why the alpine plant cover looks the way it does today. Compared to other alpine habitats, snowbeds are regarded as especially sensitive to temperature increase from climate change. With this in mind, this thesis aims to answer how seed rain differs between snowbeds and surrounding terrain. Previous studies have investigated seed rain in snowbeds but the spatial comparison to surrounding terrain has not been done before. In this study, seed rain was measured using artificial traps, comparing three snowbeds sites with three sites representing the surrounding terrain in Latnjajaure, northernmost Sweden. The seed rain is compared in terms of seed abundance, species richness and percentage of species and seeds in the seed rain that have full-grown plants represented close to the traps. The results show that graminoid seed abundance and total species richness are significantly higher in snowbeds compared with surrounding terrain. In some snowbeds a large amount, around 80%, of seeds, primarily graminoids, lack representation in the nearby plant community. This suggests that graminoid seeds have a higher tendency to spread with wind and/or snowdrifts compared to seeds from herbs and shrubs. It is clear that seeds are dispersed heterogeneously across the alpine landscape and that some snowbeds end up with a majority of seeds from species that do not grow there. The total alpine biodiversity will decrease in the future if the seeds that land in snowbeds succeed in germinating and outcompete the specialist growing there today.

Keywords: seed rain; snowbeds; alpine zone; seed dispersal; climate change

Sammanfattning

Fröspridning är en grundläggande process för växters etablering i nya områden och snölegor är ett unikt och viktigt habitat i den alpina miljön. Kunskap om skillnader i frönedfall mellan snölegor och närliggande terräng kan hjälpa oss att förstå framtida förändringar i växtsamhällen. Det kan också vara ett redskap för att förstå varför växtsamhällen ser ut som dom gör idag och precisering av eventuella naturvårdsåtgärder. Jämfört med andra alpina habitat så är snölegor speciellt känsliga för förändringar i klimatet. Med detta i åtanke försöker den här uppsatsen besvara hur frönedfall skiljer sig mellan snölegor och omgivande terräng. Det finns tidigare litteratur som undersökt alpint frönedfall men ingen som försökt besvara denna frågeställning. I den här studien så mättes frönedfall med artificiella fröfällor och tre lokaler i snölegor jämfördes med tre lokaler som representerar omgivande terräng i Latnjajaure, nordligaste Sverige. Fröregnet jämförs i avseende på antal frön, artrikedom och andel arter och frön som har fullt utvecklade växtindivider representerade i växtsamhället närliggande fröfällorna. Resultaten visar att antal graminidfrön och artrikedom av frönedfall i snölegor är signifikant högre än i omgivande terräng. I vissa snölegor så kommer en stor andel av frön, runt 80%, från växter som inte finns representerade i växtsamhället nära fröfällorna. Sannolikt har graminidfrön en högre tendens att spridas med vind och/eller snödrev jämfört med frön från ris och örter. Det är tydligt att frön sprids heterogent över det alpina landskapet och att det i vissa snölegor hamnar en majoritet av frön från växter som inte växer där. Den totala alpina biodiversiteten riskerar att minska om de frön som hamnar i snölegor i framtiden lyckas gro och utkonkurrera de specialister som nu växer där.

Nyckelord: frönedfall; snölegor; alpin zon; fröspridning; klimatförändringar

Introduction

General

Seed dispersal is a fundamental process for plants in general (Howe and Smallwood, 1982) and snowbeds constitute a unique habitat for specialized alpine plants (Bjork and Molau, 2007). Determining where seeds end up in the alpine landscape is crucial for understanding plant dispersal patterns. The knowledge of how seed rain in snowbeds differs from surrounding terrain provides important insight to understand future vegetation shifts and can help pinpoint possible restoration efforts. Also, in a retrospective ecological perspective, it could be a part of understanding why the alpine plant cover looks the way it does today.

The ongoing climate change is more severe in the arctic than in other, non-polar, regions of the earth. Already the arctic temperature rise is at least doubled compared to the global increase (ACIA, 2004). The increasing temperature has many effects, including: decreasing snow cover, thawing permafrost, increased precipitation and vegetation shifts (ACIA, 2004). Numerous studies show that snowbed habitats are especially threatened by climate change compared to other alpine habitats (Matteodo et al., 2016, Schob et al., 2009, Bjork and Molau, 2007). Lowland species from the boreal region (Kudo et al., 1999) and species usually found in intermediate snow habitats (Heegaard and Vandvik, 2004) will have the opportunity to establish in snowbed habitats with continued climate change. Furthermore, it has been observed in the Swiss alps that snowbed plant communities tend to shift towards a species composition more similar to the siliceous alpine grasslands as the climate warms (Matteodo et al., 2016). The arrival of grassland species is likely a consequence of longer growing seasons resulting in earlier snowmelt (Matteodo et al., 2016). Already, a snowbed plant community, located in southern Scandes has been reported to completely disappear within a 30 year period (Kullman, 2005).

The ongoing climate change also affects seed dispersal (Corlett and Westcott, 2013). Modelling alpine seed dispersal in relation to climate change has shown that alpine plants have limited capacity for long-distance seed dispersal (Morgan and Venn, 2017). This limited capacity suggest that most plant species will not be able to track ongoing climate change, as their seed dispersal capabilities are too slow (Cang et al., 2016), referred to as “migration-lag” (Corlett and Westcott, 2013).

Seed rain

Seed rain is the total amount of seeds deposited to the ground. Seeds can be dispersed from their mother plant by different agents, such as water, wind, animals or humans (Howe and Smallwood, 1982, Matlack, 1987, Nathan and Muller-Landau, 2000). Spence (1990) states that to fully understand the distribution and variation in aboveground plant cover and soil seed banks the measurement of seed rain, including what interacts with it, e.g. herbivores, annual variation, is an important aspect. Some studies suggest that sexual reproduction by seed is rare compared to vegetative reproduction in arctic or alpine environments (Thompson, 1978), or that reproduction altogether is rare (Bell and Bliss, 1980). However, seed production in years with warm summers has been shown to be immense (Molau, 1993).

Studies done on seed rain in the alpine zone indicates that plant dispersal distances tend to be relatively short, usually under 1m (Marchand and Roach, 1980, Spence and Shaw, 1983). Furthermore, seeds that lack obvious morphological attributes to disperse effectively with wind or animals can in the alpine zone be a major component of the seed rain (Marchand and Roach, 1980, Spence and Shaw, 1983). While many questions remain regarding the role of seed dispersal in alpine and arctic environment, it is clear that without it many areas, in particular land areas after deglaciation events would still be barren land (Molau and Larsson, 2000).

