

NORWEGIAN UNIVERSITY OF LIFE SCIENCES



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Ås, May 2012

Lise Tingstad



## Abstract

The climate is predicted to become warmer and wetter during the next decades. With this, we may expect tree establishment at higher altitudes. Upward migration of trees has already been observed several places in the northern hemisphere. A rising tree line is also an expected consequence of climatic change in many areas in Scandinavia. This study represents a seed sowing experiment conducted along climatic gradients in south-western Norway. The gradients were established in 2008 along the natural precipitation gradient from the coast towards the inland. The study plots were located at different altitudes that represent the temperature gradient. Survival of the seedlings was registered in 2010 and 2011, and all seedlings were harvested at the end of the field season in 2011. The establishment of spruce (*Picea abies*) and pine (*Pinus sylvestris*) seedlings differed significantly along natural temperature and precipitation gradients. However, significantly more seedlings established at intermediate and alpine localities compared to lowland localities, and therefore no temperature limitations could be shown in this study. Root biomass and root length of seedlings of both species were found to decrease with increasing altitude. Gap plots and intact vegetation plots were compared to assess the effect of competition from the surrounding vegetation. This comparison revealed that competition is one important factor that may limit tree seedling establishment, especially at the lowland localities due to higher competition rates. Further, different light and nutrient conditions may impact the allocation pattern of the seedlings. Plants in alpine allocated more resources to root growth, while seedlings at lowland localities allocated more resources to the aboveground tissues. Climatic conditions can have a large impact on the tree line dynamics. The tree line can serve as a biological indicator for changes in the vegetation with possible consequences at the ecosystem level. The alpine habitats are vulnerable, since the native alpine plant species are weak competitors compared to many faster growing lowland species. With the increasing temperatures it is likely that we will see an increase in the tree line altitudes. My results are in line with these projections, and the conifer trees might be capable of establishing in alpine areas.



## Table of contents

1.0	Introduction .....	1
1.1	Aims of the study .....	4
2.0	Methods.....	5
2.1	Study area.....	5
2.2	Study species.....	8
2.3	Experimental design.....	10
2.4	Statistical analyses.....	13
3.0	Results .....	14
3.1	Number of plants.....	15
3.2	Morphological traits .....	17
4.0	Discussion .....	26
4.1	Number of plants.....	26
4.2	Morphological traits .....	32
4.3	Perspectives.....	33
4.4	Conclusion.....	35
	References .....	36



## 1.0 Introduction

Warming of our globe and changes in the climate system are unequivocal. During the 21<sup>st</sup> century, monitoring and research have revealed that glaciers and sea ice are melting, oceans rising and global mean temperatures are increasing (Coop & Givnish 2008). This human-induced climate warming is a driving force of the profound mountain landscape transformation seen in many parts of the world (Grace et al. 2002; Kullman 2001; Tranquillini 1979).

Coming from lowland and forest habitats and entering the alpine zones, one of the most protruding differences one sees is the lack of trees above a certain altitude. This ragged boundary above where there are no trees is called the tree line and is observed on all continents, except Antarctica (Tranquillini 1979). I have chosen here to use the term “tree line” in the same meaning as the “tree limit”. This refers to the climatic limitation for tree growth, following Kullman (1979) stating that the tree-limit is the elevation of the uppermost individual of a specific tree species. The tree line is widely thought to be temperature-sensitive and hence responsive to climatic warming (Holtmeier & Broll 2005; Kozłowski et al. 1991; Kullman 2002; Körner & Paulsen 2004). Several studies have indicated that climate warming in the 20<sup>th</sup> century has caused tree-limit advance in many places (Harsch et al. 2009; Kullman & Engelmark 1990; Kullman 2001; Körner & Paulsen 2004; Payette & Filion 1985; Tranquillini 1979). The situation is not globally uniform, and in some areas the tree line response might reflect local spatial variability. There are, for example, locations where the tree line is stable and does not seem to respond to increasing temperature, although the net global outcome is that tree lines are rising upslope (Harsch et al. 2009) and poleward (Dullinger et al. 2004). Both field data and model experiments indicate that the tree line responds rapidly to changes in temperature, but also that sensitivity to warming may vary substantially in space and time (Lloyd et al. 2003).

