Norwegian University
of Life Sciences

Master's Thesis 2016   60 ECTS

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences

Establishment, survival and dispersal limitations of pioneer plants in a Norwegian glacier foreland as revealed by seed sowing, transplantation and seed bank experiments

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Master in Ecology

2016

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ACKNOWLEDGEMENTS

This thesis was written at the Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, under the supervision of Professor Mikael Ohlson at NMBU and co-supervisor Professor Geir Hestmark, at the University of Oslo (UiO). I would first like to thank my supervisor Mikael Ohlson for the opportunity to write a master thesis with fieldwork in the magnificent Jotunheimen, and to all the support and guidance during fieldwork and all the way to the final stage of this master thesis. I will also thank my co-supervisor Geir Hestmark for help, guidance and comments during my work with this master thesis.

I would like to thank my friends and the student association *BB Cowboys* for five great years at the Norwegian University of Life Sciences, Ås. I would also like to give a special thanks to the people that helped during the fieldwork. Thanks to Lucas and Martina in the first part of the fieldwork. Thanks to my friend and classmate Silje S. Vågen for help in field and in lab, and all the help watering my plants the times I was away. I would like give a special thanks to my parents, Lisbeth Bergene and Ole Petter Strømme, for support and motivation, and for being the greatest field assistance and “Sherpa service” the last day of fieldwork. At the University, I would like to thank May Tove Alseth for help regarding the statistic program R. I would also like to thank Jorunn Haugen and David Arnott for proofreading my thesis.

Finally, I would like to give a big thanks to Thomas Skjelbred for all the help regarding the fieldwork, for always supporting and motivate me. Thank you so much for being there for me all the time and always understanding, you are the best!

Norwegian University of Life Sciences
Ås, Norway 15th May 2016

Anne-Sofie Bergene Strømme

ABSTRACT

Glaciers are melting and retreating on a global scale due to climate change. Rapid glacier retreat leave behind large areas of barren ground, in which primary succession and plant establishments can start. However, a typical feature in glaciers forelands is that vascular plants are lacking in a distinct area close to the front of melting glaciers. To explain the absence of plants in this unpopulated area, I have conducted seed sowing, transplantation, and soil seed bank experiments to explore the establishment and survival success in eight pioneer species (i.e. *Saxifraga stellaris*, *Poa alpina, Poa arctica, Oxyria digyna, Arabis alpina, Cerastium cerastoides, Arabis petraea* and *Beckwithia glacialis*) along a chronosequence in the glacier foreland of Hellstugubreen in Jotunheimen, central Norway. Interestingly, my results from the field experiments showed that the study species generally had significantly higher germination success, survival, vitality and better performance in the unpopulated area nearest to the glacier as compared to in the positions furthest away from the glacier. Moreover, the soil seed bank experiment revealed that there was no seed bank in the unpopulated area closest to the glacier front. From these results, I draw the main conclusion that dispersal limitation, and not germination- and survival limitations, explained the absence of plants in the unpopulated area in front of the Hellstugubreen glacier. In addition, to understand what environmental factors that limits the growth of the important pioneer species, i.e. *A. alpina*, I conducted a growth experiment under four controlled combinations of temperature and light conditions. Here, my results showed that *A. alpina* grew better under cold and high light conditions, and that the proportion of fertile individuals were significantly reduced with increased temperatures.

Key words: Norwegian glacier, Hellstugubreen, glacier foreland, melting glaciers, plant establishment, seed germination, survival- and dispersal limitation

SAMANDRAG

Isbrear smeltar og trekkjer seg tilbake globalt grunna klima endringar. Når isbrear trekkjer seg raskt tilbake blir det lagt att eit stort område av naken grunn der primærsuksesjon og plantekolonisering kan byrja. Men eit typisk karakteristikk på isbre-forland er mangelen på vaskulære planter i eit klart område framom isbrefronten på ein smeltande isbre. For å forklare manglelen på planter i detta område utan busetnad, gjorde eg eit såfrø-, transplanterings- og jord frøbank eksperiment for å utforske etablering og overlevingssuksess hjå åtte pioner artar (som *Saxifraga stellaris, Poa alpina, Poa arctica, Oxyria digyna, Arabis alpina, Cerastium cerastoides, Arabis petraea* and *Beckwithia glacialis*) langs ein tidsserie i isbre-forlandet av Hellstugubreen i Jotunheimen, i sentral Noreg. Mine resultat frå felteksperimenta viste interessant at studieartane hadde generelt signifikant høgare spiringssuksess, overleving, vitalitet og betre yting i det området utan busetnad nærmast isbreen, samanlikna med i posisjonen lengst unna isbreen. I tillegg, viste jord frøbank eksperimentet at det var inga frøbank i det området utan busetnad nærmast isbreen. Frå dessa resultata, trakk eg hovudkonklusjonen at det var spreiingsavgrensing, og ikkje spirings- og overlevingsavgrensing, som forklara mangelen på planter i det området utan busetnad ved fronten av Hellstugubreen isbre. I tillegg, for å forstå kva miljøfaktorar som avgrensar vekst hjå den viktige pionerarten *A. alpina*, gjorde eg eit veksteksperiment under fire kontrollerte kombinasjonar av temperatur og ljos forhold. Her viste resultata at *A. alpina* veks betre under kaldt og høgt ljos forhold, og at andelen fertile individ vart signifikant redusera med høgare temperatur.

Nøkkelord: Norsk isbre, Hellstugubreen, isbre-forland, smeltande isbrear, planteetablering, frøspiring, overleving- og spreiingsavgrensing

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INTRODUCTION

Today, glaciers are melting and retreating all over the world because of climate change, mainly in terms of higher summer temperatures and less winter precipitation (IPCC 2014; Jomelli et al. 2011; Nesje et al. 2008; Oerlemans 2005). The global decreasing trend of glaciers began after the maximum of the "Little Ice Age" (LIA), early 17th century to late 19th century, and the rate of this decrease has accelerated rapidly (Jomelli et al. 2011; Nesje et al. 2008; Watson et al. 1997). For example, since 1850 AD, more than 30-40 % of the glaciers in the European Alps have disappeared (Primack 2012), and during the last 30 years (yr) the total area of Norwegian glaciers have decreased by 11 % (Andreassen et al. 2011). Since 2000 AD, the situation has become even worse for the Norwegian glaciers as some, mainly in eastern Norway, have retreated more than 100 m over a period of less than a decade (Andreassen et al. 2011; Nesje et al. 2008). Yet, there are regional variations as West Norwegian glaciers actually increased in the early 2000's, but today, all the Norwegian glaciers have a general declining trend (see Appendix I). However, the world's climate has varied greatly through time (Hanssen-Bauer et al. 2015), and during the last 2,6 million yr there have been more than 20 ice ages, with approximately 15-20 000 yr intervals (Ramberg et al. 2013). Climate has also varied significantly on a shorter Holocene time scales e.g. from about 8000 to 4000 yr ago, all Norwegian glaciers were at least once completely melted away (Hanssen-Bauer et al. 2015; Nesje et al. 2008).

Retreating glaciers provide excellent opportunities to study and conduct scientific research on primary successions and plant colonization (Matthews 1992). Ellenberg (1988) states; "*nowhere can succession be studied more profitably than in the valley below the front of a large glacier*". Successions involve processes of gradual and directional changes in species composition and the ecosystem structure (Krebs 2008; Matthews 1992). In ecology, receding glaciers serves as a common model to study ecological changes over time (Diemer & Prock 1993; Marcante et al. 2009; Matthews & Whittaker 1987; Matthews 1992; Philippot et al. 2011). The area uncovered after glacier retreat is called glacier foreland (Matthews 1992). Glacier forelands provide an unique type of field laboratory as they comprise the timescale from the maximum expansion of ice at the LIA up to the present and recently deglaciated land, which is also referred to as a glacier chronosequence (Matthews 1992; Philippot et al. 2011). A glacier chronosequence is thus a temporal sequence that contains long term dating of the terrain age, providing a substitution of space-for-time, giving the distance from the glacier as a proxy for the soil age (Matthews 1992).

In Norway, studies on primary succession and vegetation in glacier foreland have a long tradition, see e.g. the pioneer study of Fægri (1933) about plant succession in glacier forelands of Jostedalen, and Elven

(1978a) and (Elven 1978b) who studied forelands at Hardangerjøkulen. Moreover, from studies in Jotunheimen, with emphasis on Storbreen glacier foreland, have Matthews et al. produced more than 200 scientific papers with a geo-ecological approach on primary succession and vegetation (Matthews & Whittaker 1987; Robbins & Matthews 2009; Robbins & Matthews 2010; Robbins & Matthews 2014). Matthews and colleagues have also produced a general textbook about primary succession in glacier forelands (Matthews 1992). Examples on other studies in Jotunheimen, regarding the vegetation of vascular plants and their succession in glacier forelands are: Whittaker (1993) in Storbreen glacier foreland, Haugland (2006), Haugland and Beatty (2005) at Styggedalsbreen, Slettmarkbreen and Vestre Memurubreen, and Berg (2014) and Dalen (2014) with a population approach in Hellstugubreen glacier foreland.

Rapid glacier retreats leaves behind large areas of ice-free barren ground in which the process of plant colonization can start (Hagvar & Ohlson 2013; Marcante et al. 2014). However, plant colonization in glacier forelands is a slow and relatively fragmented process (Marcante et al. 2009; Marcante et al. 2012). Recently deglaciated terrain represents an extreme environment with harsh conditions, the soil does not contain any organic matter, there are relatively low resource levels and generally low plant abundance (Matthews 1992; Stöcklin & Bäumler 1996; Whittaker 1993). Abiotic factors like short growth season, time of melting, freezing temperatures, cold wind, heat and drought during the growth season are some reasons for limited colonization in glacier forelands, especially in recently deglaciated areas (Jones & del Moral 2009; Körner 2003; Marcante et al. 2014; Sandvik et al. 1999). However, the limited colonization is also dependent on biotic factors such as the distance to donor populations and species propagules, dispersal, growth and survival rate in glacier forelands, as well as predation risk (Erschbamer & Mayer 2011; Jones & del Moral 2009; Körner 2003).

According to Chapin et al. (1994) and Erschbamer and Mayer (2011), primary succession and vegetation in glacier foreland can be explained by species life histories. The first arrivals of plants after glacier retreats are called pioneer species (Matthews 1992; Robbins & Matthews 2009). Pioneer species and early colonization species are often fast growing and known for their high dispersal capability and rapid germination rate (Chapin et al. 1994; Whittaker 1993). Pioneer species are often described as r-strategists with early reproduction, producing a lot of small seeds and low mature height (Bohn et al. 2014; Chapin et al. 1994; Erschbamer & Mayer 2011; Stöcklin & Bäumler 1996). Pioneer species appear sporadic at early stages of primary succession, and increases relatively quickly after establishment (Matthews & Vater 2015; Whittaker 1993). However, over time the abundance of pioneer species decline, and the vegetation will be gradually replaced by late successional species (Matthews & Whittaker 1987; Matthews & Vater 2015; Whittaker 1993). Glacier forelands are characterized by gradual changes in disturbance regimes (Matthews & Vater 2015), content of soil organic matter, nutrient availability, pH and temperature along the chronosequence (Haugland 2006; Stöcklin & Bäumler 1996). In addition, the interspecific competitions for water, nutrient, space and light increases with terrain age and distance from the glacier (Matthews & Vater 2015), as well as the presence or absence of microorganisms (Oehl et al. 2011). Still, the environmental factors like altitude (Robbins & Matthews 2010), micro-topography (Matthews & Whittaker 1987) and locally environmental factors are equally important, if not more relevant in species composition in glacier forelands (Rydgren et al. 2014).

In the light of this background, my objectives in this master thesis was to study selected aspects of plant establishment and survival across a chronosequence in the glacier foreland of Hellstugubreen, Jotunheimen, with eight pioneer plant species i.e.; *Saxifraga stellaris* (nomenclature for plant names follows Lid & Lid 2007), *Poa alpina*, *Poa arctica*, *Oxyria digyna, Arabis alpina, Cerastium cerastoides*, *Arabis petraea* and *Beckwithia glacialis*. A typical feature of the Hellstugubreen foreland is the occurrence of a very distinct 50 m unpopulated area in the front of the glacier (Berg 2014; Dalen 2014). This recently deglaciated area represents 4-6 years exposed soil (Appendix II). My research question is to try to find out why there are no established pioneer plants in this unpopulated area. To address this, I have these questions and hypotheses dealing with three main themes:

I. **Germination limitation:** Firstly, is the lack of pioneer species due to seed germination problems, even if seeds manage to spread into the unpopulated area? To test this hypothesis, I conducted a seed sowing experiment, and I hypothesized that there would be no or few germinated seeds inside the unpopulated area as compared to the situation in a vegetated control area further away from the glacier front.

II. **Survival limitations:** Secondly, is the lack of pioneer species inside the unpopulated area due to the plants problems of survival through the growth season, even after successful germination? To test this hypothesis, I conducted a plant transplantation experiment. I hypothesized that the plants inside the unpopulated area would have less vitality and less survival as compared to the control area.

III. **Dispersal limitation:** Thirdly, is the lack of pioneer species inside the unpopulated area due to dispersal limitation, meaning that no or few seeds manage to spread into this area? To test this hypothesis, I conducted a seed bank study, and I hypothesized that the seed bank inside the unpopulated area would be absent or significantly smaller than in the vegetated areas located at longer distances from the glacier front.

Finally, to better understand the ecology of *A. alpina*, which is an important pioneer species in glacier forelands (Matthews & Vater 2015), I conducted a growth experiment under controlled environmental conditions to examine its performance under four different temperature and light conditions. Here, I expected that *A. alpina* would grow better under cold and high light conditions, and that high temperature would decrease its vitality.

MATERIALS AND METHODS

STUDY AREA – HELLSTUGUBREEN GLACIER FORELAND

Hellstugubreen also known as Hellstugubrean on official maps (61^{o}34’ N and 8^{o}26’ E) is a north-facing u-shaped valley glacier situated in the mountain range of Jotunheimen, southern Norway (Andreassen et al. 2011; NVE 2009) (Fig. 1). Jotunheimen, named by O. A. Vinje, derives from Nordic mythology, meaning the home of giants (Steigan & Rønning 1997). Jotunheimen became a National Park in 1980 with 1151 km^2 of protected area, including the highest mountain in Norway, Galdhøpiggen, 2469 m.a.s.l. (Miljø-Direktoratet 2015). In Jotunheimen National Park, the main land use are outdoor recreation activities as well as agriculture with grazing by domesticated animals, e.g. reindeer, there is also good possibility for teaching and research in Jotunheimen (Miljø-Direktoratet 2015).