Snowbeds

Snowbeds form in tundra biome where winter snow accumulates. Especially, this occurs in the alpine zone due to wind re-distribution of snow, rugged terrain and favorable slope directions. Some species, and even communities, can only be found in snowbed habitats, thus, alpine biodiversity is heavily dependent on their preservation (Billings and Bliss, 1959). Also, snowbeds can provide water and nutrients to adjacent ecosystems after they have thawed (Bowman, 1992). Due to continuous melting during the summer months snowbeds offer large herbivores high-quality food in the late season (Fox, 1991). Snowbeds also provide the Norway lemmings (*Lemmus lemmus*) with grazing opportunities and shelter in the subnivean layer between the ground and snow during summer months (Nagy et al., 2003).

In snowbeds the plant cover is lower than surrounding terrain, this favors adaptation towards enduring or coping with prevailing conditions in snowbeds rather than competition with other species (Bjork and Molau, 2007). Specialized snowbed species tend to be capable of dealing well with two stress factors, low soil temperature and short growing season (Schob et al., 2009). Somewhat simplified this means that a high number of specialist species in snowbeds is at risk of being replaced by a low number of generalist species with increasing climate change. The two stress factors favouring specialist species will diminish with climate change and an experiment simulating this possible scenario showed that, on a small scale, species richness in snowbeds decreased by 50% (Schob et al., 2009).

Aims

No previous study has compared seed rain in snowbeds and surrounding terrain using the same trapping method. However, seed rain and snowbeds has been the target for several studies in the same area as this one, Latnjajaure close to Abisko. Seed rain has been measured along an altitudinal gradient over a three year period, concluding that seed rain varies annually as well as altitudinally (Molau and Larsson, 2000). Furthermore, in an effort to streamline seed rain trapping methods one study sampled the top layer of snow in snowbeds, regarded as the “grey blanket”, and showed that they matched the results from artificial traps in (Molau and Larsson, 2000) and even surpassing them on some points (Larsson and Molau, 2001). To further investigate trapping efficiency, horizontal seed dispersal and correlation between species richness and mean summer temperatures an additional study was made (Larsson, 2003).

The previous research carried out in this area provides an excellent basis for further investigations of the impact of snowbeds on alpine seed rain. With the mechanisms of snowbed formation in mind, in particular re-occurring wind patterns emerging on snowbeds, it is reasonable to assume that the abundance of seeds with obvious morphological attributes to disperse with wind should be higher there. This thesis aims to answer the following questions:

1. Is there a difference in seed abundance and species richness in seed rain between snowbeds and surrounding terrain?
2. Is there a difference in the abundance of seeds with morphological attributes facilitating wind dispersal in the seed rain between snowbeds and surrounding terrain?
3. What proportion of the seeds and species in the seed rain is represented in the local plant community close to the collection sites?

Materials and methods

Study site and data collection

This study was conducted at Latnjajaure field station close to Abisko, northernmost Sweden (Figure 1). Most of the year Latnjajaure is covered with snow and the climate is distinguished by snow-rich, mild winters and cool summers, more exact weather data provided in Table 1. As most

other alpine areas it is a mosaic of different vegetation communities, varied in terms of water availability, soil nutrients and pH (Molau and Larsson, 2000). Typical dominant species in the area are *Cassiope tetragona*, *Carex bigelowii* and *Dryas octopetala* (Molau and Alatalo, 1998).

Table 1. Mean temperature, annual precipitation and sunshine for 2017, recorded by the closest weather station in Katterjokk (SMHI, 2017).

Weather station	Mean temperature (°C)	Precipitation (mm)	Sunshine (h)
Katterjokk 2017	-0,8	869	1347

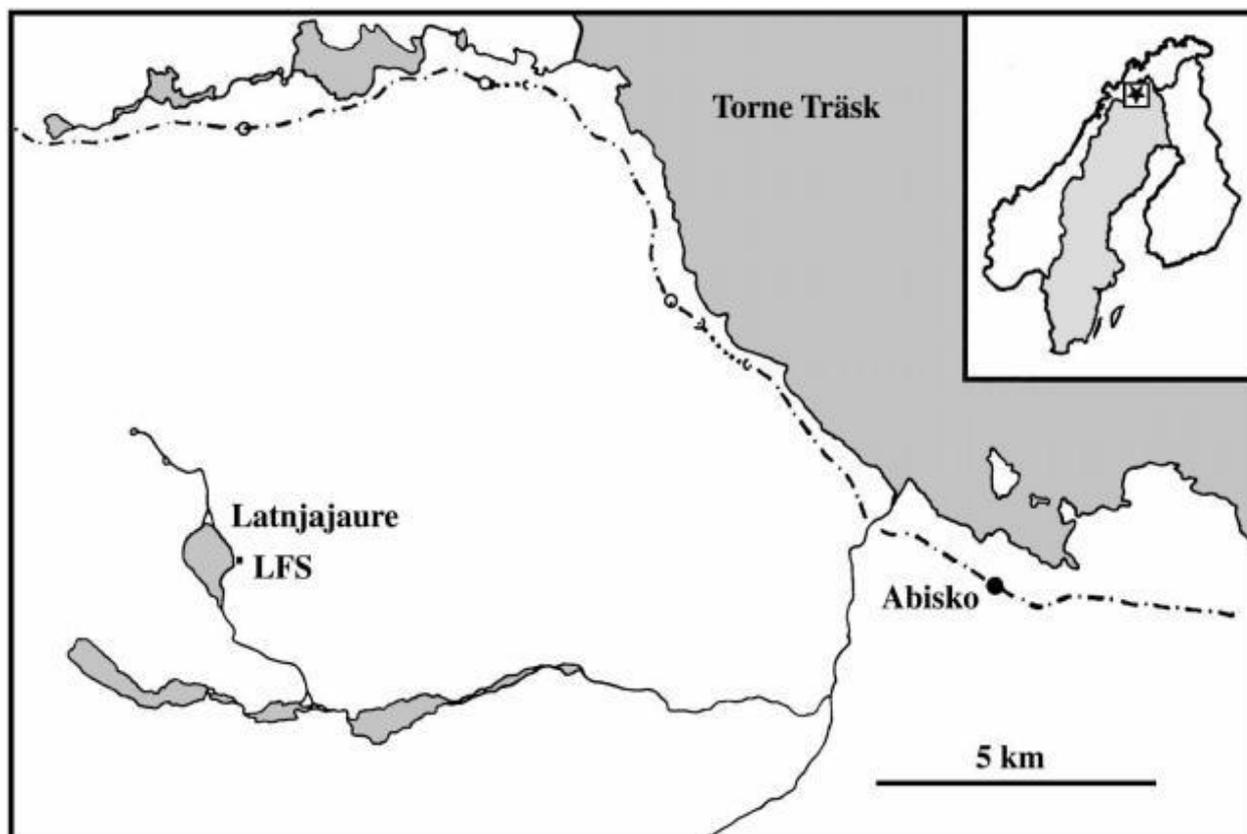


Figure 1. Location of the study site (Molau and Larsson, 2000).