Increase and decrease of tree line altitude are not per se a new phenomenon, but has occurred since the Holocene era (12 000 years ago). The boreal forest expanded northwards and upwards beyond the present-day limit during a period of high-latitude warming in the early and mid-Holocene (Foley et al. 1994; Körner & Paulsen 2004). Historical studies have shown that the treeline has followed the variations in temperature quite closely (Foley et al. 1994; Kullman & Öberg 2009), and growing season temperature is widely considered to be the primary factor controlling treeline formation (Harsch et al. 2009). Also in Fennoscandia post-



glacial tree line histories have evidenced elevational tree range shifts in obvious response to climate change (Kullman & Kjällgren 2006). We may therefore expect a rapid advancing tree line with the on-going changes in climate. Even though tree lines have been moving in earlier times, the way this is occurring now is worth our attention. It is faster and different species are migrating (Larsson 2004). During the past 100 years, the tree lines of boreal forest species have shifted upwards according to a rate of 100 m per 0.6 degrees centigrade (Grace et al. 2002). The hypothetical temperature rise of 5 °C would then result in a 700 meter elevational tree line shift (Grace et al. 2002). Woody species are known to be especially temperature-sensitive, as only a few degrees change in the mean temperature can affect their growth rate significantly (Kozlowski et al. 1991). An increase in temperature has been predicted to generate changes in precipitation (IPCC 2007), and at least in the western parts of Norway the precipitation will most likely increase in the coming years (Hanssen-Bauer et al. 2003). Precipitation is known to have a direct effect on plant recruitment (McCarty 2001; Walther et al. 2002), and it may change plant community composition, partly due to changes in seed and seedling success (Fay & Shultz 2009). Hence, treelines can function as a biological indicator of climate change.

Upward migration of the tree line can profoundly change the alpine ecosystems as we know them today. Presence or absence of a tree layer can affect wind and snow deposition, and in addition the existence of snow cover can provide shelter, increase the minimum temperatures and reduce the risk of desiccation for plants underneath the snow (Hofgaard 1997). As the climate warms, lowland species are finding new, suitable habitats in previously unavailable, alpine areas. Alpine species have unique adaptations to their environment, but are weak competitors (Krebs 2001; Sætersdal & Birks 1997). Hence, they may be displaced by highly competitive lowland species, such as trees. If areas previously above tree line in a few years will be scattered with trees, or even forested, it is assumed to have a large impact on the biodiversity and the floral composition of the alpine ecotone (Grace et al. 2002; Krebs 2001). The possible loss of alpine species as a result of the upward migration of subalpine forest is an important concern (Smith et al. 2003). In a climate perspective, the transition from alpine, open heathlands to forested areas can generate a negative feedback. Dark forest will reduce the albedo-effect (Hofgaard 1997) and enhance further warming of the soil, making it even more favourable for new tree seedlings to establish and potentially speeding succession. Trees also produce more seeds at higher temperatures, which should increase the already high potential reproduction rate for trees in a warmer climate (Brubaker 1986; Fenner 2000). An advancing tree line or a denser forest below the tree line is also projected to have important

implications for the global carbon cycle by increasing the terrestrial carbon sink (Grace et al. 2002).

Seedling establishment is a critical life history stage for trees (Castro et al. 2004; Germino et al. 2002; Körner & Paulsen 2004). Seedlings are especially vulnerable to climatic factors, predation and pathogens (Erefur et al. 2008). Natural regeneration consists of many phases, e.g. flowering, seed maturation, seed germination and early survival of seedlings, and certain climatic conditions must be fulfilled during several years before successful regeneration can take place (Juntunen & Neuvonen 2006). Simultaneously, tree seedlings are influenced by factors like site history, human impact and disturbance, wildfires, plant diseases and insect infestations (Holtmeier & Broll 2005). All these factors operate on a medium-large spatial scale, but there are also growth requirements at finer scales down to the level of the individual seedling. Every seedling needs a supply of carbohydrates produced by photosynthesis, plant hormones that aid in integrating the different physiological processes, nitrogen and other mineral elements and enough water to maintain cell turgor. In addition all plants need environmental conditions suitable for the biochemical and biophysical processes involved in growth (Kozlowski et al. 1991). This means that the tree lines position will be influenced by a wide range of factors (Germino et al. 2002; Kullman 2004; Smith et al. 2003).