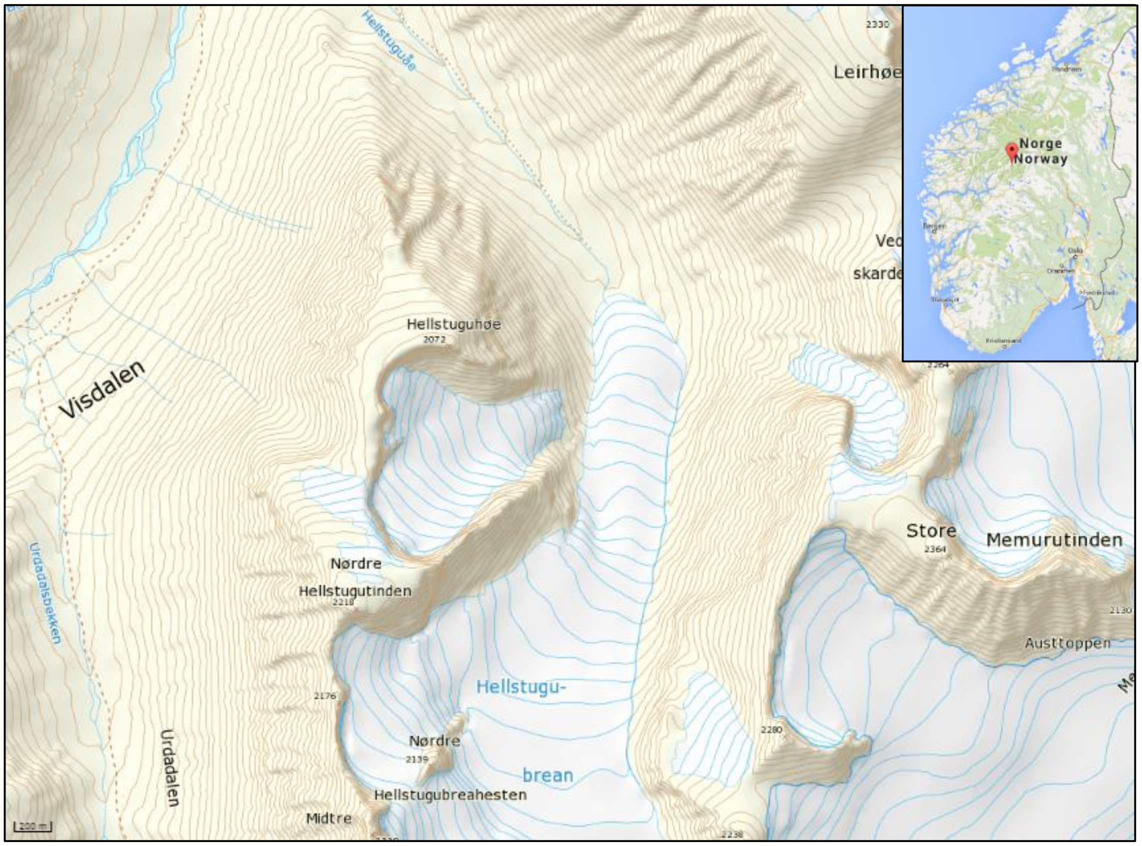

Figure 1. Map over Hellstugubreen glacier foreland and location of Jotunheimen in Central Norway (red dot in insert picture). Map from kartverket.no

In Jotunheimen there are about 300 glaciers, accounting for about 10 % of the Norwegian glaciers, and they have all decreased significantly in the last decade (Miljø-Direktoratet 2015). Hellstugubreen glacier is the third largest glacier in Jotunheimen, and shares a border with Vestre Memurubreen (Andreassen et al. 2011; Miljø-Direktoratet 2015). Hellstugubreen glacier has an area of 2,9 km^2 and lies between 1482 to 2229 m.a.s.l., with half of the glacier above 1800 m.a.s.l. (Andreassen et al. 2011; NVE 2009). The Hellstugubreen glacier reached maximum around 1740-1750 AD (Hoel & Werenskiold 1962).

Hellstugubreen glacier has long-term data of the glacier retreat (NVE 2009). The glacier front measurements at Hellstugubreen began in 1901 by Quaternary Geolog P. A. Øyen from the Geological Museum of UiO (Hoel & Werenskiold 1962). From 1927 to 1946 most of the observation of glaciers in Jotunheimen were carried out by civil engineer A. Koller and professor W. Werenskiold (Hoel & Werenskiold 1962). The annual mass balance measurement at Hellstugubreen began in 1962 by glaciologist O. Liestøl from the Norwegian Polar Research Institute and the Norwegian Water Resource and Energy Directorate (NVE) (NVE 2009; Oerlemans 1992). NVE has published a huge data set in the report series titled "Glaciological investigations in Norway" with yearly front changes, mass balances and glacier velocities since 1963 (Appendix I), giving a well-documented time- and space-sequence of the frontal change. The data from 1962 to 2015 varied greatly from year to year, but has a clear general decreasing trend (Andreassen et al. 2011) (Appendix II and III). The fastest frontal retreat was between 1940 and 1980 (NVE 2009) and the total glacier front retreat from the 1750 end moraine is 1 600 m (Fig. 2). From 1901, the glacier front has retreated 1138 m (Fig. 2 and see Appendix II).

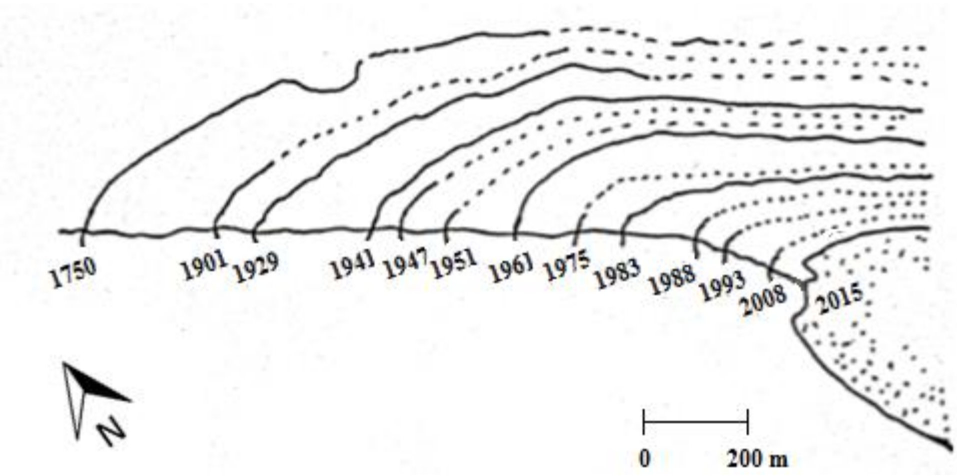

Figure 2. Hellstugubreen glacier foreland, with dated glacier positions from 1750-2015. Based on and developed from Hestmark et al. (2005).

Jotunheimen was created in the Caledonian orogeny (500-405 MA) when Baltica (now Europe and Russia) and Laurentia (now North America and Greenland) collided (Ramberg et al. 2013). Jotunheimen, including Hellstugubreen glacier foreland, is a part of the complex Jotun- and Valdres-Nappe, and the bedrock in Hellstugubreen foreland contains highly metamorphic rocks pyroxene granulite with composition from gabbro to quartzite (NGU 2016; Ramberg et al. 2013; Solli & Nordgulen 2013). The vegetation in the glacier foreland of Hellstugubreen has been surveyed by Robbin & Matthews (2009; 2010), Berg (2014) and Dalen (2014). Hestmark et al. (2004a, 2004b, 2005, 2007) studied the population dynamic of lichens inside the glacier foreland of Hellstugubreen. The area inside the foreland is affected by grazing domestic reindeers (as observed during the fieldwork). Outside the foreland (moraine age older than 10 000 yr), alpine meadow dominate the mature vegetation.

At Hellstugubreen, the climate is relatively dry compared to the western part of Jotunheimen. The closest meteorological station is Juvasshøe weather-station (created in 1999, 1894 m.a.s.l.), 13,8 km from Hellstugubreen. The annual mean normal temperatures from 1961-1990 was -4,5 ^{o}C, with lowest temperatures observed in January (-12,2^{o}C) and highest temperatures in August (4,2^{o}C) (Eklima 2016). Data from 1961 to 2015 show annual precipitation between 1500-2000 mm. A large proportion of the precipitation falls as snow – the first fall occur generally in late August or early September (Fig. 3), and annual normal snow depth is around 150-200 cm (NVE 2016).

Figure 3. The Hellstugubreen glacier foreland in 5-7 August (left) and 4-5 September (right) in 2015.
Photo: Anne-Sofie Bergene Strømme

STUDY SPECIES

General species information in this section is obtained from Nilsson and Elven (1995), Lid and Lid (2007) and Mossberg and Stenberg (2007). Other sources are referred to in the text.

Saxifraga stellaris (Fig. 4 A).

Saxifraga stellaris (Engl.: Starry saxifrage, Norw.: Stjernesildre) is a common perennial alpine plant within the family *Saxifragaceae*, that prefers wet or moist conditions, e.g. snow beds, moss mats, marshes, along mountain streams, brooke sides, creeks, lakes or spring edges. In Norway, *S. stellaris* has a wide distribution within the alpine regions and is observed up to 1970 m.a.s.l. in Jotunheimen. *S. stellaris* is normally between 4-15 cm in height, and has short rhizomes, leaf in 1-20 rosettes and 5-17 light green leaves on short shafts, often toothed obovate shape with some hair. The leaves are wintergreen and adapted to start photosynthesis early in the growing season (Sandvik et al. 1999). *S. stellaris* flowers in July to August, and rametes may remain in vegetative stage one to several yr before flowering (Sandvik 2001). *S. stellaris* has one to several leafless reddish stems, covered with glandular hair with one to several flower on each stem. The flowers resembles a star, with 4-6 mm white and pointed corolla with two yellow or red spots. The anthers are pinkish with orange pollen, and the ovule is normally red, rarely white. *S. stellaris* has a mixed breeding system (both self-pollination and cross-pollination), and produces a large number of seeds with self-pollination, however to reach maximum seed set it needs to be pollinated by insects (Sandvik et al. 1999). *S. stellaris* has no apparent structure for dispersal, and has a maximum dispersal distance of 40 m (Stöcklin & Bäumler 1996).

Poa alpina (Fig. 4 B)

Poa alpina (Engl.: Alpine meadow-grass, Norw.: Fjellrapp) is a common alpine plant within the family *Poaceae*, that requires calcareous soil and wet or moist conditions, e.g. snow bed, mountain ledges and mountain scree. In Norway, *P. alpina* is one of the most common grasses in the alpine areas, and is observed up to 2140 m.a.s.l. in Jotunheimen, but it is also observed in dryer areas in the lowland. *P. alpina* is normally 15-40 cm high, with 1-2 joint nods low down on the stem together with light grey sheets and the leaves are 2-5 cm dark green with 2-3 mm long ligules. *P. alpina* flowers in July to August and the spikelets are 4,5-9 mm reddish or brown-violet with 3-6 flowers dense in the top of the straw. *P. alpina* grows in tussocks, and has two different reproductive strategies, i.e. sexual reproductions producing seeds and asexual reproduction (pseudo-viviparous), producing plantlets of maternal tissue (clones) (Gurevitch et al. 2006; Winkler et al. 2010). In moist alpine areas and pioneer stages the viviparous form of *P. alpina* is more important, and with ongoing succession the occurrence of this form reduces or completely disappears (Winkler et al. 2010). The viviparous reproduction in *P. alpina* is an adaptation to colder conditions, since plantlets have higher frost tolerance as compared to seedlings (Winkler et al. 2010). *P. alpina* has no apparent structure for dispersal, and has a low maximum dispersal distance (<1 m) (Stöcklin & Bäumler 1996).

Poa arctica (Fig. 4 C)

Poa arctica (Engl.: Arctic bluegrass, Norw.: Jervrapp) is a relatively rare various alpine plant within the family *Poaceae*, that prefers calcareous soil in the mountains with dry or moist conditions, e.g. landslip areas and tundra. In Norway, *P. arctica* has mostly a northern distribution, but is also observed in the alpine areas in the middle part of Norway. *P. arctica* is normally 15-35 cm high, the leaves are 1-2,5 mm darkgreen wide with 1,5-3 mm long ligules, and the spikelets are 4,5-9 mm dark violet with 2-4 flowers. *P. arctica* grows in tussocks or mats, and reproduce sexually with seeds or asexually with plantlets.

Oxyria digyna (Fig. 4 D)

Oxyria digyna (Engl.: Mountain sorrel, Norw.: Fjellsyre) is a common perennial alpine plant within the family *Polygonaceae*, that prefers wet or moist conditions, e.g. snow beds, mountain springs or brooklets, but it is also observed in bird mountains. In Norway, *O. digyna* has a wide distribution in alpine areas and is one of the highest flowering plants in Scandinavia, observed up to 2370 m.a.s.l. at Galdhøpiggen, Jotunheimen. *O. digyna* is 5-15 cm high, with a lot of 0,5-3 cm green kidney-shape leaf rosettes with one or several upright reddish thick stems without leaf and hair. *O. digyna* normally flowers in June to August, and has 50-350 small flowers in the top of the stem, hanging with 4 perianth, 6 stamen and 2 stigma. *O. digyna* produces wing shape seeds an adaption to wind dispersal, however it has a low maximum dispersal distance (<1 m) (Stöcklin & Bäumler 1996), and *O. digyna* normally reproduce sexually by seeds, but may also spread vegetative with rhizomes.

Arabis alpina (Fig. 4 E)

Arabis alpina (Engl.: Alpine rock-cress, Norw.: Fjellskrinneblom) is a common perennial alpine plant within the family *Brassicaceae*, predominantly found in moist areas, e.g. snow beds, springs or brooke sides, often in association with calcareous soil (Torang et al. 2015). In Norway, *A. alpina* has a wide distribution in mountains, and is one of the most important pioneer species in young terrain and in glacier forelands (Matthews & Vater 2015), and it is observed at 1980 m.a.s.l. in Vågå, Oppland, but is also observed in the lowland. *A. alpina* is normally 10-30 cm high and has one or few hairy grey-green leaf rosettes, with one stem that has toothed pointed leaves. *A. alpina* flowers in July to August and the flowers are gathered in corymb with 3-4 mm small sepals with four white 6-10 mm long corolla, and *A.*

petraea produces several 20-35 mm long and 1,5-2 mm wide fruits, containing large amount of seeds. According to Torang et al. (2015) *A. alpina* has a mixed breeding system and can also reproduce through stoloniferous growth (runners). *A .alpina* can grow in tufts, colonies or alone, and has a low maximum dispersal distance (<1 m) (Stöcklin & Bäumler 1996).

Cerastium cerastoides (Fig. 4 F)

Cerastium cerastoides (Engl.: Starwort Mouse-ear, Norw.: Brearve) is a common perennial alpine plant within the family *Caryophyllacea*, that prefers wet conditions, e.g. snow beds, wet gravel, spring edges or brooklets. In Norway, *C. cerastoides* has a wide distribution in alpine areas, and is observed at 2040 m.a.s.l. in Lom, Oppland. *C. cerastoides* is normally 5-20 cm high with short horizontal creeping reddish stems, with 7-15 mm light green leaves without hair and often 2-4 flowers on each branch with green support leaves. The flowers have 6-10 mm long half cleaved white corolla with three styles, and 4-6 mm green sepals with some glandular hair. *C. cerastoides* normally flowers in July to August and produces several 7-10 mm capsules with six teeth, containing large amount of seeds. *C. cerastoides* has a mixed breeding system (Totland & Schulte-Herbruggen 2003), and it can live in colonies or grow solitary and can sometimes forms mats. *C. cerastoides* has no apparent structure for dispersal and has a low maximum dispersal distance (<1 m) (Stöcklin & Bäumler 1996).