Plastic mats (Finnturf™) were placed at six different sites (three snowbed sites, two meadow sites and one heath site). All the sites are close to each other, both in terms of altitude (Table 2) and spatially. The plastic mats were laid out in late July 2017, ahead of the annual dispersal of seeds for all species in the area. Each site consisted of four mats (area one mat: 0,25 m²) spaced 1 m apart and attached to the ground with nails in the corners. All material deposited on the mats was collected in early July 2018, dried and stored in paper bags for analysis. The seeds analyzed in this project are regarded as the production of 2017.

The sorting and classification took place at Botanhuset in Gothenburg. The samples were filtered with a 2x2 mm metal net. All seeds were sorted out from the filtered material using a stereo loupe. Using a reference collection all seeds were classified to either genus (only some *Luzula* and *Carex* species) or species. The following taxa were counted as having seeds with morphological attributes facilitating dispersal by wind: Asteraceae, *Betula*, *Eriophorum angustifolium*, *Rumex acetosa* ssp. *lapponicus*, *Trichophorum cespitosum* and *Dryas octopetala*. Nomenclature follow that of “Den nya nordiska floran” (Mossberg and Stenberg, 2003). The term

seed in this thesis includes other diaspores, such as bulbils from *Bistorta vivipara* and macrospores from *Selaginella selaginoides*.

Information of the local plant community composition close to the plastic mats was based on previous observations (Molau 2018, personal communication). A species is defined as being present at a site if it is found inside the same habitat patch as the plastic mats.

Table 2. Description of the sites.

Site	Vegetation type	Meters above sea level
Heath (H)	Dry heath	1000
Meadow a (Ma)	Mesic meadow	1000
Meadow b (Mb)	Mesic meadow	1000
Snowbed a (Sa)	Meadow snowbed	900
Snowbed b (Sb)	Meadow snowbed	1000
Snowbed c (Sc)	Meadow snowbed	1100

Data analysis

The variation among the sites was tested using one-way ANOVA. Levene's test was used to test for homogeneity of variance. If the assumption was violated a log-transformation was performed on abundance data and arc sin-transformation was performed on proportion data prior to running the ANOVA. Significant results from the ANOVA test were analyzed further using Tukey HSD post hoc tests to determine which sites differed from each other. The significance level of $p < 0,05$ was used for all tests and values lower than 0,0001 are presented as $p < 0,0001$.

Results

Seed abundance

In this study a total of 3150 seeds were classified, 2388 in the snowbed sites and 762 in the surrounding terrain sites. Mean seed abundance for all sites was 525 seeds m^{-2} , in snowbeds 796 seeds m^{-2} and in surrounding terrain 254 seeds m^{-2} . Three seeds of *Betula pubescens ssp. czerepanowii* were classified, two in Sa and one in Sb (Table 3, appendix). The closest individual is 1,5 km away from the collection sites and at least at 300 m lower altitude (Molau, 2018 personal communication).

The one-way ANOVA test comparing mean seed abundance among the sites resulted in $F=11,77$ and $p < 0,0001$ indicating significant among-site variation. The Tukey HSD post hoc test showed that all snowbed sites (Sa, Sb, Sc) and one meadow site (Mb) were significantly different from the heath site (H) and the other meadow site (Ma) (Figure 2).

Separating the seeds into functional groups graminoid, herb, shrub and tree gives a more in-depth explanation of how the abundance differ among the sites. Too few tree seeds were found to conduct any statistical analysis. Mean seed abundance for graminoid (one-way ANOVA, $F=22.72$, $p < 0,0001$), herb (one-way ANOVA, $F=8.28$, $p < 0,0001$) and shrub (one-way ANOVA, $F=27.79$, $p < 0,0001$) varied significantly among the sites. The Tukey HSD post hoc test identified significant differences among all functional groups (Figure 3a, 3b, 3c). However, the only group showing consistent significant difference in regard to snowbed versus surrounding terrain is graminoids (Figure 3a).

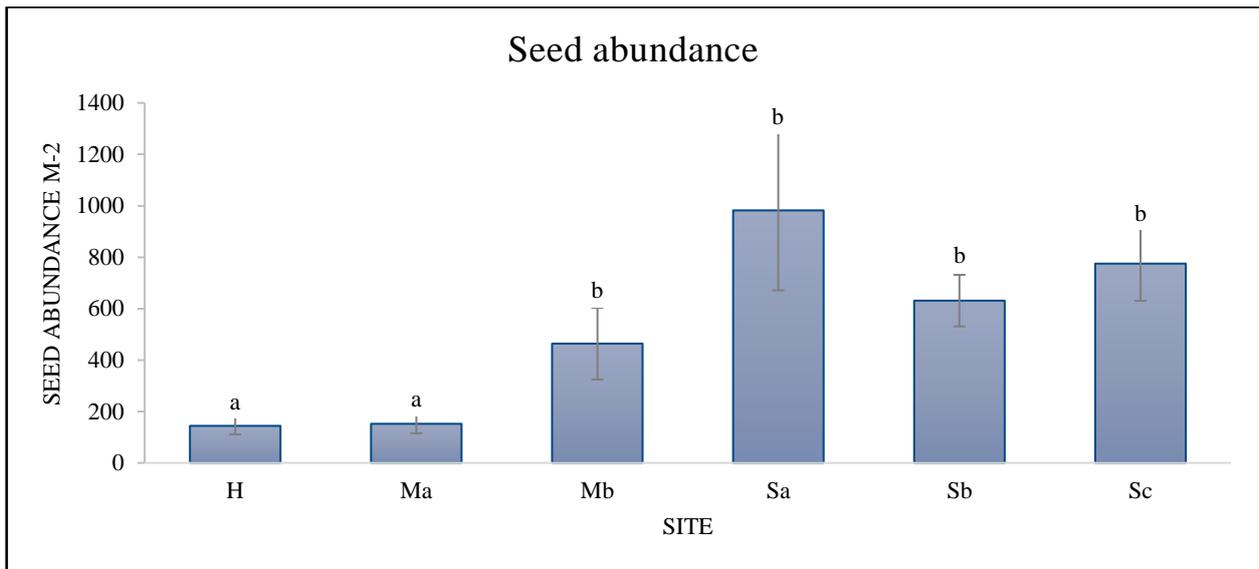


Figure 2. Mean seed abundance m⁻² for each site. If the same letter appears above different bars they are not significantly different (Tukey HSD post hoc: p<0,05). N=4. Error bars show standard error.