The importance of seedling establishment to the position of alpine tree line is recognized, yet few studies have measured factors directly influencing establishment of young conifer seedlings during their first years (Germino et al. 2002). Differences in allocation within the plants is an important aspect when studying growth patterns across different climatic conditions (Skarpaas et al. 2012). Here, I present the results from a seed-sowing experiment across a wide range of contrasting local climates to assess how different climatic conditions impact on seedling establishment and growth of three common tree species in southern Norway. To my knowledge, no such studies have yet been conducted in Norway. The results can be valuable in predicting how the tree line will be impacted by climate change and what changes we can expect to happen in the alpine ecotone. Responses to a warmer climate is relevant and important information as the situation is today, and also for years to come (Coop & Givnish 2008).

## 1.1 Aims of the study

In this study, I take the advantage of natural climatic east-west precipitation and temperature gradients in southern Norway to study the effects of climate change. Many experiments including climate change and plants use artificial heating or in other way manipulate the microclimate. This often influences the whole microclimate and not only the one (or few) factor(s) that are under study. For example, open top chambers (OTC's) are widely used to simulate temperature rise (Hollister & Webber 2000), but these chambers might also decrease moisture or change the exposition for instance to wind and herbivores. Using a natural climate gradient, this study may produce more realistic results. My experimental plots are placed in meadow ecosystems, and the pattern of seedling survival in this biotope is important due to the predominance of this ground-cover type in the alpine ecotone.

This study looks at rather short-term responses (over a few years). The goal is to use these responses to simulate the longer-term responses of the tree seed establishment to a changing climate. To study the growth and allocation of tree seedlings under differing climatic conditions, I looked at seedlings both in intact vegetation and in gap plots where the competitive vegetation had been removed.