Arabis petraea (Fig. 4 G)

Arabis petraea (Engl.: Northern Rock-cress, Norw.: Aurskrinneblom) is a rare perennial alpine plant within the family *Brassicaceae*, found in landslip areas often with magnesium rich rocks. In Norway, *A. petraea* is observed at 1730 m.a.s.l. in Lom, Jotunheimen. *A. petraea* is normally 5-20 cm high without hair, the stem is dark violet upright or crawling with short rhizomes, and the leaf rosettes are toothed with end cleft, and the stem leaves are dark green slim and blunt. *A. petraea* flowers in June to August and the flowers have 3-7 mm corolla normally white, rarely light red-violet, and it produces few 15-45 mm long and 1,2-1,5 mm wide fruits.

Beckwithia glacialis (Fig. 4 H)

Beckwithia glacialis (earlier *Ranuculus glacialis*) (Engl.: Glacier buttercup, Norw.: Issoleie) is a common perennial plants within the family *Ranunculaceae*, that is listed as NT (near threatened) on the Norwegian Red List (Artsdatabanken 2016). *B. glacialis* prefers moist conditions with wet gravel found in e. g. snow beds, screes or steam edges and is relatively abundant in unstable habitats (Schonswetter et al. 2003). *B. glacialis* is one of the highest flowering plants in Scandinavia, and is observed at 2370 m.a.s.l. in Lom, Oppland. *B. glacialis* is 5-25 cm high with one or several relatively thick violate upright blank stems with ligule around the leaf base and with 1,2-6 cm wide blank dark green three-clefted lamina. *B. glacialis* needs normally 1-3 seasons before flowering and flowering occur often 2-3 weeks after snowmelt in July to August (Sandvik et al. 1999). One ramete produces 4-6 leaves and one to few 1,8-3,8 cm wide flowers (Totland & Alatalo 2002). The sepal is red brown and relatively furry, and the corolla is first white at the start of the growing season and it turn dark purple after pollination. *B. glacialis* has large reproductive capacity, and flowering individuals are able to produce an average of about 500 seeds (Jarvinen 1984), and the seeds are normally 2-3 mm hairless and with a bent beak. *B. glacialis* reproduces sexually and the estimated expected mean life for an established individual is 27 yr (Jarvinen 1989).

Figure 4. The pioneer species *Saxifraga stellaris* (A), *Poa alpina* (B), *Poa arctica* (C), *Oxyria digyna* (D), *Arabis alpina* (E), *Cerastium cerastoides* (F), *Arabis petraea* (G) and *Beckwithia glacialis* (H) in the Hellstugubreen glacier foreland. Photo: Anne-Sofie B. Strømme, 2015, except (B) Geir Hestmark, 2012.

DATA COLLECTION

Germination field experiment

In July 2014, I harvested seeds from seven pioneer species, i.e. *S. stellaris, P. alpina*, *O. digyna*, *A. arabis, C. cerastoides*, *A. petraea* and *B. glacialis,* from the glacier foreland of Hellstugubreen. In September 2014, I placed the harvested seeds of *S. stellaris, P. alpina*, *O. digyna*, *A. arabis* and *C. cerastoides* in 10 plots randomly selected in each of the two study positions in the glacier foreland. Position 1 (barren ground) was 10-15 m from the glacier, moraine age 0-3 yr, and position 2 (existing vegetation) was 1100 m from glacier, moraine age 106-109 yr. The seeds of *B. glacialis* and *A. petraea* were not included, since I only collected the seeds of *A. petraea* to see the difference between *A. alpina* and *A. petraea*, and the seeds of *B. glacialis* were not mature. Each plot was 60 cm x 60 cm and contained five blocks of 20 cm x 20 cm, with 50 seeds for each species (Fig. 5; also see Fig. 7 that shows the positions and number of seed sowing plots in the foreland). I placed in total 5000 seeds into the glacier foreland. The distance from plot to plot ranged from 0,5-5 m. The percent germinated seeds in each plot were measured during the growth season 2015. Hence, the extremely short growing season in 2015, only two measurements were possible because of snow covering the plots closest to the glacier. The first possible measurements were conducted 21-22 August and the second 4-5 September. The growth substrate were divided into 2 categories; fine substrate (1) and rough substrate (2).

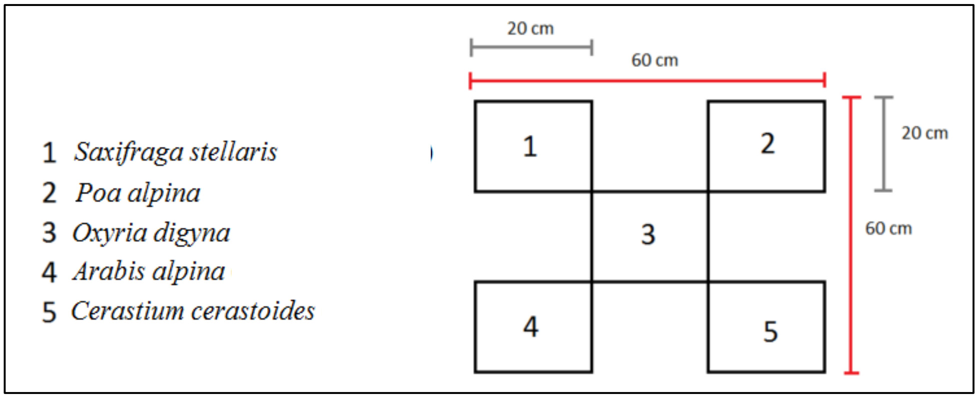

Figure 5. The field setup in the germination experiment in Hellstugubreen glacier foreland. Twenty plots (60 cm x 60 cm) each containing five blocks (20 cm x 20 cm) with *Saxifraga stellaris, Poa alpina*, *Oxyria digyna*, *Arabis alpina* and *Cerastium cerastoides.*

Germination lab experiment

The rest of the harvested seeds from Hellstugubreen glacier foreland July 2014, were stored cold and dark in paper bags (about 5 ^{o}C) after harvesting. I placed the seeds 48 days in a garden during the winter 2014, and afterwards I placed the seeds 27 days in a freezer (-20 ^{o}C) to give them natural stratification before the lab experiment started. The experiment was conducted in a greenhouse in SKP, The Center for Plant Research in Controlled Climate at NMBU. The conditions in the greenhouse were 20 ^{o}C in 16 hours daytime and 12 ^{o}C in 8 hours night-time, with armature Gavita gan 4-550 AL 230 V superego, and lamps Osram powerstar HQI-Bi 400 W/D daylight E40 300 W per m^{2}. The greenhouse conditions had 70% relative humidity (RH) and an automatic irrigation system. Seeds from each species were placed 20 days in 14 pots with 10 seeds in each pot, with commercially produced organic garden soil (Tjerbo Gardner Soil, 900 mg/L N, 35 mg/L P and 190 mg/L K, pH 5,5-6,5). After germination onset I sprayed the seedlings with commercial nutrition, Plantagen liquid plant food 1,16 kg, 7.0 % N, 1.3% P, 5.0 % K, pH 4-8. The measurement for *A. alpina* ended after 13 days, since the seedling at that time needed to be transplanted into pots with only 2-3 seedlings. Additionally, 50 seeds of *S. stellaris* and *O. digyna* were placed in 5 pots in 15 days with machine sand (0-8 mm, from Franzefoss crunchers in Vinterbro, Akershus) and covered by plastic foil to ensuring moist conditions. The timing of germination and percent germinated seeds were closely measured throughout the experiments. To determine metabolic activity in those species that did not germinate, the seeds of *S. stellaris* and *O. digyna*, together with *Avena sativa* (Norw.: Havre) as comparison, were tested with colourless *2, 3, 5 – Triphenyl – 2 H – tetrazodium chloride*, *98 %* in a 0,5% solution. Dehydrogenase activity changes the colourless tetrazodium chloride to red colour triphenyl formazane as an indication for vital cells.

Transplantation field experiment

In July 2015, I sampled 50 plants from each of the seven pioneer species, i.e. *S. stellaris, P. arctica, O. digyna, A. arabis, C. cerastoides, A. petraea* and *B. glacialis* from the glacier foreland and transplanted them into two positions in the glacier foreland of Hellstugubreen. Position 1 (barren ground) was 10-15 m from the glacier, moraine age 0-3 yr, and position 2 (existing vegetation) was 860 m from glacier, moraine age 72-73 yr. There were in total 50 plots, each plot containing seven plant species (Fig. 6; also see Fig. 7 that shows the positions and number of transplantation plots in the foreland). The plants were sampled with roots and soil, using a small garden shovel, and then transported in plastic trays and watered after they were transplantated in the soil. I measured the height (cm), width (cm), number of leaves and number of flowers for each plant, except number of leaves in *P. arctica* and *C. cerastoides* due to time-consuming efforts. The plants state, alive or dead/senescent were also included in the recordings. Hence, the short growing season in 2015, the recordings were only conducted four times during the growth season, with approximately 14 days between the measurements (18-21 July; 5-7 August; 21-22 August; and 4-5 September). At the last recording, I harvested fruits from five *A. alpina* plants in each position, since *A. alpina* was the only species that had mature seeds/fruits in both positions. The number of seeds and fruits in *A. alpina* were counted in lab. Photographs were taken at each recording to later compare the plants at the beginning and at the end of the experiment in the two positions (see Fig. 12 for selected plants throughout the study in the positions).

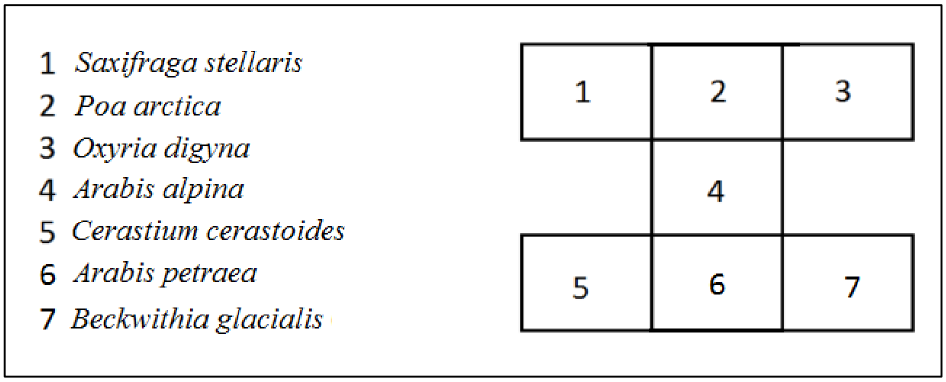

Figure 6. The field setup in the transplantation experiment. Fifty plots contained seven blocks for each of the species, *Saxifraga stellaris, Poa arctica, Oxyria digyna, Arabis alpina, Cerastium cerastoides, Arabis petraea* and *Beckwithia glacialis.*

Soil seed bank experiment

I sampled 60 soil seed bank samples with an aluminium cylinder (5 cm x 10 cm, approximately 190 cm^3) at the end of summer 2015 (4-5 September) from the glacier foreland of Hellstugubreen, see Fig. 7 and Table 2 for sampling design and positions from which the samples were collected. Vegetation cover; low (< 20 %), intermediate (20-60 %) and high (> 60 %), and species identification (according to Mossberg & Stenberg 2007) was done at each sample (25 cm x 25 cm, with the sample in the middle). Immediately after collection, I placed the soil seed-bank samples in a cooling refrigerator bag, and afterwards in a dark cooling room (4-5 ^{o}C) for 74 days. The seed bank experiment was conducted in a greenhouse at SKP at NMBU. The conditions in the greenhouse was 20 ^{o}C in 16 hours daytime and 12 ^{o}C in 8 hours night-time, with armature Gavita gan 4-550 AL 230 V superego, 70% relative humidity (RH), automatic irrigation system, and sticky paper to remove unwanted insects. The samples were placed in aluminium boxes (20 cm x 15 cm) with drainage holes and kept moist (watering every other day). After 14 days, I gently stirred and covered the samples with plastic foil to ensure moist conditions. The timing of germination and number of seedlings were measured during 47 days, and afterwards the seedlings were transplanted one by one in commercial produced and full-ferilized sowing soil.

Soil analysis

I collected 15 soil samples with an aluminium stir (5 cm x 10 cm, approximately 190 cm^3) at the end of the summer season 2015 (4-5 September) from the glacier foreland of Hellstugubreen (Fig. 7). I collected 5 soil samples at position 1, inside the unpopulated area closest to the glacier (0- 50 meters from the glacier front, moraine age 0-3 yr), 5 soil samples at the intermediate position, where the pioneer vegetation seemed to reach maximum (250 meters from the glacier front, moraine age 29-32 yr), and 5 soil samples at position 2 (860 meters from the glacier front, moraine age 72-73 yr) (Fig. 7). Immediately after collection, I placed the soil samples in a cooling refrigerator bag, and afterwards in a dark cooling room (4-5 °C).

In the pH analysis, I mixed 15 beakers with 10 mL sieved soil (2 mm) and 20 mL deionisert (filtrated) water for 20-30 minutes. The pH in the beakers were measured at 20°C with a Laboratory pH meter, IonLab pH720 with electrode SenTix 81 pH 0..14/0..100°C/3mol/KLC, that were calibrated with a calibration buffer pH 4,00 at 20°C. The electrode was washed with deionisert water between the measurements. For the loss of ignition (LOI), I sieved 15 soil samples through 2 mm sieve and placed them in porcelain crucible and dried them in a drying cabin (Termaks type 230V 50Hz 1430W), at 105°C in 16 hours. The samples were cooled in an executor (Silica gel) for two hours. Then I weighed the samples with a Sartorius ED224S before and after the samples were placed in an incineration, Nabertherm Controller B170, at 550 °C in 4 hours.