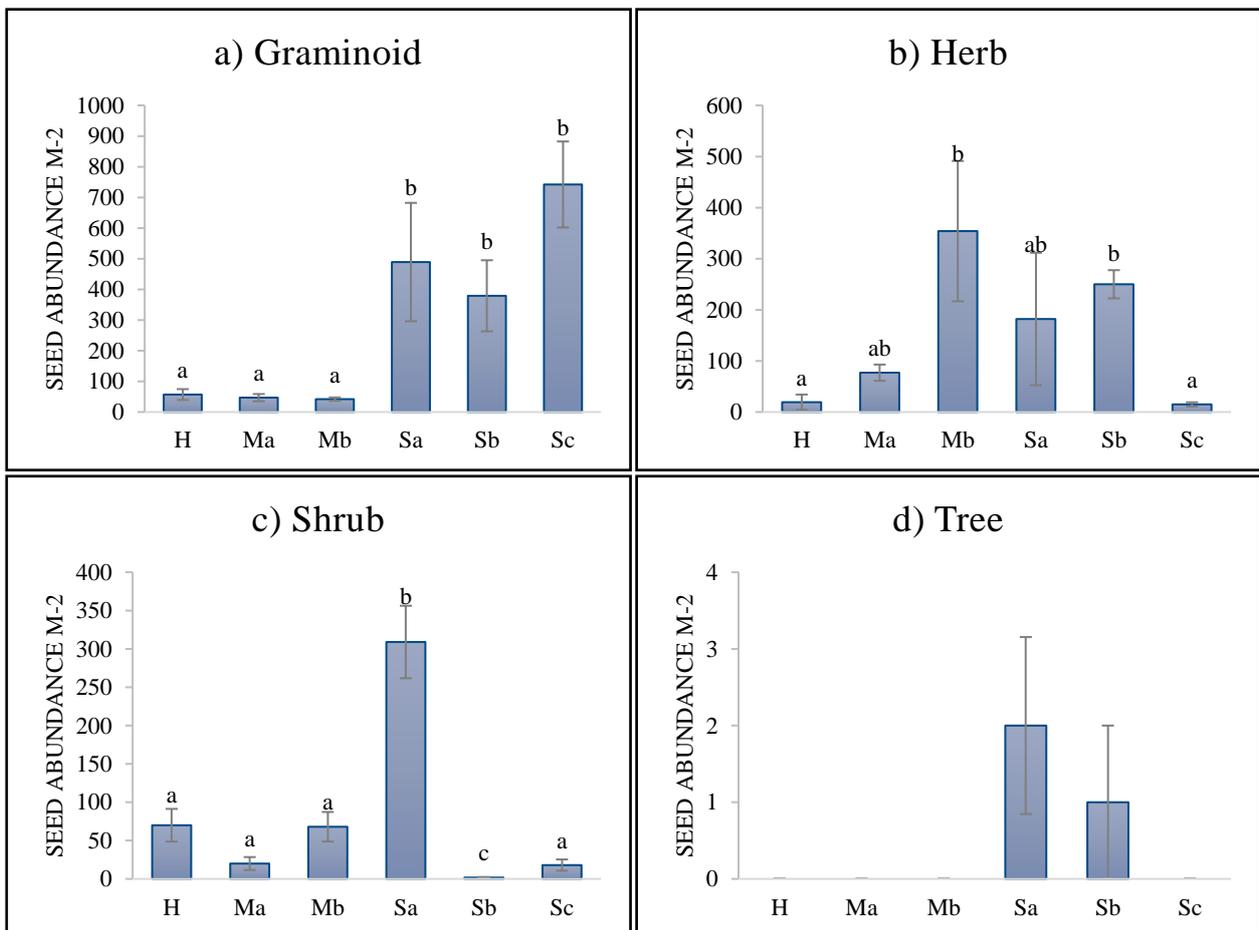
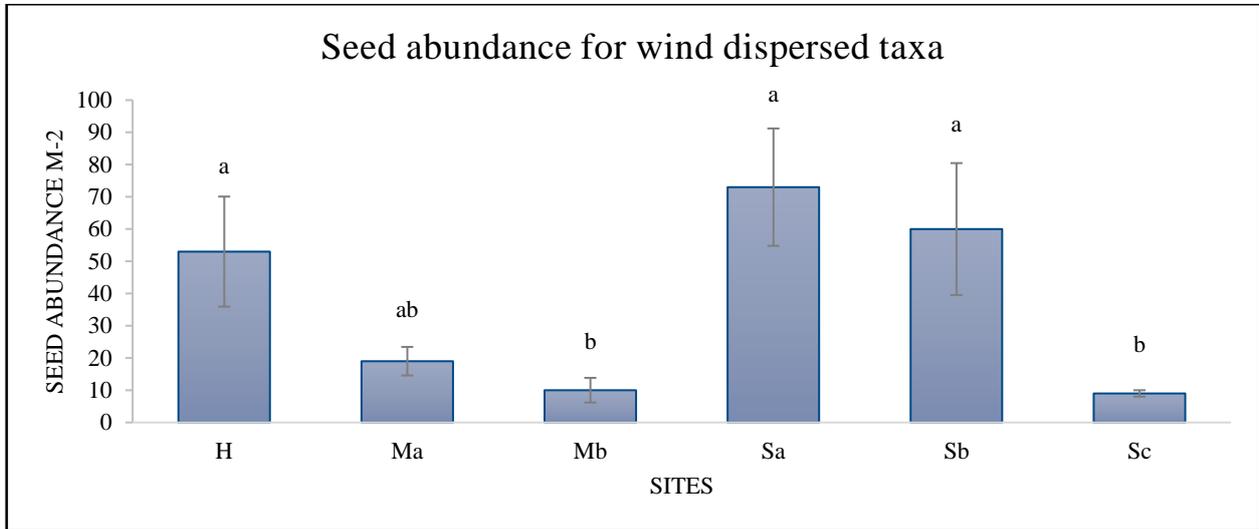


Figure 3. a) Mean graminoid seed abundance m⁻² for each site. b) Mean herb seed abundance m⁻² for each site. c) Mean shrub seed abundance m⁻² for each site. d) Mean tree seed abundance m⁻², since so few seeds were classified in this functional group no statistical test were possible. If the same letter appears above different bars they are not significantly different (Tukey HSD post hoc: p<0,05). N=4. Error bars show standard error.