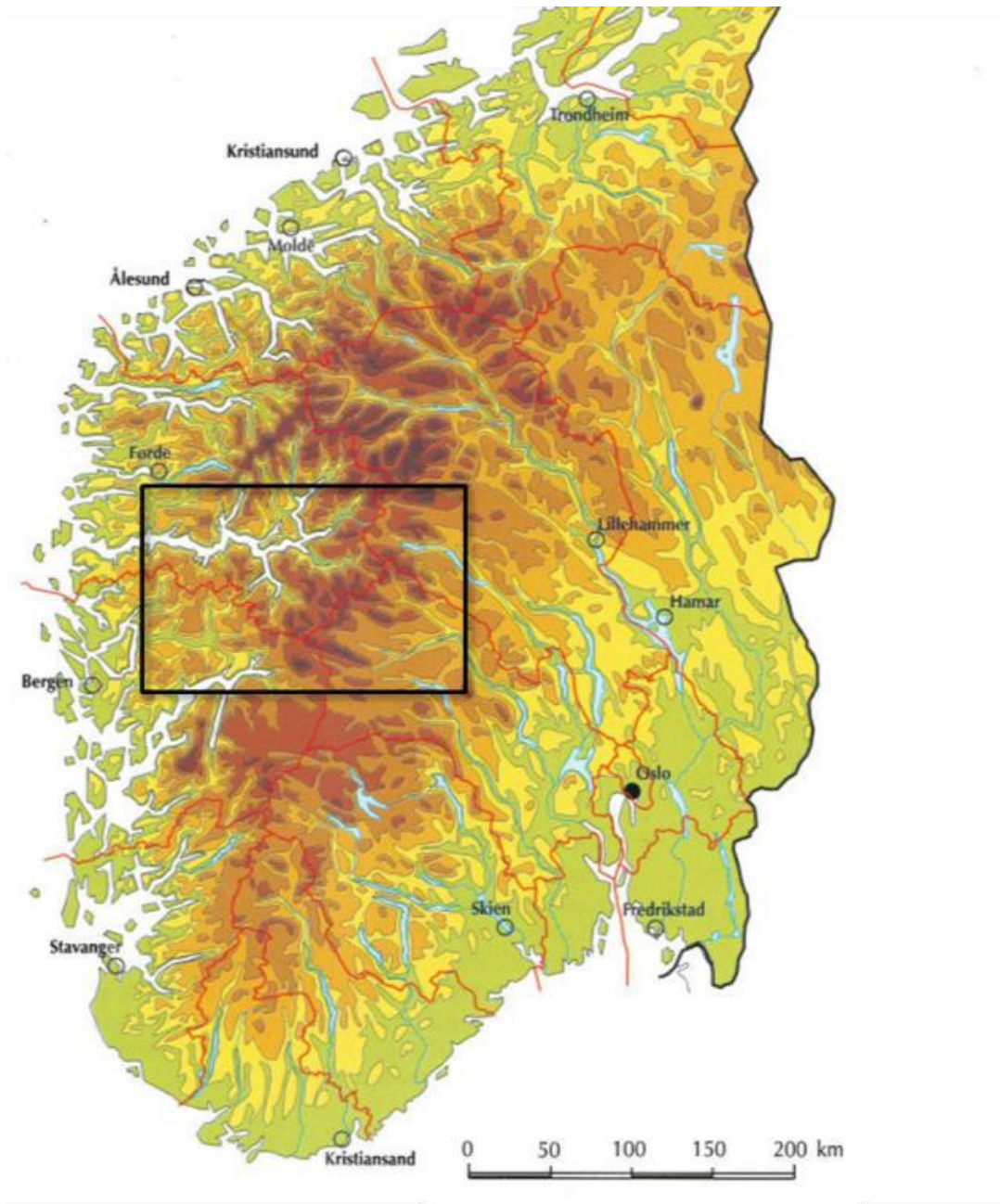
Based on the studies mentioned above I hypothesized that:

- i. Tree seedlings would establish better in warmer and wetter climate (at the lower west end of the study area) because these localities are presumed to have the most favourable climatic conditions for establishment; namely highest temperature and most precipitation.
- ii. More seedlings would emerge and grow in gaps compared to intact vegetation due to the high competition in the intact plots. This competition is thought to be most profound for intact plots in lowland localities.
- iii. Seedlings growing at more marginal localities (intermediate and alpine) will proportionally allocate more resources to roots than to aboveground tissue.