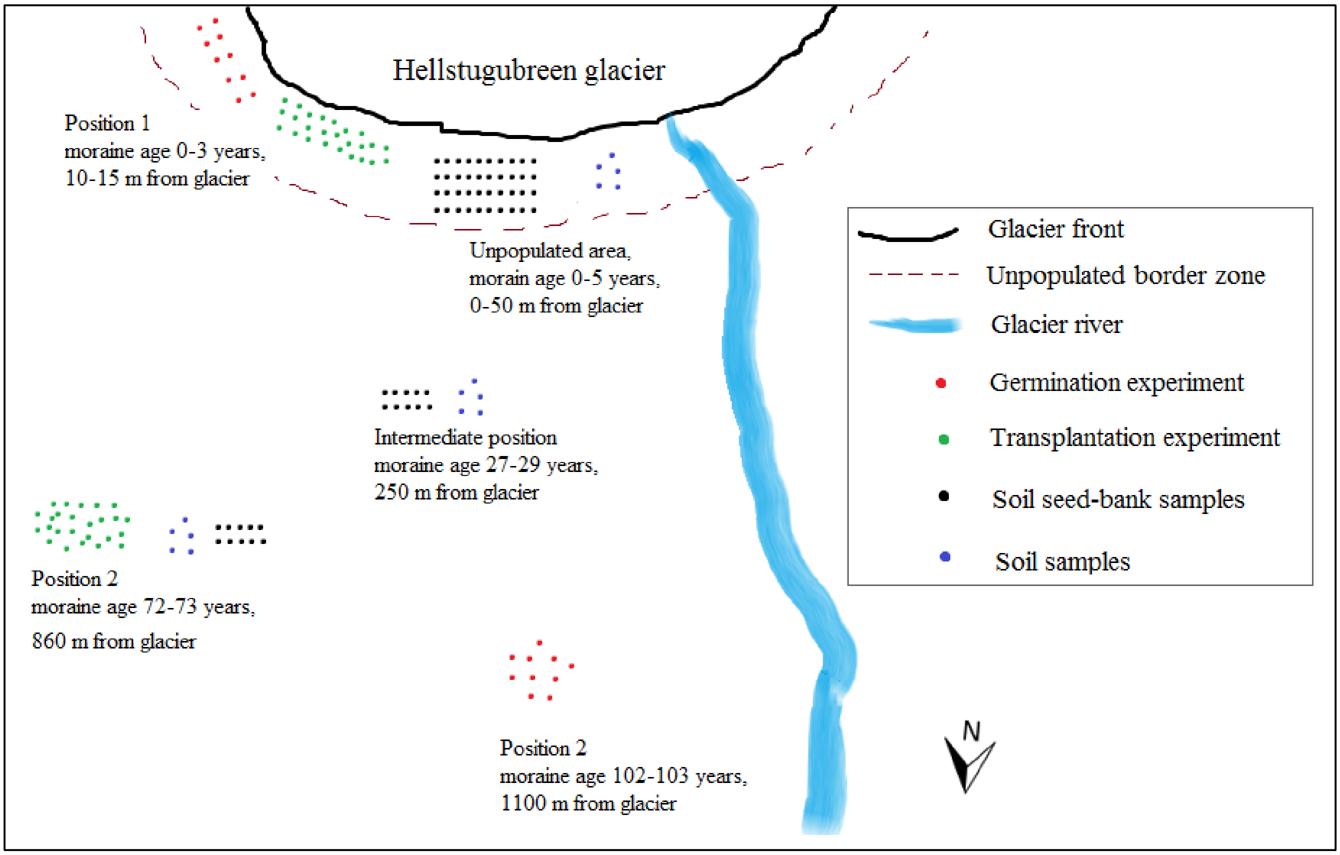

Figure 7. Overview over the experiments and sample sites done in Hellstugubreen glacier foreland summer 2014 and 2015. The different color show the different experiments and samples; red dots are germination experiment (summer 2014-2015), green dots are transplantation experiment (summer 2015), black dots are soil seed-bank samples (autumn 2015) and blue dots are soil samples (autumn 2015). The number of dots indicates number of plots or samples at each location.

Growth experiment with *A. alpina*

I used 107 plants of *A. alpina* from the germination lab experiment and transplanted them one by one in pots with a 50/50 mixture of machine sand (0-8 mm) and commercial organic garden soil from Tjerbo, and placed them in two growth-chambers. One of the growth-chamber had 22 ^{o}C in 18 hours daytime and 15 ^{o}C in 6 hours night time, and the other chamber had 18 ^{o}C in 18 hours daytime and 9 ^{o}C in 6 hours night time (Fig. 8). The growth chambers had equal armature (Gavita gan 4-550 AL 230 V superagro) and white light (Philips, master HPI-T Plus 400 W/230 V) with 65 % relative humidity (RH) and automatic irrigation system and each chamber had sticky papers to remove unwanted insects. In addition the plants were watered every other day with commercial nutrition, Plantagen liquid plant food 1,16 kg, 7.0 % N, 1.3% P, 5.0 % K and pH between 4-8. Around half of the plants in each chamber were placed under a shade cloth, with about 75 % light reduction, giving four different treatments (Fig. 8). The average irradiance (PPF, photons m^{-2} s^{-1}) were measured with a photometer sensor at two fixed positions immediately over the plants in each treatment (Fig. 8).

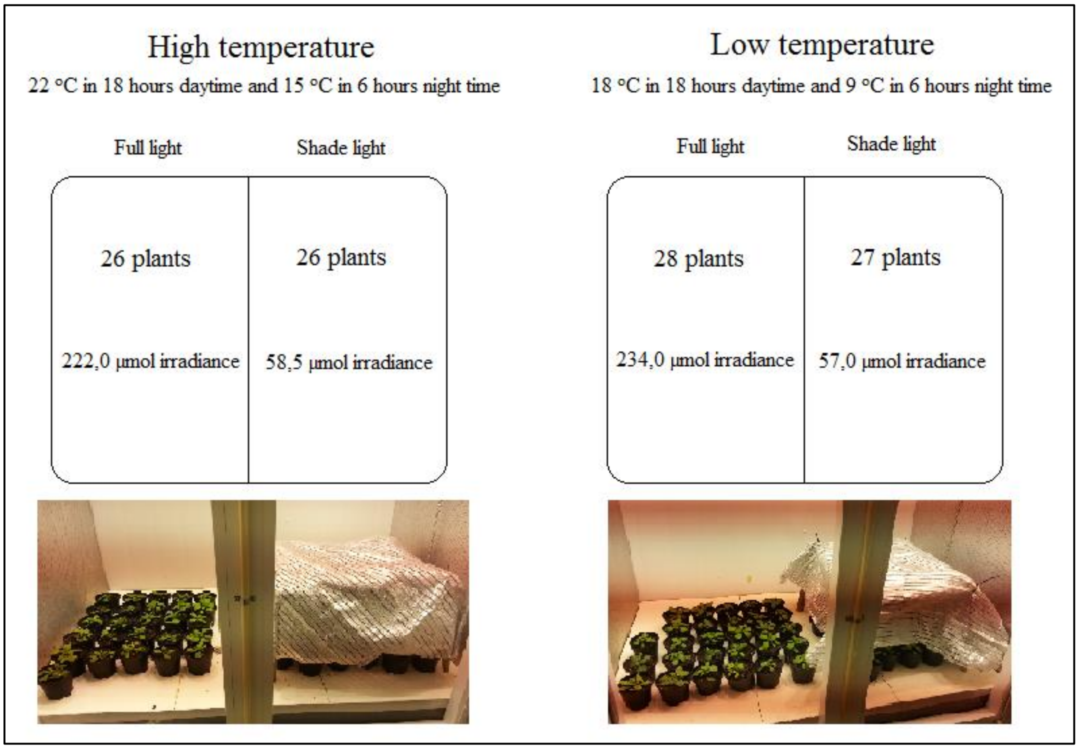

Figure 8. Overview over the experimental setup in the two growth chambers with the four treatments in the total growth experiment, with temperature, hours, type of light, number of plants and µmol irradiance in each treatment. Treatment 1 (high temperature and high light), Treatment 2 (high temperature and low light), Treatment 3 (low temperature and high light) and Treatment 4 (low temperature and low light).

The flowering onset and proportion flowering plants in *A. alpina* were closely measured, and the experiment was completed after 47 days. At the end of the experiment the total leaf area (cm^2) were measured using a LiCor 3100 area meter, and the total amount of leaves, stems, reproductive mass (flowers and fruits) for the surviving plants were placed in paper bags and dried in a Termak TS8136 drying cabin for 4 days. Due to the consuming effort and difficulties of washing away the soil without damaging the root, the roots of only five representative plants in each treatment were included in the experiment. The total dried mass of leaves, stems, reproductive mass and roots for each plant were measured using a Sartorius ED224S weight. In addition, total vegetative weight, above ground biomass (AGB) and leaf density (leaf weight/leaf area) were calculated in Microsoft Excel 2010. Reproductive effort$_1$ (reproductive weight/ total vegetative weight (%) - from now on referred to as RE$_1$) and reproductive effort$_2$ (reproductive weight/leaf area (mg cm^{-2}) - from now on referred to as RE$_2$) were only calculated for fertile plants.

STATISTICAL ANALYSIS

All statistical analysis were made in RStudio and R Commander (R version 3.2.3), and the response variables were subjected to regression analysis, t-test or analysis of variance (ANOVAs), and the latter were followed by Tukey post hoc tests to check for difference among means. All figures were made in Microsoft Excel 2010.

The germination in field was tested with a multi-way ANOVA, type II test, there time of recordings, species and substrate were used as factors and the germination percent as response variable. The germination in lab were tested with regression analysis and multi-way ANOVA, type II test, there time and species were used as factors and the germination percent as response variable. Post hoc Tuckey test was used to test differences among species. The transplantation in field was tested with multi-way ANOVA there time of recordings, positions (chronosequence) and species were used as factors and development of height, width, number of leaf and flowers as response variables. At the end of the transplantation, seeds and fruits of *A. alpina* were tested with a Welch two sample *t-test,* there positions (chronosequence) were used as factors and the number of fruits per plant, seeds per fruit and total number fruits per plant were used as response variables. In addition, the flowering onset and total growth analysis in *A. alpina* in lab, were tested with multi-way ANOVA, there treatment and time were used as factors and the percent flowering onset, leaf area, leaf-, stem-, reproductive-, and root-mass, total vegetative weight, above ground biomass, leaf density, reproductive effort (RE_1 and RE_2) as response variables. Soil analysis from the glacier foreland was tested with one-way ANOVA, there the pH-values and percent LOI were used as response variables and positions (chronosequence) as factors.

Examination of variable distributions revealed strong positive skewness among the majority of the variables and log-transformations were used to achieve an approximation to normality for these variables. As transformations could not entirely correct the non-normal distributions, I have also analyzed the data with non-parametric statistical methods, i.e. Mann-Whitney U-tests and Kruskal-Wallis one-way analysis of variance (data not shown). However, none of these analyses gave results that contradicted those from the parametric tests. Thus, I have used the results from the parametric tests for simplicity.

RESULTS

GERMINATION LIMITATION

Germination field experiment

All of the study species, i.e. *S. stellaris, P. alpina, O, digyna, A. alpina* and *C. cerastoides* had seeds that germinated in the position nearest to the glacier (Table 1), while none of the study species had seeds that germinated in the position furthest away from the glacier (1100 m from the glacier front, moraine age 102-103 yr). There was a significant response among type of substrates, species and time of recordings in the position closest to the glacier (multi-way ANOVA, type II test: $F = 6{,}37$: $p < 0{,}001$). At the first recording the only germination appeared in substrate 1, where *O. digyna* had highest germination, and *S. stellaris* and *P. alpina* did not germinate at all (Table 1). At the second recording, germination was observed in both substrates, but it were clearly higher in substrate 1 (Table 1). *O. digyna* was the only species that decreased the number of established seedlings at the second recording, and it decreased by 50 % (Table 1). *S. stellaris* showed no significantly establishment in any of the substrates, not even at the last recording (Table 1).

Table 1. Average percent germination ± SE (A), and percent established seedlings ± SE (B) in the pioneer species *Saxifraga stellaris, Poa alpina, Oxyria digyna, Arabis alpina* and *Cerastium cerastoides* in position 1 (moraine age 0-3 yr, 10-15 m from the glacier) in the glacier foreland of Hellstugubreen, in substrate 1 (fine substrate) and 2 (rough substrate). First recording 21-22 August 2015, second recording 4-5 September 2015.

	Species	**Substrate 1**	**Substrate 2**
(A) First recording	*S. stellaris*	0 ± 0	0 ± 0
	P. alpina	0 ± 0	0 ± 0
	O. digyna	36,00 ± 3,06	0 ± 0
	A .alpina	5,33 ± 3,53	0 ± 0
	C. cerastoides	8,67 ± 4,37	0 ± 0
(B) Second recording	*S. stellaris*	0,67 ± 0,67	0 ± 0
	P. alpina	21,33 ± 10,73	1,14 ± 0,40
	O. digyna	18,00 ± 8,33	6,86 ± 4,42
	A. alpina	14,67 ± 9,33	12,86 ± 2,96
	C. cerastoides	11,33 ± 6,57	10,29 ± 4,10

Germination lab experiment

Seeds of *P. alpina, A. alpina, C. cerastoides* and *A. petraea* were the only study species that germinated in lab, and *A. alpina* had the significantly fastest and highest germination percent (Fig. 9). Here, it should also be mentioned that seeds of *A. alpina* germinated while stored under dark and cold conditions. The slowest germination onset and lowest germination percent appeared in *P. alpina,* however, there were no significant difference between *P. alpina* and *C. cerastoides* (Fig. 9). The seeds of *S. stellaris*, *O. digyna* and *B. glacialis* did not germinate at all, not even in the additionally experiment. The seeds of *O. digyna* and *S. stellaris* did not show any metabolic activity when tested with 0,5 solution of tetrazodium chloride since the seeds did not change colour to red.

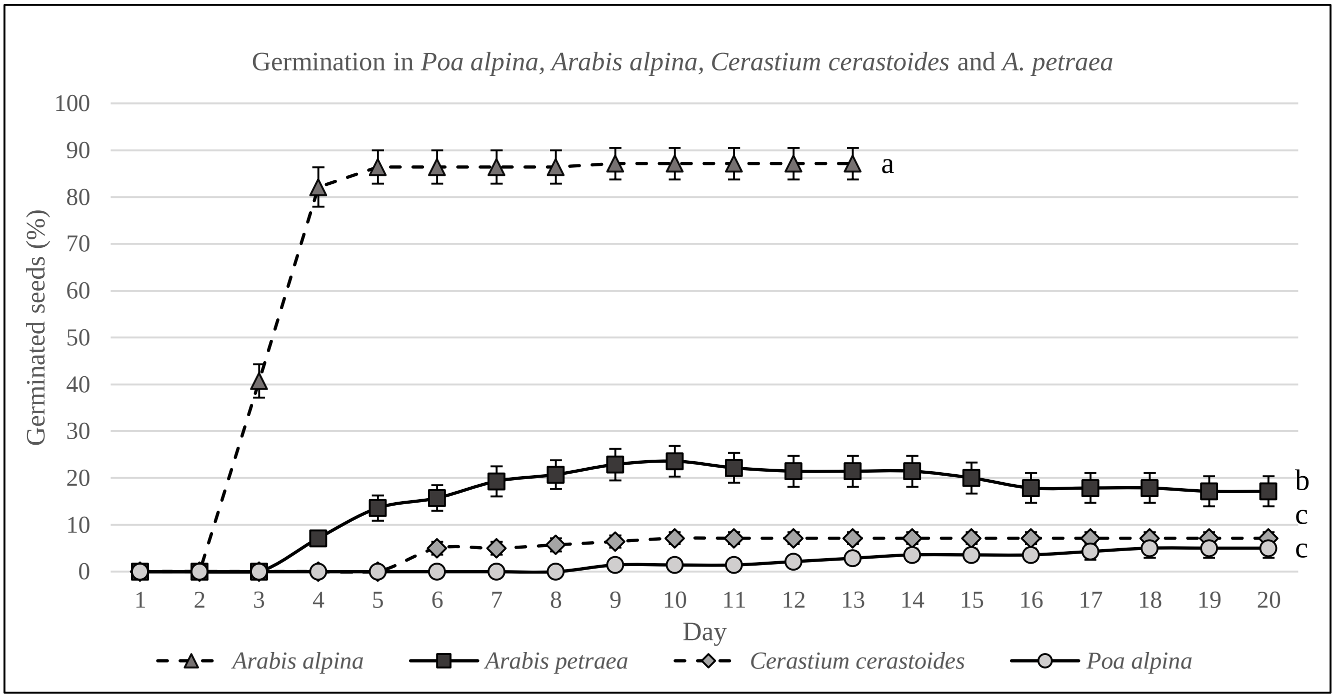

Figure 9. Germination percent in seeds from pioneer species *Poa alpina, Arabis alpina, Cerastium cerastoides* and *Arabis petraea* with SE during 20 days (except *A. alpina* which ended after 13 days). Different letters indicates significant difference among species (ANOVA, *F* = 175,2 ; *P* < 0,001).