Seed abundance for wind dispersed taxa

There was significant among sites variation in the abundance of seeds from taxa with morphology directed towards wind dispersal (one-way ANOVA, $F=8,08$, $p=0,0004$). Results from the Tukey HSD post hoc test show that sites Sa, Sb and H differed significantly from sites Mb and Sc (Figure 4). Site Ma did not differ significantly from any other site (Figure 4).



Figur 4. Seed abundance m⁻² for each site only comparing seeds with morphological attributes facilitating dispersal with wind. If the same letter appears above different bars they are not significantly different (Tukey HSD post hoc: $p<0,05$). $N=4$. Error bars show standard error.

Species richness

In total, 45 species were classified among all the sites, 38 in the snowbed sites and 30 in the surrounding terrain sites. The highest total number of species in an individual site was 33 in Sa. Since plant species are more or less aggregated depending on dispersal strategy both the total number of unique species for each site, summarizing all species from the 4 mats (Figure 5), and the mean number of species (Figure 6) is presented. As seen by the higher species number in figure 5 than figure 6 the distribution of species among the replicates in each site was uneven. The mean richness of all species present varied significantly among the sites (one-way ANOVA, $F=5.19$, $p = 0.004$). The post hoc test identified significant differences in mean number of species between Sa and H ($p = 0.008$), Sa and Ma (0.021), and Sb and H (0.027) (Figure 6a).

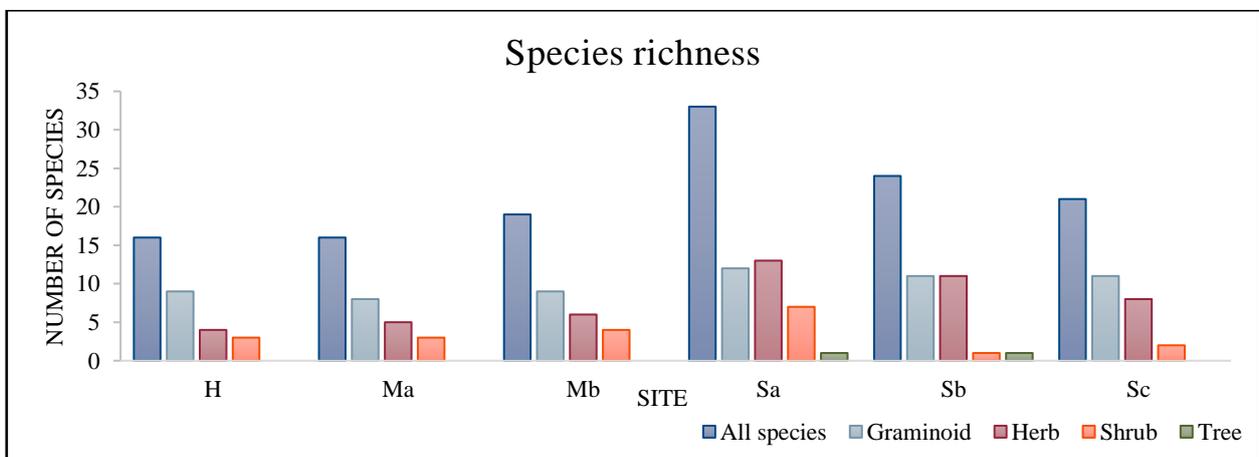


Figure 5. Total number of unique species in all of the replicates for each site.

As with seed abundance the mean number of species was also analyzed on the level of functional group. Mean number of species for graminoid seeds (one-way ANOVA, $F=7.04$, $p=0.0008$), herb seeds (one-way ANOVA, $F=3.79$, $p=0.016$) and shrub seeds (one-way ANOVA, $F=13.5$, $p<0,0001$) varied significantly among the sites. The Tukey HSD post hoc test identified significant differences for all three groups but only herb and graminoid show results somewhat consistent with snowbed versus surrounding terrain (Figure 6b, 6c, 6d)

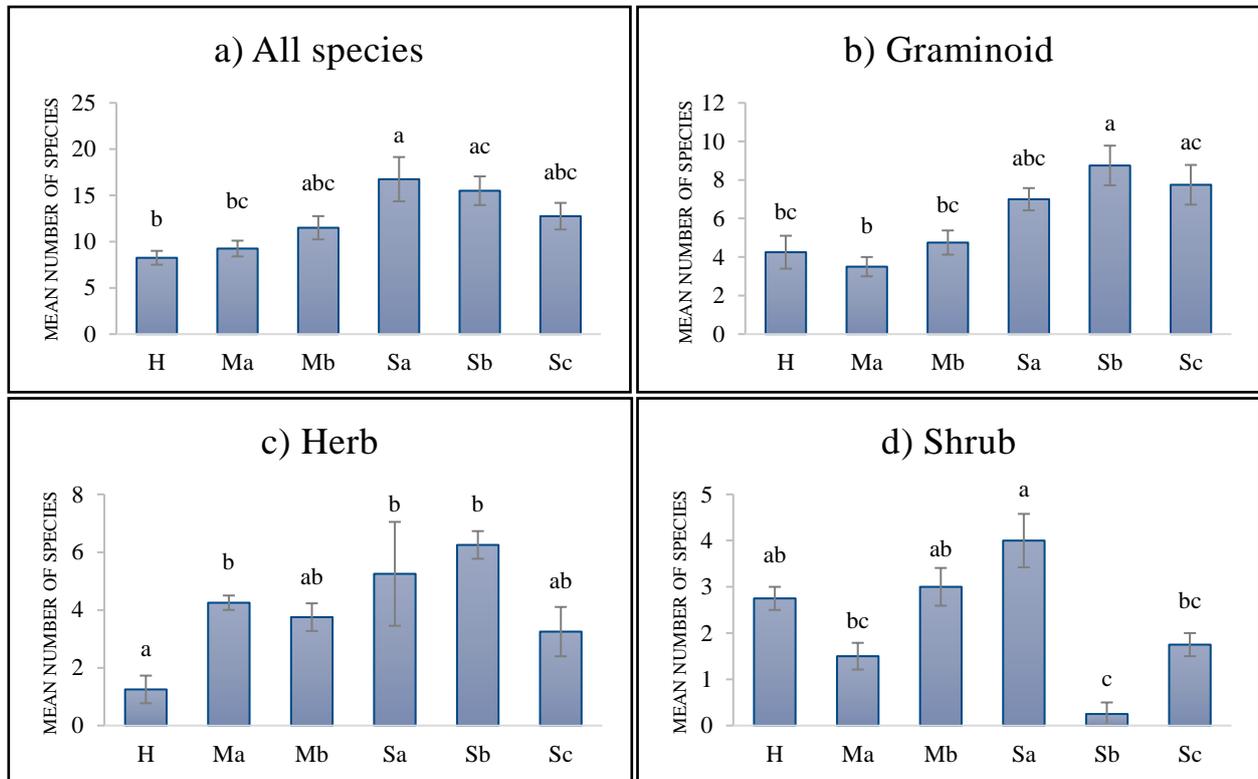


Figure 6. a) Mean species richness for all species in each site. b) Mean species richness for graminoids in each site. c) Mean species richness for herbs in each site. d) Mean species richness for shrubs in each site.