Transplantation field experiment

All the study species, except *O. digyna* and *P. arctica*, showed clearly higher mortality in the position furthest away from the glacier (Fig. 10 and 11) and *S. stellaris* had the highest mortality, 72 % (Fig. 10). *P. arctica* survived in both positions, and *O. digyna* had none mortality in the position nearest to the glacier, and low mortality in the position furthest away from the glacier (Fig. 11). At the last recording new leaves were observed in *O. digyna* in both positions, and accordingly, some of the plants had recovered from a senescent state (semi-dead state) to vital state (Fig. 10 and see Fig. 12). There were significant interactions for all the measured traits (development of height, width, number of flowers and leaves) among study species, time of recordings and positions during the growth season 2015 (Appendix IV). All species, except *O. digyna* and *P. arctica*, performed significantly weaker in the position furthest away from the glacier as compared to the position nearest the glacier, in which the performance was generally stable throughout the study (Fig. 10, 11 and see Fig. 12 for selected plants throughout the study in the positions). In *P. arctica* the height were significant higher in the position furthest away from the glacier, but the width and number of flowers did not show any significantly difference between the positions (Fig. 11). In *O. digyna* there were no significantly difference between the positions and most of the traits decreased in both positions, however, the width and number of leaves increased from the third to the last recording in the position furthest away from the glacier (Fig. 10 and Fig. 12)

However, there were some clear species-specific patters, i.e., *S. stellaris* had most flowers in the position furthest away from the glacier at the second recording, but it declined at the third and last recording, and at the last recording the position closest to the glacier had eventually highest number of flowers (Fig. 10). The height of *A. alpina* increased in both positions at the second recording, but at the third and last recording, it declined in the position furthest away from the glacier, while it continued to increase nearest to the glacier (Fig. 10). In *A. petraea*, the number of flowers and leaves declined at the third and last recording in both positions, but only the number of leaves were significantly lower in the position furthest away from the glacier (Fig. 10). Additionally, at the position furthest away from the glacier, the number of flowers in *C. cerastoides* were significantly higher at the second recording, for then to decline at the last recording to lower levels than in the position closest to the glacier (Fig. 11).

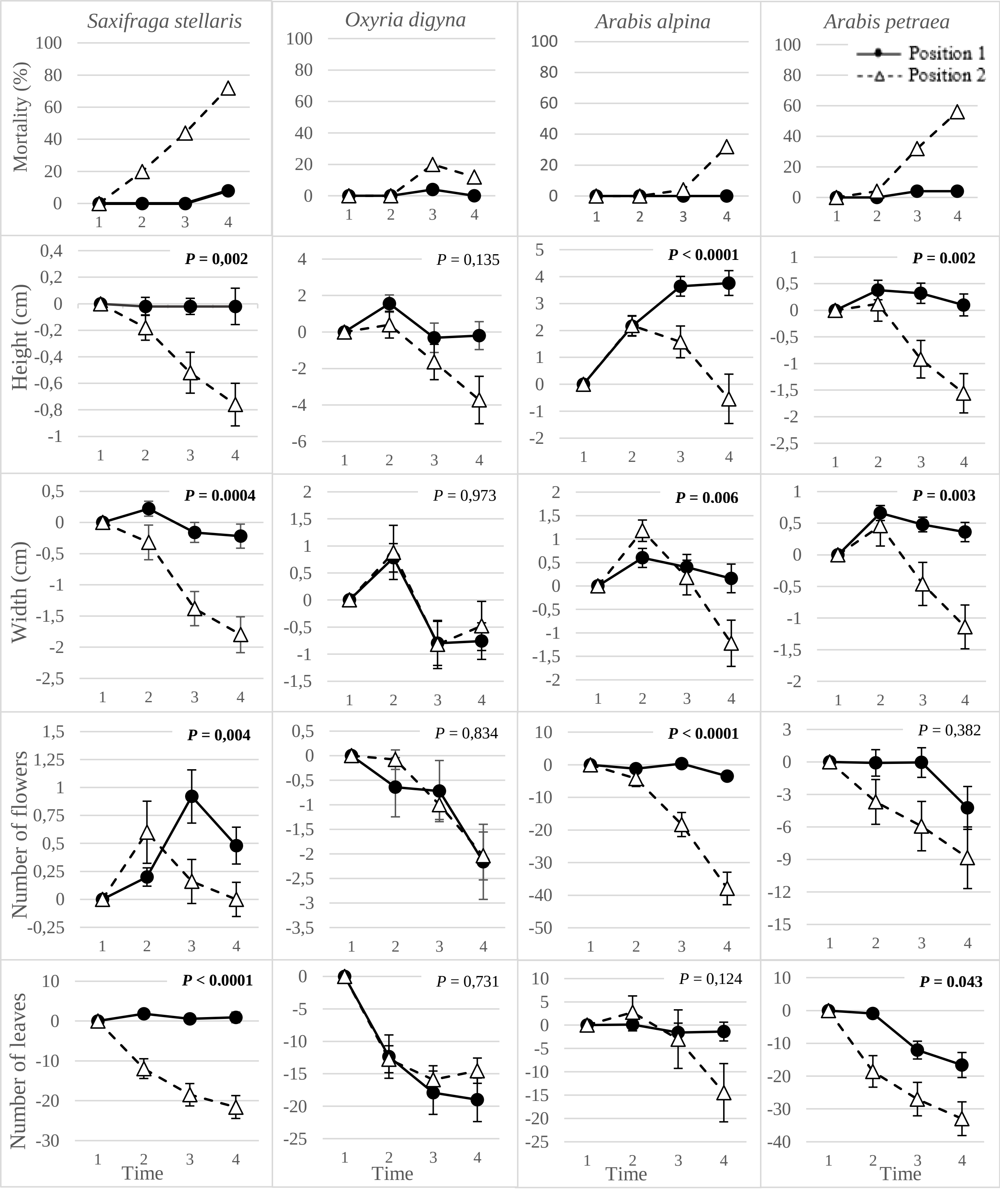

Figure 10. The transplantation of adult plants in the glacier foreland of Hellstugubreen in 2015 in position 1 (10-15 m from the glacier, moraine age 0-3 yr, *n* = 175) and position 2 (860 m from the glacier, moraine age 72-73 yr, *n* = 175). The proportion mortality (%) and the average development of height (cm), width (cm), number of flowers and leaves from the first recording with SE in *Saxifraga stellaris*, *Oxyria digyna*, *Arabis alpina*, *Arabis petraea.* Recordings were done at time 1 (18-21 July), time 2 (5-7 Aug.), time 3 (21-22 Aug) and time 4 (4-5 Sep). **Note different vertical scale among species.** *P*-value indicate the interaction term between measurements and positions. The significant level is 0,05 and marked in bold.

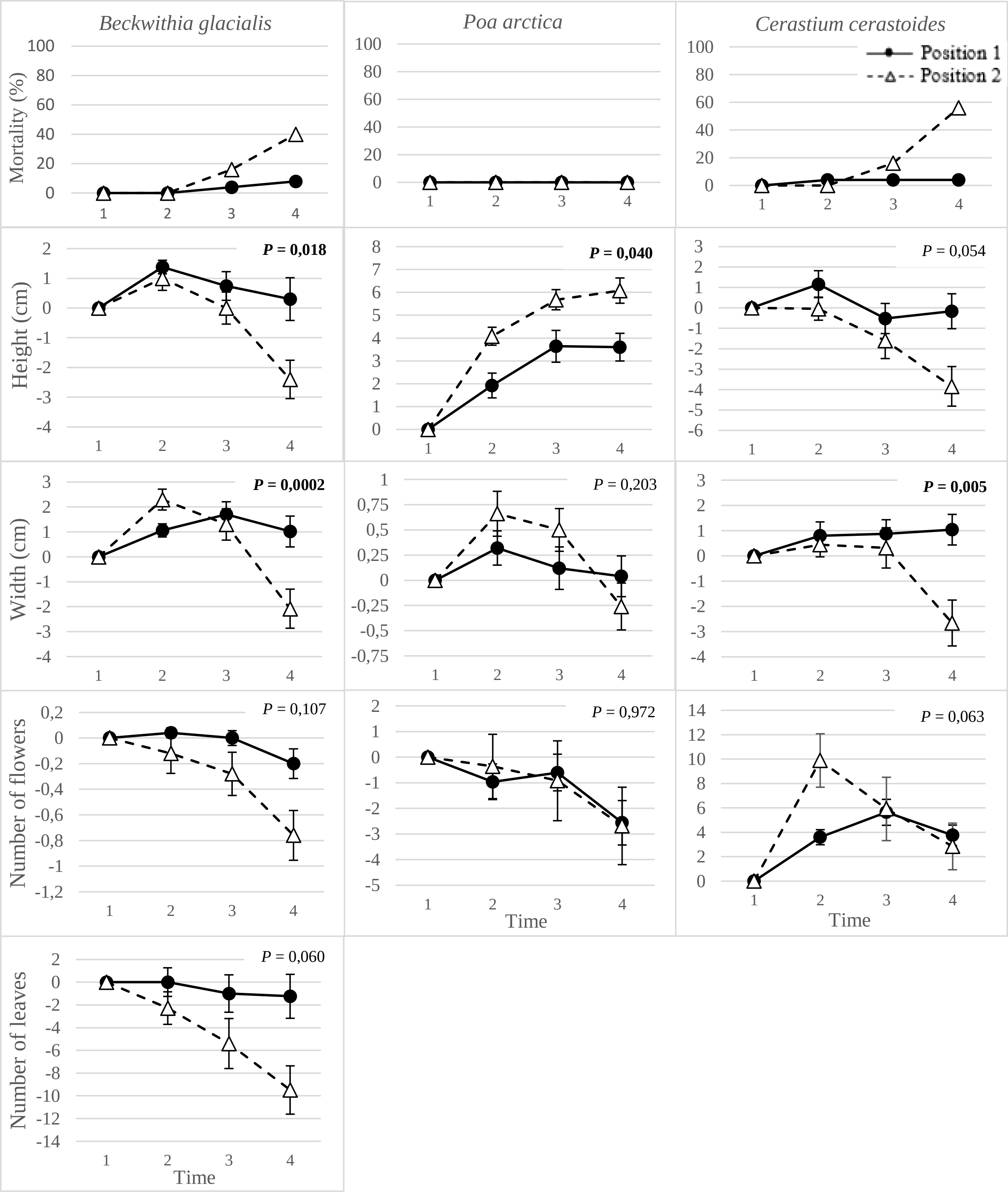

Figure 11. Transplantation of adult plants in the glacier foreland of Hellstugubreen in 2015 in position 1 (10-15 m from the glacier, moraine age 0-3 yr, *n = 175*) and position 2 (860 m from the glacier, moraine age 72-73 yr, *n* = 175). The proportion mortality (%) and the average development of height, width, number of flowers from the first recording with SE in *Beckwithia glacialis* (in addition development of leaves), *Poa arctica* and *Cerastium cerastoides.* Recordings were done at time 1 (18-21 July), time 2 (5-7 Aug.), time 3 (21-22 Aug) and time 4 (4-5 Sep). **Note different vertical scale among species**. *P*-value indicate the interaction term between measurements and positions. The significant level is 0,05 and marked in bold.

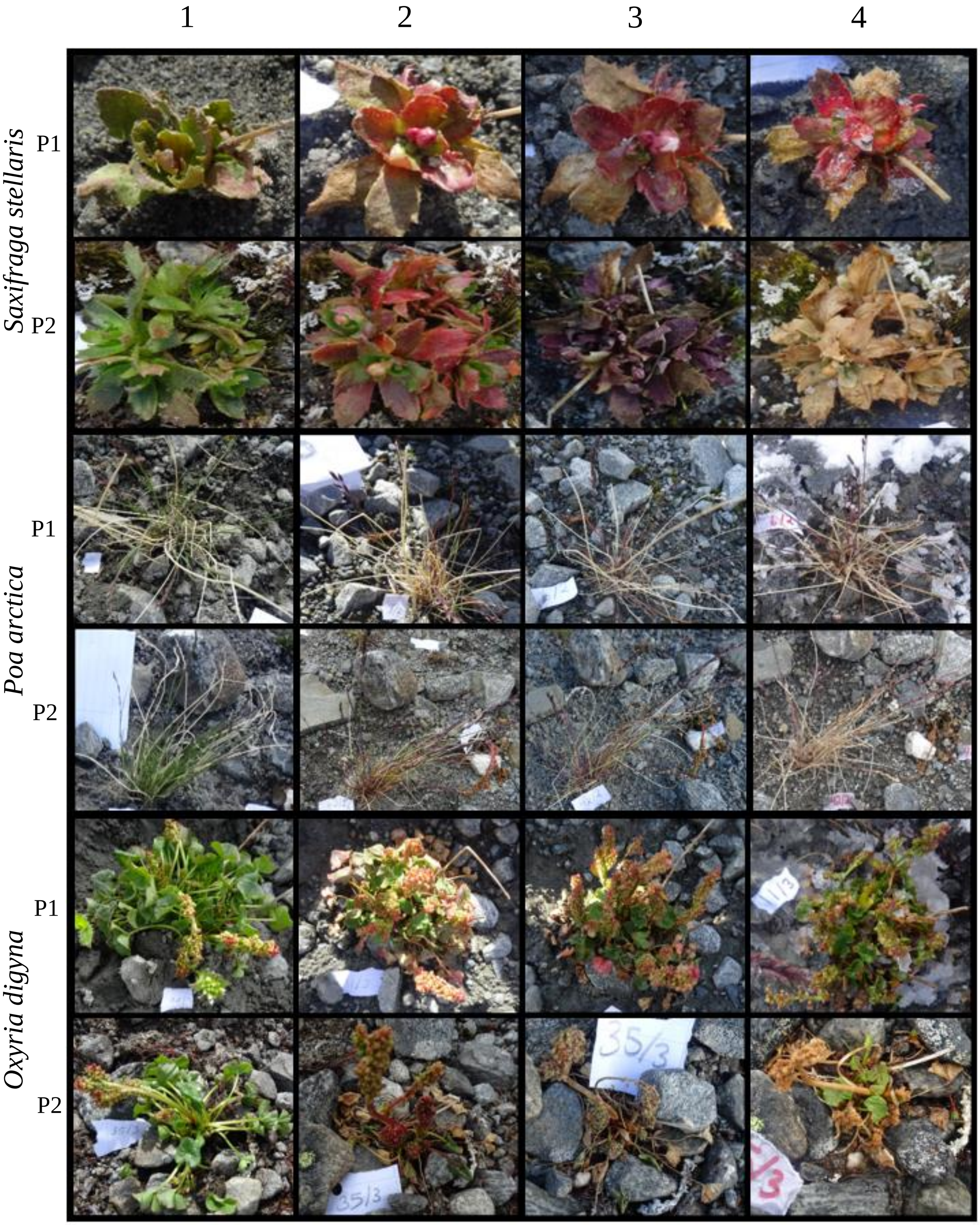

Figure 12. Pictures from selected plants throughout the transplantation experiment in position 1 (P1) and position 2 (P2) at four recordings, as depicted horizontally at the top of the pictures; 1 = 18-21 July, 2 = 5-7 August, 3 = 21-22 August and 4 = 4-5 September for all study species. Note that some of the pictures are taken at different angles, and stones and gravel have been moved in order to anchor number tags in strong wind. Photo: Anne-Sofie B. Strømme, 2015.

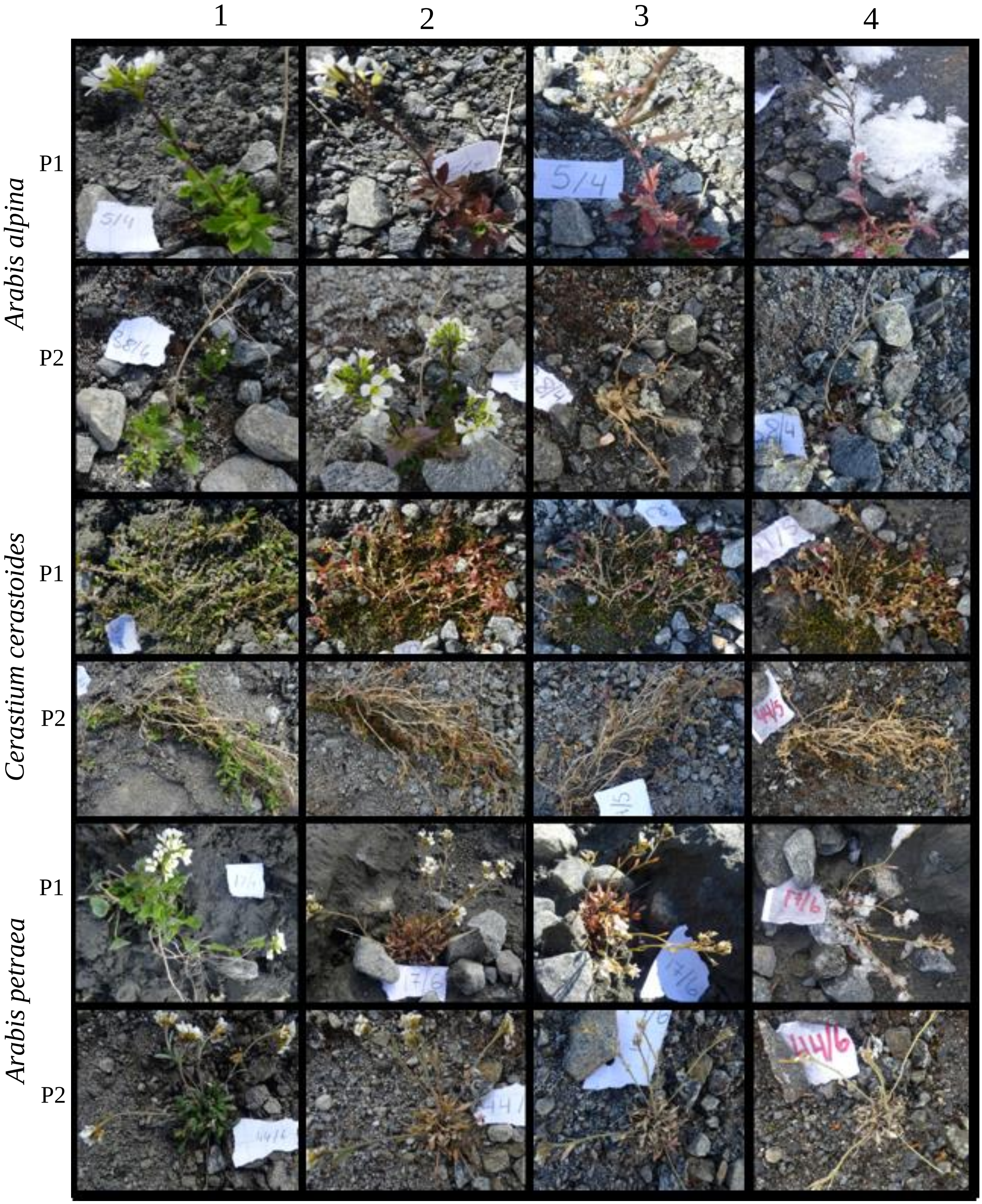

Figure 12. Continued.

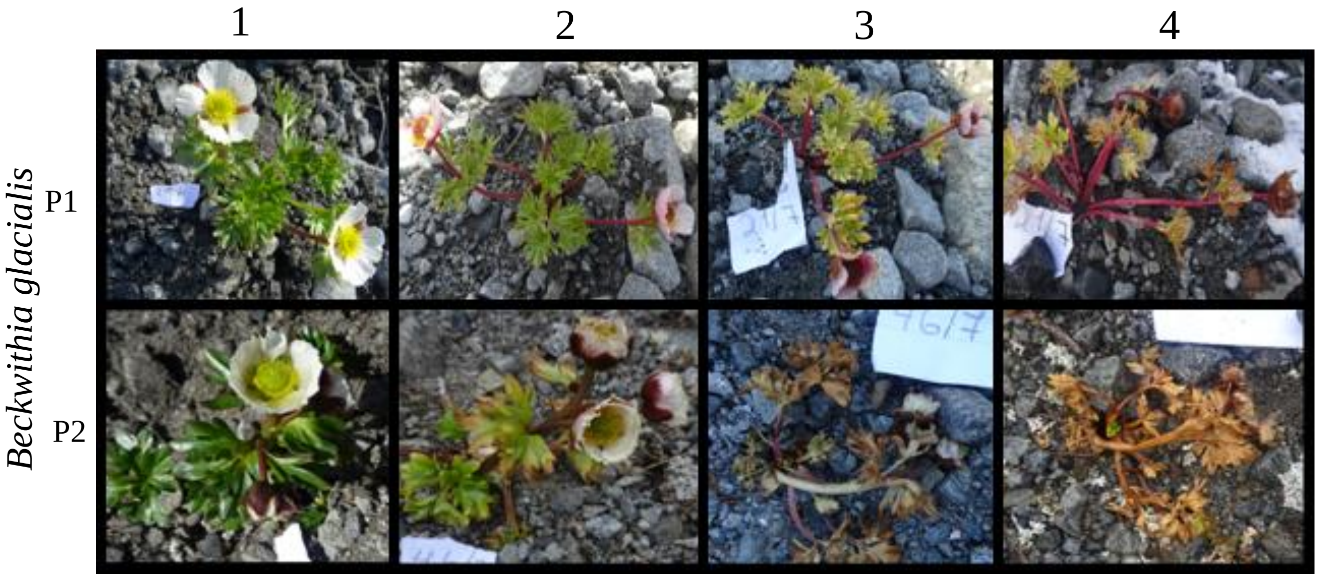

Figure 12. Continued.

Reproduction in *Arabis alpina*

The total number of seeds produced in *A. alpina* after the transplantation experiment were significantly higher in position nearest to the glacier (319 ± 83 seeds per plant), as compared to position furthest away from the glacier (90 ± 30 seeds per plant). The number of seeds per fruit were also significantly higher in the position closest to the glacier, although, the average fruits per plant did not show any significant difference between the positions (Fig. 13).

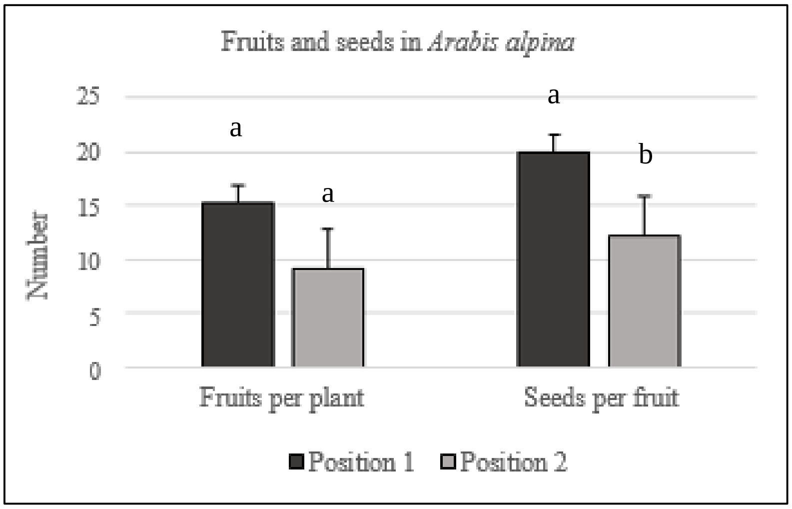

Figure 13. The average fruits per plant and seeds per fruit in *Arabis alpina* in position 1 (0-50 m from the glacier front, moraine age 0-3 yr, *n* = 5), and position 2 (860 m from the glacier front, moraine age 72-73 yr, *n* = 5). Different letters indicate significant difference among positions (*t- test* results are shown in Appendix V).

Soil analysis

The pH-value from the glacier foreland of Hellstugubreen were significantly higher in the position nearest to the glacier, than in the intermediate positions and the position furthest away from the glacier, there were no significant difference between the latter positions (Fig. 14). The organic material, measured in loss of ignition (LOI) did not show any significant difference between the positions, but the position furthest away from the glacier showed a trend of larger range as compared to the position nearest to the glacier and the intermediate position (Fig. 15).

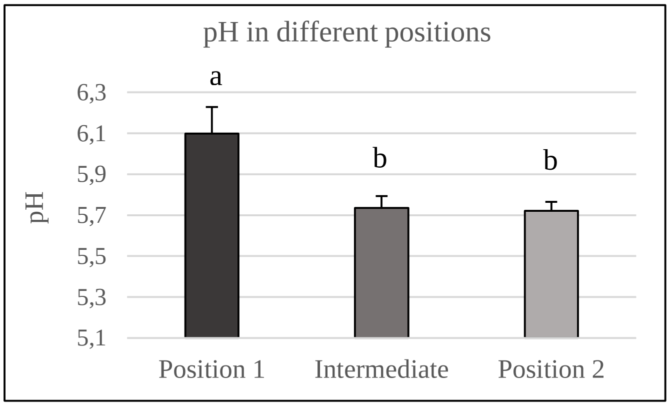

Figure 14. The pH in three positions in the glacier foreland of Hellstugubreen. Position 1, moraine age 0-5 years (0-50 m from the glacier) (*n* = 5), intermediate position (250 m from the glacier, moraine age 26-29 yr, *n* = 5) and position 2 (860 m from the glacier, moraine age 72-73 yr, *n* = 5). Different letters indicate significant difference among positions (one-way ANOVA, *F* = 6,07; *P* < 0,05).

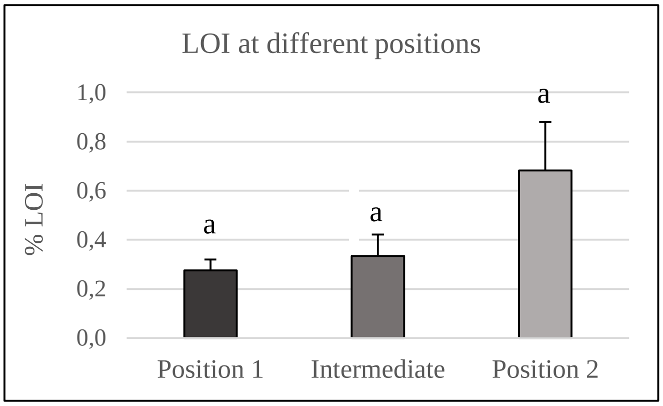

Figure 15. The percent loss of ignition (LOI) in three positions in the glacier foreland of Hellstugubreen. Position 1 (0-50 m from the glacier, moraine age 0-5 yr, *n* = 5), intermediate position (250 m from the glacier, moraine age 26-29 yr, *n* = 5) and position 2 (860 m from the glacier moraine age 72-73 yr, *n* = 5). Different letters indicate significant difference among positions (one-way ANOVA, *F* = 1,64; *P* = 0,24).

Soil seed bank experiment

In general, very few seeds germinated from the soil seed bank samples, actually, in total only 11 seeds germinated from the 60 soil samples. In the unpopulated area, only one seed (*C. cerastoides*) germinated (Table 2). Further away from the glacier, six seeds of *C. cerastoides* germinated in the intermediate position and four seeds (graminoides) germinated in the position furthest away from the glacier (Table 2). The vegetation cover inside the unpopulated area was very sparse and characterized by only sporadic appearance from the study species within in sample sites, i.e. *A. alpina*, *O, digyna* and *C. cerastoides* (Table 2). At the intermediate position, the vegetation cover was higher, and the study species *S. stellaris* and *P. alpina* were also observed at the sample plots. At the position furthest away from the glacier, the early pioneer species i.e. the study species were absent, and late pioneer species i.e. *Luzula arcuata* (Engl.: Curved wood-rush, Norw.: Buefrytle), *Silene acaulis* (Engl.: Cushion pink, Norw.: Fjellsmelle), and *Salix herbacea* (Engl.: Dwarf willow, Norw.: Musøre) were more abundant (Table 2).

Table 2. Number of seeds germinated and vegetation cover (low < 20 %, intermediate 20-60 % and high > 60 %) from sixty soil seedbank samples collected in the Hellstugubreen glacier foreland along a chronosequence at the end of the growing season 2015 (collected 4-5 September).

Position and number of samples	**Distance from the glacier (m)**	**Moraine age (yr)**	**Soil seed bank**	**Vegetation cover**
Unpopulated area (*n* = 40)	10-15	0-3	0 individual	Low (only lichens and mosses)
	15-25	3-4	1 individual (*C. cerastoides)*	Low (only mosses)
	25-35	5-6	0 individual	Low (mosses and some early pioneer species)
	35-45	6	0 individual	Low (mosses and some early pioneer species)
Intermediate position (*n* = 10)	250	26-29	6 individuals (*C. cerastoides)*	Intermediate (mosses and early pioneer species)
Position 1 (*n* = 10)	860	72-73	4 individuals (graminoides)	High (lichens, mosses and later pioneer species)

The highest proportion flowering plants of *A. alpina* in lab appeared in treatment 3, despite the latest flowering onset (Fig. 16), and the fact that three plants died during the experiment (Appendix VII). The earliest flowering onset appeared treatment 1, but the proportion flowering plants stagnated in the end of the experiment (Fig. 16), additionally three plants died (Appendix VII). There was no significant difference in proportion flowering plant between treatment 2 (one dead plant, Appendix VII) and treatment 4 (all plants survived, Appendix VII) (Fig. 16).