If the same letter appears above different bars they are not significantly different (TukeyHSD post hoc: $p<0,05$). $N=4$. Error bars show standard error.

Local plant community represented in the seed rain

The proportion of seeds/species in the seed rain represented in the local plant community differed significantly among the sites, both for seeds (one-way ANOVA, $F=97,04$, $p<0,0001$) and species (one-way ANOVA, $F=47,75$, $p<0,0001$).

45%-61% of the species classified from the seed samples in the snowbed sites had plants represented in the local plant community around the plastic mats (Figure 7a). The heath site (H) did not differ significantly from the snowbeds with 63% (Figure 7a). The two meadow sites (Ma and Mb) differed significantly from all other sites with all species or close to all species represented in the local plant community (Figure 7a).

Taking the seed abundance into account two sites (Sa and Sc) are significantly different from the others (Figure 7b). 16% of seeds in Sa and 23% in Sc come from species present within a couple of meters around the plastic mats (Figure 7b). Also, H and Sb, with 84% and 82% respectively of seeds that have species present a couple of meters around the plastic mats, are significantly different from the rest (Figure 7b). There was a strong correlation between seed abundance and local plant community composition at the meadow sites with nearly all of the seeds originating from species growing near the plastic mats (Figure 7b).

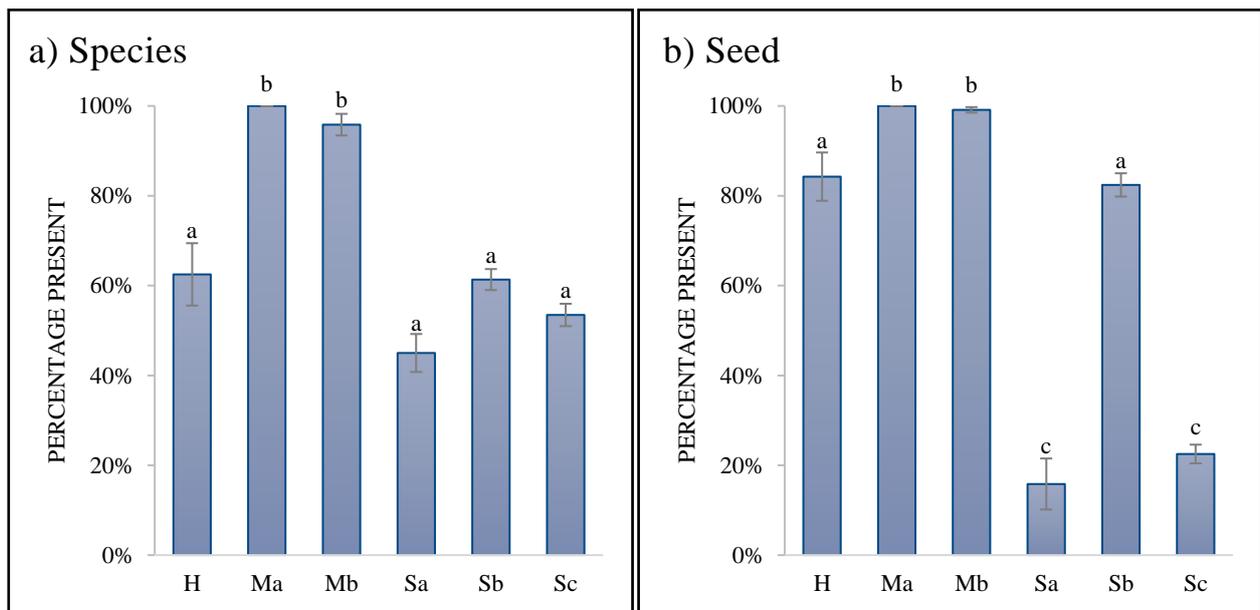


Figure 7. a) percentage of species classified from the seed samples that are represented in the local plant community. b) percentage of seeds that originate from species represented in the local plant community (Molau, 2018 personal communication). If the same letter appears above different bars they are not significantly different (Tukey HSD post hoc: $p < 0.05$). $N=4$. Error bars show standard error.

Discussion

All snowbed sites had a significantly higher seed abundance than two of the sites representing the surrounding terrain (Figure 2). Only comparing the functional group graminoids among the sites showed that all snowbed sites had a significantly higher seeds abundance compared to the other sites (Figure 3a). Seed abundance from wind dispersed taxa show no clear difference regarding snowbed versus surrounding terrain, even though some among sites variation was observed (Figure 4). There was considerable among sites variation in species richness, although it was generally higher at the snowbed sites (Figure 5 and 6). Furthermore, two of the snowbed sites, Sa and Sc, have seed rain with a high proportion of seeds coming from species not represented in the local plant community close to the plastic mats (Figure 7).

Mean seed abundance in the seed rain for all sites was in this study 525 seeds m^{-2} . A previous study with data collected along an altitudinal gradient ranging from 400-1600 meters above sea level from the same area as this one showed a mean annual seed rain with 284 seeds m^{-2} (Molau and Larsson, 2000). In perspective, a study in New Zealand measured $1921 \text{ seeds m}^{-2} \text{ y}^{-1}$ (Spence, 1990) and another in the Hawaiian forest measured $5713 \text{ seeds m}^{-2} \text{ y}^{-1}$ (Drake, 1998), showing that seed rain is still low in alpine environments compared to the tropics. The mean seed abundance for snowbeds in this study is 796 seeds m^{-2} , which agrees with other studies with seed abundance data from snowbeds in the same area that show numbers ranging between $60\text{-}1363 \text{ seeds m}^{-2}$ (Larsson and Molau, 2001, Larsson, 2003).