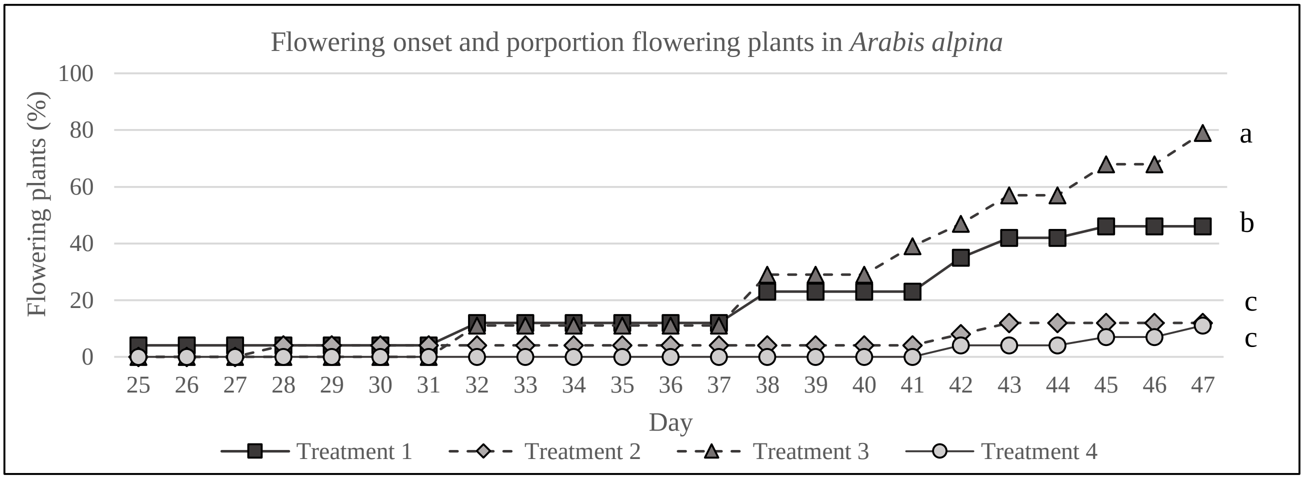

Figure 16. Flowering onset and proportion flowering plants (%) in *Arabis alpina* in four treatments. Treatment 1 (high temperature, high light), Treatment 2 (high temperature, low light), Treatment 3 (low temperature, high light) and Treatment 4 (low temperature, low light). Different letters indicate significant difference among treatments and time (ANOVA, $F = 79{,}4$; $P < 0{,}001$).

Further in the growth experiment, leaf mass and above ground biomass, together with the two measures of reproductive effort, showed a similar response pattern on the treatments, with highest values for treatment 1, for then to gradually decline to lowest levels in treatment 4, i.e. in the low light and low temperature treatment. However, the difference between the treatments were only significant for leaf mass and above ground biomass (Fig. 17). There was a significant effect of light treatments in leaf area and leaf density, as the leaf density was significantly higher in the high light treatments than in the low light treatments. In contrast, the leaf area was significantly highest in one of the low light treatments, i.e. in treatment 2; the combination of high temperature and low light (Fig. 17). The light treatments had also a significant impact on reproductive mass, as it was significantly reduced under the two low light treatments (Fig. 17). The stem mass response on the treatments were difficult to interpret, as the mass peaked under two opposite combinations of high and low temperatures and high and low light (Fig. 17). There were found no significant difference in root mass among the treatments (this was likely due to methodological difficulties when sorting out the roots from the soil).

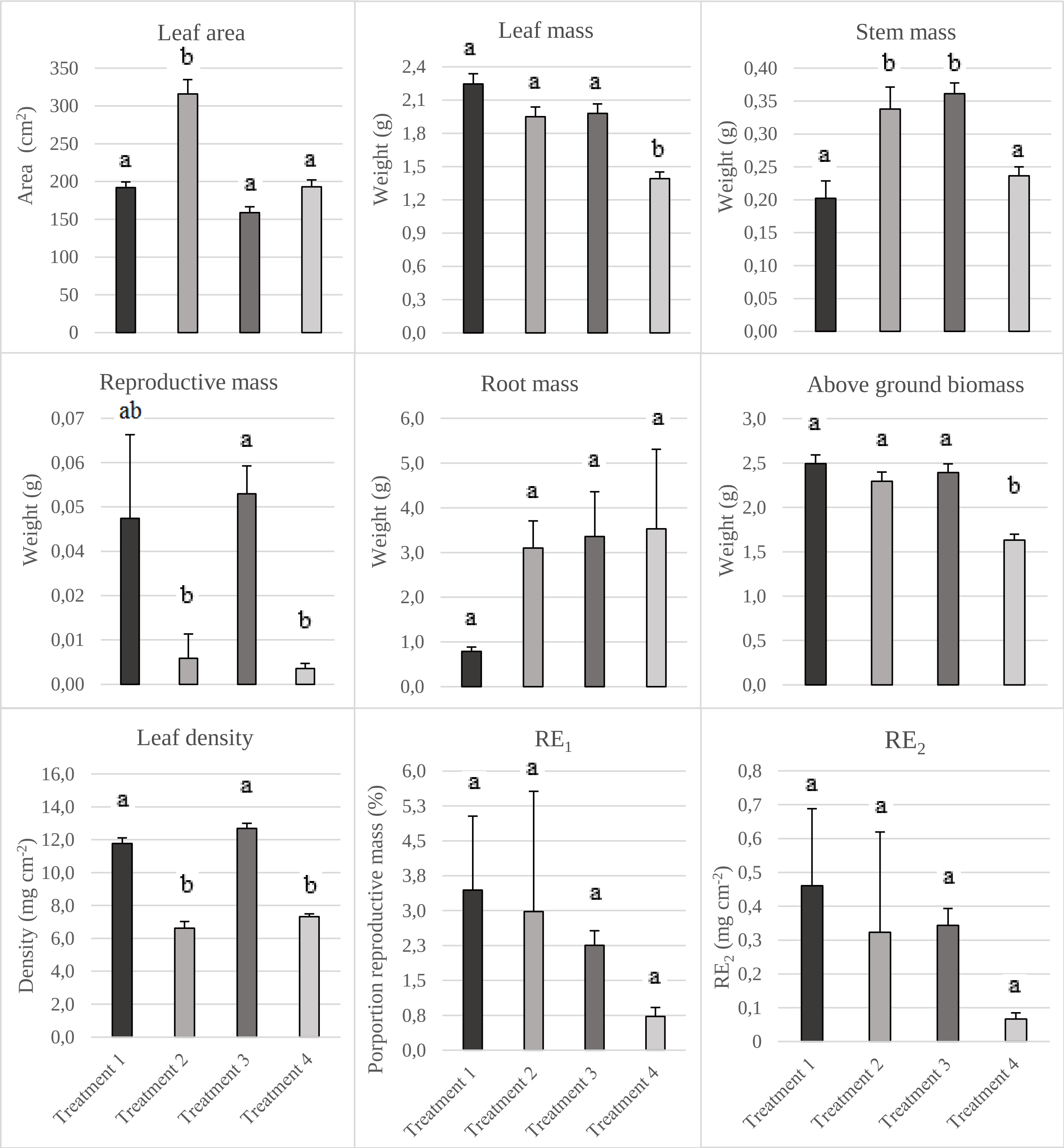

Figure 17. The growth experiment whit the pioneer species *Arabis alpina*. Leaf area (cm^2), leaf mass (g), stem mass (g), reproductive mass (g), root mass (g), above ground biomass (AGB) (g), leaf density (mg cm^{-2}), reproductive effort: RE$_1$ (reproductive mass/ vegetative mass (%)) and RE$_2$ (reproductive mass/leaf area (mg cm^{-2})) with SE were measure in four treatments. Treatment 1 (high temperature, high light, n = 23), Treatment 2 (high temperature, low light, n = 25), Treatment 3 (low temperature, high light, n = 25), and Treatment 4 (low temperature, low light, n = 27). Different letters indicate significant difference among treatments (one-way ANOVA results are shown in Appendix IV).

DISCUSSION

No vascular plants grow closer than approximately 50 m from the glacier front on moraine that is younger than 6 yr in the Hellstugubreen glacier foreland (Berg 2014; Dalen 2014), and a similar pattern has been documented at the nearby Storbreen glacier foreland (Matthews & Vater 2015; Whittaker 1993). However, immediately outside this unpopulated area at the front of Hellstugubreen, Berg (2014) and Dalen (2014) found high numbers of seed producing plants who could likely easily spread their seeds and establish in the unpopulated area, but they do not. Why? To try to answer this question, I have addressed three main themes in my thesis, i.e. germination-, survival- and dispersal limitation. Below I will discuss these themes in the light of my main results.

GERMINATION LIMITATION

All of the study species in the germination experiment (i.e. *S. stellaris, P. alpina, O, digyna, A. alpina* and *C. cerastoides*) germinated in the position closest to the glacier, i.e. only 10-15 m from the glacier front on moraine that was 0-3 yr old (Table 1). This result shows that these pioneer seeds are capable to germinate in the unpopulated area closest to the Hellstugubreen glacier, which in turn suggests that the lack of plants in the unpopulated area should be due to survival and/or dispersal limitations, which will be discussed later on.

In alpine areas, species are adapted to a harsh climate (Körner 2003). Stress factors as freezing temperatures, heat and drought have been considered to be main reason for high seed mortality and low plant establishment during the first growth season, but in particularly after the first and second winter seasons (Körner 2003; Marcante et al. 2012; Marcante et al. 2014; Stöcklin & Bäumler 1996). Seeds of pioneer species have often higher frost resistance than their seedlings, and frost resistance decrease rapidly after germination onset (Marcante et al. 2012). If frost resistance in early development stage is insufficient, freezing temperatures during the growing season could be the dominant factor in seedlings mortality (Körner 2003; Marcante et al. 2012). It would have been interesting to continue monitoring the germination experiment over the next few seasons, to follow the long-term establishment of seedlings in the Hellstugubreen glacier foreland.

There were in general low germination (< 22 %) closest to the glacier, however, all of the study species showed significantly higher germination in the fine soil substrate compared to the rough substrate (Table 1). Similar results are found in a Swiss glacier foreland (Stöcklin & Bäumler 1996). The fine soil substrate, mostly consisting of fine till derived from the glacier, was probably more suitable for seed germination because it was saturated by glacier meltwater and melting snow (see Matthews & Vater 2015), and thereby providing more moist conditions and less drainage as compared to the rough substrate (Körner 2003; Stöcklin & Bäumler 1996). With increasing time and distance from glacier, the amount of fine substrates decline due to wind and surface wash (Matthews & Vater 2015), while the rough substrate increases. The rough soil substrate in recently-deglaciated areas can be very unstable, as disturbance in terms of thawing of seasonally-frozen ground (Matthews & Vater 2015) creates sorted and patterned ground conditions (Haugland & Beatty 2005), which can explain the lower germination in the rough substrate as compared to the fine substrate (Table 1). The disturbance and freezing temperatures are more frequent and more severe closest to the glacier front, for to decline along the chronosequence with increasing terrain age (Haugland 2006; Matthews 1999), although disturbance from frost sorting can appear in terrain age up to 20 yr (Matthews & Vater 2015).

None of the study species in the germination experiment germinated in the position furthest away from the glacier, i.e. 1100 m from the glacier front on moraine that was 102-103 yr old. The lack of germination is probably explained by a decline in water availability and increasing vegetation cover (Matthews 1999; Matthews & Vater 2015; Stöcklin & Bäumler 1996). Both inter- and intraspecific competition increases with terrain age and vegetation cover (Matthews & Vater 2015), and since pioneer species are relatively poor competitors, the existing vegetation can inhibit establishment of pioneer species in later successional stages (Erschbamer & Mayer 2011; Jones & del Moral 2009; Moen 1993). However, Schlag and Erschbamer (2000) have observed that existing vegetation and "stone borders", may serve as safe sites for seed germination in early succession stages.

All of the study species, except *A. alpina*, showed higher germination in field (*in situ*) than in lab (*ex situ*). In the germination lab experiment, the only study species that germinated were *P. alpina, A. alpina*, *C. cerastoides* and *A. petraea*. The fastest germination and highest germination percent appeared in *A. alpina*, 87 %, while the other species had slower germination onset, and under 20 % germination success (Fig. 9). The study species *S. stellaris*, *O. digyna* and *B. glacialis* did not germinate in lab at all, and the seeds of *O. digyna* and *S. stellaris* did not show any metabolic activity when tested with tetrazodium chloride, indicating that the seeds were dead (Marcante et al. 2012; Marcante et al. 2014). All the seeds were stratified with as natural conditions as possible, however freezing the seeds while wet could be the main reason for low germination percent and dead seeds. According to Heide (2005), *O. digyna* does not need any type of stratification to germinate, however, cold and wet condition may have beneficial impact (Bell & Bliss 1980). The wing shape seeds of *O. digyna* makes the seeds remain on the soil surface, in which the seeds requires necessary frost resistant to survive the autumn and winter season (Marcante et al. 2012), indicating that wet seeds should tolerate quite low freezing temperatures. Research from Marcante et al. (2012) in a glacier foreland in the Alps, showed that pioneer species, e.g. *O. digyna*, often have higher frost resistance when grown in field (*in situ*). This may indicate that some pioneer species require a special type of stratification, maybe only possible in glacier forelands. However, species responded individualistically, and *A. alpina* seeds were clearly not affected by freezing when being in a wet stage, which may explain the high and rapid seed germination in my greenhouse experiment, as well as the germination of seeds in cold and dark conditions.

Freezing temperatures and high levels of disturbance are claimed to limit plant colonization as plants require given levels of stability to establish (Matthews & Vater 2015). However, my result showed that seeds are capable to germinate despite the harsh conditions and disturbances closest to the glacier, and a similar observation has been documented by Stöcklin and Bäumler (1996) and by Schlag and Erschbamer (2000) in glacier forelands in the Alps. According to Schlag and Erschbamer (2000), seeds of late successional species are able to germinate on young moraine when they are placed there. However, since both dispersal and establishment failure limit colonization on recently exposed soils in glacier forelands, late successional forest species would have difficulties migrating upwards in response to global climate change (Jones & del Moral 2009). My result showed that the germination failure could thus not explain the lack of plants in the unpopulated area in front of the Hellstugubreen glacier, which leads to my second hypothesis; i.e. can plants survive the growth season after a successful germination?

SURVIVAL LIMITATIONS

The study species, i.e. *S. stellaris, A. alpina, C. cerastoides, A. petraea* and *B. glacialis* showed clearly higher survival, vitality and performance (measured in height, width, number of flowers and leaf) in the position closest to the glacier (Fig. 10, 11 and 12). This indicate, that after a successful germination, these pioneer species are able to survive the growing season as adult plants inside the unpopulated area, at least for one growth season. Interestingly, these results contradict most of the scientific research done in glacier forelands regarding the harsh climate and disturbance closest to glacier fronts (Erschbamer et al. 2008; Jones & del Moral 2009; Matthews & Vater 2015; Robbins & Matthews 2010; Whittaker 1993), and to the best of my knowledge there are no other studies that have used plant transplantation experiments in glacier forelands to reveal what factors that actually limit plant survival. It would thus have been very interesting to continue monitoring the transplantation experiment over the next few seasons. Here, I expect a considerable lower second season survival, as adults plants have lower frost resistance than seeds and seedlings (see Marcante et al. 2012).

The vitality and performance in the position nearest to the glacier were generally stable throughout the study season, while in the position furthest away from the glacier, i.e. 860 m from the glacier on 72-73 yr old moraines, the vitality and performance were significantly lower for most of the species, except for *O. digyna* and *P. arctica* (Fig. 10 and 11). All the plants of *P. arctica* survived the experiment, and they showed significantly lower performance in the position closest to the glacier (Fig. 11). *P. arctica* were harvested from a relatively recently dry mountain scree from one of the side slops in the glacier valley. For *P. arctica,* the dry conditions in the positions furthest away from the glacier were obviously more favourable than the moist conditions in the positions closest to the glacier (see Lid & Lid 2007). *O. digyna* showed no significant difference between the positions, and both positions exhibited decreasing performance. According to Whittaker (1993) is *O. digyna* occurrence not related to terrain age, which can explain no significant difference between the positions. At the third recording, some plants of *O. digyna* were deemed senescent (semi-dead state) because the observed plant parts appeared completely dried out and dead. However, at the last recording new leaves were observed, leading to a "decrease in mortality" (semi-dead state) in both positions (Fig. 11 and see Fig. 12). A similar observation have been made by Heide (2005), who found that old leaves wilted and new buds and leaves were produced when *O. digyna* started to induce dormancy, which likely is an adaption to survive the winter with few buds and leaves which can start photosynthesis directly after snowmelt in the next season.

The mortality were clearly higher in the position furthest away from the glacier, and *S. stellaris* had the highest mortality, 72 % (Fig. 10 and 12). The position furthest away from the glacier was relatively dry the whole growth season, and since *S. stellaris* and most of the other study species requires or prefer wet and moist conditions, less water availability could probably explain the high mortality rate. Additionally, the position furthest away from the glacier had higher vegetation cover, including some dense carpets of mosses and lichens, leading to a hard interspecific competition, in which pioneer species often loses (Erschbamer & Mayer 2011; Jones & del Moral 2009). In this context, the size and activity of the below ground soil community may also be of importance, due to competition between the transplanted plants and the below ground community for limiting nutrients such as e.g. N, P and K (Grønli et al. 2005). The larger LOI in the position furthest away from the glacier (Fig. 15) indicates more organic material in the soil, and thus probably a larger and more active belowground community, something the transplanted plants nearest to the glacier did not encounter. Plants in recently deglaciated areas are non-mycorrhizal, and the density of below ground communities increases with terrain age (Oehl et al. 2011; Tscherko et al. 2003). The pH were also significantly lower in the position furthest away from the glacier as compared to the positions closest to the glacier (Fig. 14), this agrees with a rapid decrease in pH along the chronosequence with increased terrain age (Lambers et al. 2008; Matthews et al. 2014). Soil pH is also a major determinant of soil nutrient availability, and rain exposure, soil leaching in combinations of an increase vegetation cover gives rise to accumulation of soil organic matter, which in turn leads to an increase in soil acidity (Lambers et al. 2008).

Recently deglaciated areas has relatively high P availability (Lambers et al. 2008), and as most of the study species prefers wet or moist conditions with some calcareous soil condition, the conditions in the unpopulated area were clearly more favourable than the conditions further away from the glacier. Additionally, fruit and seed set in *A. alpina* were also clearly higher in the position closest to the glacier (Fig. 13), which indicates that this pioneer plant is able to successfully reproduce as well as survive inside the unpopulated area in front of Hellstugubreen glacier. My results showed that the germination and survival failure could thus not explain the lack of plants in the unpopulated area in front of glaciers, which leads to the third hypothesis; i.e. is the lack of plants inside this unpopulated area due to dispersal limitation?

DISPERSAL LIMITATION

The results from the soil seed bank experiment showed that the seed bank was very small in the glacier foreland of Hellstugubreen (Table 2). Only one seed (*C. cerastoides*) germinated in the unpopulated area, i.e. 15-25 m from the glacier on moraine that was 3-4 yr, which indicated that there was no seed bank in the unpopulated area, which clearly confirmed my third hypothesis, that the lack of plants in the unpopulated area in front of Hellstugubreen glacier is explained by dispersal limitation. Similar results, which corroborate the lack of a seed bank close to glacier fronts are found by Stöcklin and Bäumler (1996), Erschbamer et al. (2001) and Marcante et al. (2009) from studies in glacier forelands located in the Alps.

I found a clearly limited dispersal towards the Hellstugubreen glacier front, despite the relatively fast establishment in relation to the rapid glacier retreat the last 10-15 yr (Appendix II). Dispersal limitation in glacier foreland can be explained by wind direction (Matthews & Vater 2015), water dispersal, low maximum dispersal distance (often < 10 m) and slow clonal growth (Diemer & Prock 1993; Stöcklin & Bäumler 1996). Pioneer species that produce high number of small seeds should be able to easily disperse into recently deglaciated areas, and Stöcklin and Bäumler (1996) observed an increase in trapped seeds from 125 to > 2000 diaspores per m^2 from moraine of age from 8 to 45 yr in a Swiss glacier foreland. However, Stöcklin and Bäumler (1996) also found that species restricted to early pioneer site produces less seeds, and long-lived perennials abundant in cold and disturbed areas, such as recently deglaciated areas, relies also on reproductions with horizontal spread from widely spaced ramets, runners, and rhizomes.

I expected the soil seed bank to reflect the local vegetation (see e.g. Marcante et al. 2009), however, this was not the case in Hellstugubreen glacier foreland. To improve the seed bank experiment, I could have included a stratification period (dark and 4-5 ^{o}C) to break dormancy in this year produced seeds (see Marcante et al. 2009). However, local vegetation and vegetation cover have been found to be weak predictors for soil seed bank (Diemer & Prock 1993; Milberg & Persson 1994).

GROWTH EXPERIMENT WITH *ARABIS ALPINA*

The result from the growth experiment showed that *A. alpina* had higher proportion fertile plants and more reproductive mass in the treatment with low temperature and high light (Fig. 16 and 17), which is similar to the natural conditions that *A. alpina* experience in the alpine environment today. The four treatments in the growth experiment can be linked to four climate scenarios with different combinations of temperatures and light conditions. Anthropogenic climate change can alter species compositions in ecosystems and pose a threat to biodiversity, especially in Arctic- and alpine ecosystems (Pollnac & Rew 2014; Primack 2012; Sætersdal & Birks 1997; Wookey et al. 2009). The knowledge about species responses to climate change are therefore crucial in making rational management plans for species, ecosystems and the environment.

My results showed that in the high temperature and high light treatment the proportion fertile plants in *A. alpina* were about 40 % lower than in the treatment similar to the natural conditions (Fig. 16). Hence, if the temperature raises only 4-6 ^{o}C, *A. alpina* would probably decrease its abundance due to lower vitality and less reproductive individuals. In addition, I found that the treatments with higher temperatures resulted in faster flowering onset, which can potentially lead to alpine trophic interactions, mainly in terms of mismatch between flowering onset and pollinator arrivals, which has found to correspond well with temperatures (Hegland et al. 2009; Kudo & Ida 2013).

The leaf area and leaf density in *A. alpina* responded only to light intensity, since there were no significant difference between the temperature treatments. The plants treated with lower light had as expected, larger leaf area and thinner leaves, which is an adaptions to harvest efficiently at low light intensity (Lambers et al. 2008). The plants treated with full light did not need to absorb all the available light, hence lower leaf area and thicker leaves, which is an adaption to avoid overheating and over-excitation from high light intensity (Lambers et al. 2008). The proportion fertile plants and reproductive mass were significantly lower in the two treatments with lower light, which means that *A. alpina* requires high light to produce fertile plants, and that *A. alpina* would likely be outcompeted by shading from higher plants that migrate upwards in response to climate change.

CONCLUSION

I draw the main conclusions that the first and second hypothesis i.e. germination and survival limitation, did not explain the lack of plants in the unpopulated area close to Hellstugubreen glacier. First, all the study species in the germination experiment had clearly higher germination success in the unpopulated area, and second, most of the study species from the transplantation experiment had generally higher survival, vitality and better performance in the unpopulated area. Additionally, *A. alpina* had significantly higher reproduction success inside the unpopulated area, as compared to the position furthest away from the glacier. The study species were able to establish, survive and reproduce in the unpopulated area closest to the glacier, probably because of higher water availability and less inter- and intraspecific competition from above- and below ground communities. In summary, the unpopulated area seemed favourable for most of the pioneer species. The third hypothesis, i.e. dispersal limitation, was clearly confirmed by the absence of a soil seed bank inside the unpopulated area. This suggests that pioneer species in glacier foreland are dispersal limited towards the glacier, probably because of low maximum dispersal distances, wind direction, water dispersal and slow clonal growth. The result from the growth experiment fairly agreed with my hypothesis, as *A. alpina* had the highest reproductive output under cold and high light conditions. Climate change, mainly in terms of increasing temperatures, will thus reduce the vitality of *A. alpina*, and it would probably decline its abundance in the Hellstugubreen glacier foreland.

Finally, I suggest future research should focus on: continued monitoring of the germination- and transplantation experiments over the next few seasons; seed trap experiments to determine seed dispersal patterns and distances in glacier forelands; estimates of belowground community size and activity, and how this has an impact on the vegetation; and, OTC (open top chambers) experiments to understand the ecology in alpine pioneer species in light of climate change.

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APPENDIX I: Glaciological Investigations in Norway – NVE, 1962-2010

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1988 og 1989

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APPENDIX II: Glacial Cumulative Length Change at Hellstugubreen, 1901-2015 (Modified from NVE)

Year	M melted	Total melted m	Year	M melted	Total melted m	Year	M melted	Total melted m
1901	0	Start	1944	-27	-306	1990	-8	-947
1902	0	0	1947	-43	-349	1991	-7	-954
1903	-13	-13	1948	-20	-369	1992	-9	-963
1904	-14	-27	1949	-10	-379	1993	-3	-966
1905	0	-27	1950	-19	-398	1994	-9	-975
1906	-9	-36	1951	-11	-409	1995	-6	-981
1907	5	-31	1952	-15	-424	1996	-3	-984
1908	0	-31	1953	-13	-437	1997	2	-982
1909	-4	-35	1954	-14	-451	1998	-9	-991
1910	-4	-39	1955	-11	-462	1999	-7	-998
1911	-6	-45	1956	-18	-480	2001	-4	-1002
1912	-25	-70	1957	-13	-493	2002	-17	-1019
1929	-87	-157	1958	-4	-497	2003	-10	-1029
1931	-13	-170	1959	-39	-536	2004	-5	-1034
1932	-7	-177	1961	-14	-550	2005	-4	-1038
1933	-12	-189	1962	-10	-560	2006	-15	-1053
1934	-8	-197	1963	-12	-572	2007	-10	-1063
1935	-11	-208	1964	-6	-578	2008	0	-1063
1936	-5	-213	1971	-90	-668	2009	-10	-1073
1937	-8	-221	1975	-61	-729	2010	-5	-1078
1938	-11	-232	1976	-31	-760	2011	-21	-1099
1939	-12	-244	1983	-95	-855	2012	-13	-1112
1940	-7	-251	1986	-49	-904	2013	-10	-1122
1941	-11	-262	1987	-10	-914	2014	-13	-1135
1942	-12	-274	1988	-18	-932	2015	-3	-1138
1943	-5	-279	1989	-7	-939			

APPENDIX III: Glacial Mass Balance at Hellstugubreen, 1962-2015

(Modified from NVE)

Year	Winter balance (m.w.e.)	Summer balance (m.w.e.)	Annual balance (m.w.e.)	Year	Winter balance (m.w.e.)	Summer balance (m.w.e.)	Annual balance (m.w.e.)
1962	1.181	-0.397	0.783	1990	1.772	-1.238	0.534
1963	0.933	-1.922	-0.988	1991	0.949	-1.506	-0.556
1964	0.698	-0.847	-0.148	1992	1.162	-1.124	0.037
1965	1.27	-0.786	0.483	1993	1.238	-1.037	0.2
1966	0.935	-1.646	-0.71	1994	1.22	-1.278	-0.058
1967	1.461	-0.94	0.52	1995	1.383	-1.631	-0.248
1968	1.383	-1.491	-0.108	1996	0.627	-1.459	-0.831
1969	0.948	-2.227	-1.278	1997			
1970	0.692	-1.699	-1.007	1998			
1971	1.098	-1.282	-0.184	1999			
1972	0.908	-1.476	-0.567	2000			
1973	1.172	-1.451	-0.279	2001			
1974	0.973	-0.798	0.175	2002			
1975	1.324	-1.745	-0.421	2003			
1976	1.116	-1.942	-0.826	2004			
1977	0.667	-1.433	-0.766	2005			
1978	1.036	-1.64	-0.603	2006			
1979	1.4	-1.486	-0.085	2007			
1980	0.78	-2.092	-1.311	2008	1.41	-1.468	-0.058
1981	1.048	-1.463	-0.415	2008			
1982	0.831	-1.281	-0.449	2009	1.299	-1.534	-0.234
1983	1.433	-1.384	0.048	2010	0.745	-2.085	-1.339
1984	1.197	-1.822	-0.625	2011	0.826	-2.87	-2.041
1985	1.09	-1.515	-0.424	2012	1.208	-1.216	-0.018
1986	0.734	-1.362	-0.627	2013	1.05	-1.83	-0.779
1987	1.117	-0.761	0.356	2014	1.113	-2.293	-1.19
1988	1.223	-2.429	-1.205	2015	1.213	-0.739	0.487
1989	1.577	-0.979	0.598				

APPENDIX IV: Summary ANOVA from the transplantation experiment

Summary of ANOVA three-way interactions for species, time and positions in the transplantation experiment

Variables	**Number of observations**	***F*-value**	***P*-value**
Height	*n* = 350	*F* = 2,08	***P* = 0,005**
Width	*n* = 350	*F* = 2,30	***P* = 0,001**
Number of flowers	*n* = 350	*F* = 2,08	***P* < 0,001**
Number of leaves	*n* = 250	*F* = 2,13	***P* = 0,013**

APPENDIX V: Summary *t-test* from the transplantation experiment with *Arabis alpina*

Summary of *t-test* in *Arabis alpina* at the end of transplantation in field

Variables	**Number of observations**	***t*- value**	***P*-value**
Number of fruits per plant	*n* = 10	*t* = 1,31	*P* = 0,227
Seeds per fruit	*n* = 10	t = 2,83	*P* < 0,05
Total seeds per plant	*n* = 10	*t* = 2,60	*P* < 0,05

APPENDIX VI: Summary of ANOVA growth analysis with *Arabis alpina*

Variables	**Number of observations**	***F*-value**	***P*-value**
Leaf area	$n = 100$	$F = 33{,}9$	$\mathbf{P < 0{,}001}$
Leaf mass	$n = 100$	$F = 20{,}3$	$\mathbf{P < 0{,}001}$
Stem mass	$n = 100$	$F = 10{,}6$	$\mathbf{P < 0{,}001}$
Reproductive mass	$n = 100$	$F = 4{,}6$	$\mathbf{P = 0{,}005}$
Root mass	$n = 100$	$F = 1{,}4$	$P = 0{,}266$
Above ground biomass	$n = 100$	$F = 18{,}8$	$\mathbf{P < 0{,}001}$
Vegetative biomass	$n = 100$	$F = 18{,}2$	$\mathbf{P < 0{,}001}$
Leaf density	$n = 100$	$F = 95{,}0$	$\mathbf{P < 0{,}001}$
RE_1	$n = 49$	$F = 1{,}6$	$P = 0197$
RE_2	$n = 49$	$F = 1{,}7$	$P = 0{,}184$

APPENDIX VII: Overview over *Arabis alpina* plants in the growth experiment

Overview over the number of plants at the start and end of the growth experiment and number of fertile plants in the four treatments.

Treatments		Number of plants in the start of the experiment	Number of plants at the end of the experiments	Fertile plants
Treatment 1	HT/HL	26	23	12
Treatment 2	HT/LL	26	25	2
Treatment 3	LT/HL	28	25	24
Treatment 4	LT/LL	27	27	11

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