The study comparing the method of catching seeds with plastic mats in non-snowbed sites versus collecting the top layer of snow from snowbeds and analyzing the seed content show results that corresponds well with this study (Larsson and Molau, 2001). Although the catching method for the snowbeds varied from this study they also had a higher number of seeds m^{-2} and species richness in the snowbed site (Larsson and Molau, 2001), suggesting that the seed rain is spatially diverse between snowbeds and surrounding terrain rather than being dependent of the efficiency of the trapping methods. However, they found a total of 69 different species in the snow from the snowbeds compared to 38 species found in snowbeds in this study. The species that were found

in their study but not this one consisted mostly of herbs (Larsson and Molau, 2001). Herbs is the functional group that show the highest connection between seed production and mean temperatures during summer (Larsson, 2003), which could partially explain these differences. Furthermore, comparing “grey blanket” sampling and artificial traps in snowbeds showed that seed abundance was higher in the artificial trap (Larsson, 2003). However, the “grey blanket” contained more species (Larsson, 2003), suggesting that it’s a better trapping method for determining species richness and also explaining the lower number of species found in this study.

According to the results of this study graminoid seeds are more likely to disperse to snowbeds compared to seeds from herbs and shrubs. Dispersal with water is unlikely since there is no streams from the surrounding terrain towards the snowbeds (Molau, 2018 personal communication) and if there were the water would just rinse the plastic mats due to their inability to get infiltrated. Graminoid seed dispersal facilitated by animals and wind is possible across longer distances (Morgan and Venn, 2017). However, that animals could disperse graminoid seeds to snowbeds as shown here, with numbers from around 500 seeds m⁻² and most originating from a minimum of 50-100 m away, is unlikely. Nevertheless, animal dispersal can be very important for alpine plants reaching new ranges, especially with increasing climate change (Dullinger et al., 2011). The most likely mechanism explaining high graminoid seed abundance in snowbeds is wind. Either directly by wind and/or with snowdrifts during snow covered months. Primarily because that is how snowbed formation occurs.

The high abundance of graminoid seeds compared to seeds from other functional groups indicates that traits linked to graminoid seeds enable them to spread by wind more easily. The most straightforward explanation is that it is caused by the morphological appearance of graminoid seeds. However, graminoid seeds sorted in this study have been observed to aggregate or clump together, especially seeds from *Festuca ovina* and *Poa arctica*. This could possibly make them more easily transported by wind/snowdrifts. Another explanation could be that the timing of seed dispersal from graminoids corresponds well with wind patterns emerging on snowbeds. Notably, seed abundance from wind dispersed taxa showed no clear difference regarding snowbed versus surrounding terrain. The abundance of seeds from wind dispersed taxa is also very low compared to the total seed abundance. The previous finding that seeds that lack obvious morphological attributes to disperse effectively with wind can be a large part of the seed rain (Marchand and Roach 1980, Spence and Shaw 1983) is thus supported by this study. This may be because wind exposure in the alpine landscape is much higher compared to lowland regions, causing many seeds, e.g. small seeds from Ericaceae and Poaceae families and macrospores from *Selaginella selaginoides*, to effectively disperse with wind, even without clear signs of adaptations towards it.

The snowbeds with a high proportion of seeds coming from other areas show that horizontal seed dispersal is common for many species and that they originate from a minimum of 50-100 m away. As shown with *Betula pubescens ssp. czerepanowii*, larger distances and dispersal to higher altitudes are possible. Both the horizontal (Larsson, 2003) and vertical (Molau and Larsson, 2000) dispersal is supported by previous studies (Larsson, 2003, Molau and Larsson, 2000). The findings from previous literature stating that dispersal strategies tend to be short, usually under 1 m in the alpine region (Marchand and Roach, 1980, Spence and Shaw, 1983) are certainly correct for some species but do not apply to the alpine region as a whole.

One could view the results as snowbeds Sa and Sc being saturated on seeds, exhibiting a large proportion of seeds and species in seed rain that lack representation in the plant community close to the plastic mats. Suggesting that the habitat itself is the limiting factor, not the seeds. In contrast, the two meadow sites are seed starved, maybe more species could grow in this habitat but it’s hard for plants from other areas to get seeds to disperse there. This is an important insight in understanding the risk snowbed habitats face compared to other alpine habitats in relation to climate change.

The seeds analyzed in this thesis are derived from one year only. While this gives good insight in spatial differences of seed rain it is unclear how much of it that is attributed to yearly variation. As one of the previous studies in Latnjajaure showed, seed rain varies a lot annually (Molau and Larsson, 2000). If similar results would emerge from a future study as here it would further strengthen the claim of heterogenous seed rain across the alpine landscape. Also, to see if the patterns detected in Latnjajaure can be converted to a general claim about snowbeds in arctic alpine ecosystems similar studies in other areas could be a good target for the future.

Conclusion

This study concludes that graminoid seed abundance and total species richness is higher in snowbed seed rain compared with surrounding terrain. The mechanism explaining this is suggested as being re-occurring wind patterns emerging on snowbeds, based on their involvement in snowbed formation. In some snowbeds a large amount, around 80%, of seeds, primarily graminoids, lack representation in the local plant community surrounding the seed traps. It suggests that a high amount of seeds without morphological attributes to effectively disperse with wind do so anyway. Generally, the results correspond well with previous studies done in the area, although the exact comparison made here had not been done before. Alpine areas, and snowbeds especially, are facing a major threat from climate change. The total alpine biodiversity is at risk of decreasing in the future if the seeds that land in snowbeds succeed in germinating and outcompete the specialist growing there today.

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References

- ACIA 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. *Cambridge University Press*, 2004.
- BELL, K. L. & BLISS, L. C. 1980. Plant Reproduction in a High Arctic Environment. *Arctic and Alpine Research*, 12, 1-10.
- BILLINGS, W. D. & BLISS, L. C. 1959. An Alpine Snowbank Environment and Its Effects on Vegetation, Plant Development, and Productivity. *Ecology*, 40, 388-397.
- BJORK, R. G. & MOLAU, U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic Antarctic and Alpine Research*, 39, 34-43.
- BOWMAN, W. 1992. Inputs and Storage of Nitrogen in Winter Snowpack in an Alpine Ecosystem. *Arctic and Alpine Research*, 24, 211-215.
- CANG, F. A., WILSON, A. A. & WIENS, J. J. 2016. Climate change is projected to outpace rates of niche change in grasses. *Biology Letters*, 12.
- CORLETT, R. T. & WESTCOTT, D. A. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, 28, 482-488.
- DRAKE, D. R. 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science*, 9, 103-112.
- DULLINGER, S., MANG, T., DIRNBOCK, T., ERTL, S., GATTRINGER, A., GRABHERR, G., LEITNER, M. & HULBER, K. 2011. Patch configuration affects alpine plant distribution. *Ecography*, 34, 576-587.
- FOX, J. L. 1991. Forage Quality of Carex-Macrochaeta Emerging from Alaskan Alpine Snowbanks through the Summer. *American Midland Naturalist*, 126, 287-293.
- HEEGAARD, E. & VANDVIK, V. 2004. Climate change affects the outcome of competitive interactions-an application of principal response curves. *Oecologia*, 139, 459-66.
- HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13, 201-228.
- KUDO, G., NORDENHALL, U. & MOLAU, U. 1999. Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. *Ecoscience*, 6, 439-450.
- KULLMAN, L. 2005. Gamla och nya träd på fulufjället - vegetationshistoria på hög nivå. *Svensk botanisk tidskrift*, 99, 315-329.
- LARSSON, E. L. 2003. Two ways of trapping seeds, in alpine environments, Lapland, Sweden. *Nordic Journal of Botany*, 23, 333-343.
- LARSSON, E. L. & MOLAU, U. 2001. Snowbeds trapping seed rain - a comparison of methods. *Nordic Journal of Botany*, 21, 385-392.
- MARCHAND, P. J. & ROACH, D. A. 1980. Reproductive Strategies of Pioneering Alpine Species - Seed Production, Dispersal, and Germination. *Arctic and Alpine Research*, 12, 137-146.
- MATLACK, G. R. 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant-species. *American Journal of Botany*, 74, 1150-1160.
- MATTEODO, M., AMMANN, K., VERRECCHIA, E. P. & VITTOZ, P. 2016. Snowbeds are more affected than other subalpine-alpine plant communities by climate change in the Swiss Alps. *Ecology and Evolution*, 6, 6969-6982.
- MOLAU, U. 1993. Relationships between Flowering Phenology and Life History Strategies in Tundra Plants. *Arctic and Alpine Research*, 25, 391-402.
- MOLAU, U. 2018. Personal communication, december.
- MOLAU, U. & ALATALO, J. M. 1998. Responses of subarctic-alpine plant communities to simulated environmental change: Biodiversity of bryophytes, lichens, and vascular plants. *Ambio*, 27, 322-329.

- MOLAU, U. & LARSSON, E. L. 2000. Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 78, 728-747.
- MORGAN, J. W. & VENN, S. E. 2017. Alpine plant species have limited capacity for long-distance seed dispersal. *Plant Ecology*, 218, 813-819.
- MOSSBERG, B. & STENBERG, L. 2003. Den nya nordiska floran. *Bonnier fakta*.
- NAGY, L., THOMPSON, D., GRABHERR, G. & KÖRNER, C. 2003. *Alpine Biodiversity in Europe: an Introduction*.
- NATHAN, R. & MULLER-LANDAU, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278-285.
- SCHOB, C., KAMMER, P. M., CHOLER, P. & VEIT, H. 2009. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecology*, 200, 91-104.
- SMHI 2017. Sveriges meteorologiska och hydrologiska institut: års- och månadsstatistik. Available at: <https://www.smhi.se/klimatdata/meteorologi/2.1240>.
- SPENCE, J. R. 1990. Seed Rain in Grassland, Herbfield, Snowbank, and Fellfield in the Alpine Zone, Craigieburn Range, South-Island, New-Zealand. *New Zealand Journal of Botany*, 28, 439-450.
- SPENCE, J. R. & SHAW, R. J. 1983. Observations on Alpine Vegetation near Schoolroom Glacier, Teton Range, Wyoming. *Great Basin Naturalist*, 43, 483-491.
- THOMPSON, K. 1978. Occurrence of buried viable seeds in relation to environmental gradients. *Journal of Biogeography*, 5, 425-430.

Appendix

Table 3. Complete species list for all six sites.

	H	Ma	Mb	Sa	Sb	Sc
<i>Anthoxanthum alpinum</i>	x		x	x	x	x
<i>Arabis alpina</i>						x
<i>Bartsia alpina</i>		x	x	x	x	
<i>Betula nana</i>	x			x		x
<i>Betula pubescens</i> ssp. <i>czerepanovii</i>				x	x	
<i>Bistorta vivipara</i>	x	x	x	x	x	x
<i>Calamagrostis lapponica</i>	x			x	x	x
<i>Calamagrostis stricta</i>	x					
<i>Carex atrata</i>				x	x	x
<i>Carex bigelowii</i> ssp. <i>rigida</i>	x				x	x
<i>Carex lachenalii</i>				x	x	
<i>Carex norvegica</i> ssp. <i>norvegica</i>		x	x	x		x
<i>Carex parallela</i>			x			
<i>Carex</i> sp.					x	
<i>Carex vaginata</i>		x	x	x	x	x
<i>Cassiope hypnoides</i>				x		
<i>Cassiope tetragona</i>	x	x	x	x		
<i>Cerastium alpinum</i>				x	x	x
<i>Cerastium cerastoides</i>				x		
<i>Deschampsia flexuosa</i>				x		
<i>Diapensia lapponica</i>				x		
<i>Dryas octopetala</i>		x	x	x		
<i>Empetrum nigrum</i> ssp. <i>hermaphroditum</i>	x	x	x	x	x	x
<i>Erigeron uniflorus</i> ssp. <i>uniflorus</i>	x					
<i>Eriophorum angustifolium</i>	x					
<i>Euphrasia frigida</i>		x	x		x	x
<i>Festuca ovina</i>	x	x	x	x	x	x
<i>Hieracium</i> sect. <i>Alpina</i>					x	x
<i>Kobresia myosuroides</i>		x				
<i>Luzula multiflora</i>		x				
<i>Luzula</i> sp.	x	x	x			
<i>Viscaria alpina</i>				x		
<i>Parnassia palustris</i>				x		
<i>Phleum alpinum</i>	x	x		x	x	x
<i>Poa arctica</i>			x	x	x	x
<i>Potentilla crantzii</i>				x	x	x
<i>Ranunculus nivalis</i>				x	x	
<i>Rumex acetosa</i> ssp. <i>lapponicus</i>	x				x	
<i>Saussurea alpina</i>	x					
<i>Saxifraga oppositifolia</i>			x	x		
<i>Saxifraga rivularis</i>				x		
<i>Selaginella selaginoides</i>		x	x	x	x	x
<i>Silene acaulis</i>		x	x	x		
<i>Taraxacum</i> sect. <i>Taraxacum</i> .				x	x	x
<i>Trichophorum cespitosum</i> ssp. <i>cespitosum</i>		x	x	x	x	x
<i>Trisetum spicatum</i> ssp. <i>spicatum</i>	x	x	x	x	x	x
<i>Viola biflora</i>			x	x	x	