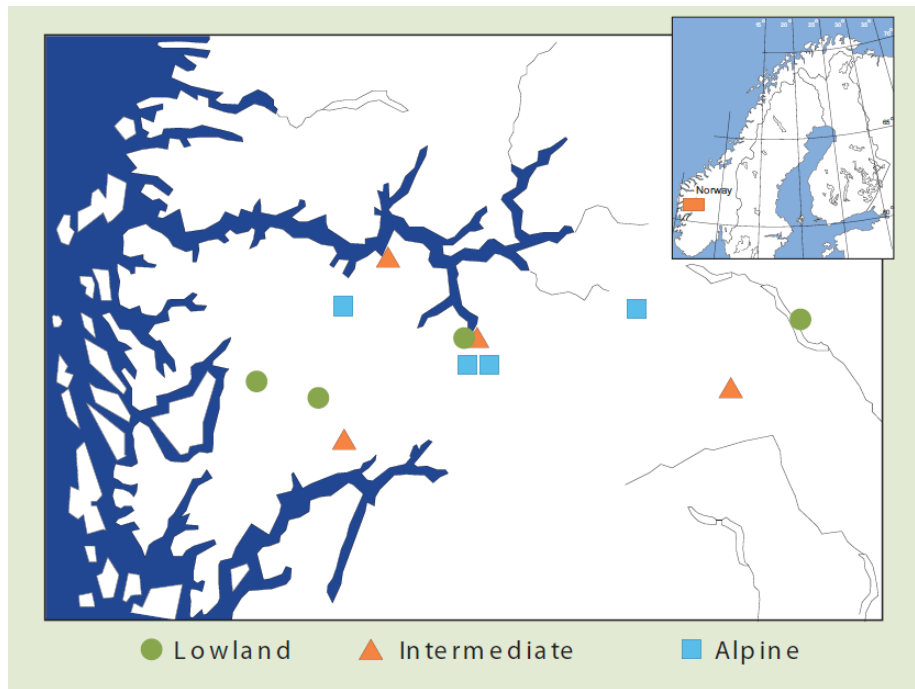
## 2.0 Methods

### 2.1 Study area

In south-west Norway there is a strong precipitation and temperature gradient from the warmer, oceanic coast towards the cooler, more continental inland (Hanssen-Bauer et al. 2003), which make the area suitable for evaluating the impacts of climate change. The whole study area stretches from Voss in the west to Fagernes in the east and includes 12 different field experimental sites (Figure 2.1). The sites used for this study were the same sites as chosen for the “SeedClim” project run by the University of Bergen. The locations were chosen for their climatic attributes (i.e. precipitation and temperature) and also for similarity in vegetation, geology and land use to facilitate comparison among sites. All sites were established in 2008 in low productive meadow ecosystems with high species diversity at a fine scale. The sites are all associated with phyllite or other calcium-rich bedrock (Berge 2010).



**Figure 2 1:** Southern Norway. The study area (grid) is marked by the black square (Moen 1999).



**Figure 2.2:** The twelve sites distributed inside the grid (see map on previous page). Lowland localities are represented by green circles, intermediate by orange triangles and alpine localities by blue squares (SeedClim, 2008).

The localities are divided into three categories based on tetra-term temperature (the mean temperature of the four warmest month per year); lowland (north-boreal), intermediate (sub-alpine) and alpine (low-alpine) (Table 2.1). The temperature gradient is hence made up by the differences in altitudinal position of the localities. The localities are further divided into 4 precipitation categories based on annual precipitation; 1 is dry, 2 is semi-dry, 3 is wet and 4 is very wet (Table 2.1). Hence there is a precipitation gradient from east to west in the study area (Figure 2.2). Climate data used here are obtained from the nearest climate station operated by the Norwegian Meteorological Institute ([www.met.no](http://www.met.no)).

**Table 2.1:** The 12 study sites with abbreviations, local name and UTM coordinates grouped into three elevation categories. Tetra term temperature (mean temperature of the four warmest months) and precipitation (mean annual) data are provided by the Norwegian Meteorological Institute (2009).

Site	Locality (local name)	UTM zone 33	UTM zone 332	Altitude	Precipitation	Temperature ° C
		<i>coordinate x</i>	<i>coordinate y</i>	<i>m asl</i>	<i>Mean annual</i>	<i>Tetra term</i>
<b>Lowland</b>						
LOW1	Fauske	180405.00	6781200.00	589	600	10.33
LOW2	Vikesland	75604.70	6774850.00	474	1161	10.5
LOW3	Arhelleren	27494.10	6756720.00	436	2044	10.6
LOW4	Øvstedalen	7643.94	6762220.00	476	2923	10.78
<b>Intermediate</b>						
INT1	Årust	157951.00	6759200.00	815	789	9.14
INT2	Høgsete	75917.50	6774330.00	700	1356	9.17
INT3	Rambæra	49407.80	6801320.00	779	1848	8.77
INT4	Veskre	35390.20	6742090.00	780	3029	8.67
<b>Alpine</b>						
ALP1	Ulvehaugen	128833.00	6785010.00	1208	596	6.17
ALP2	Låvisdalen	80587.50	6767820.00	1097	1321	6.45
ALP3	Gudmedalen	75285.30	6769540.00	1213	1925	5.87
ALP4	Skjellingahaugen	35627.60	6785870.00	1133	2725	6.58

## 2.2 Study species

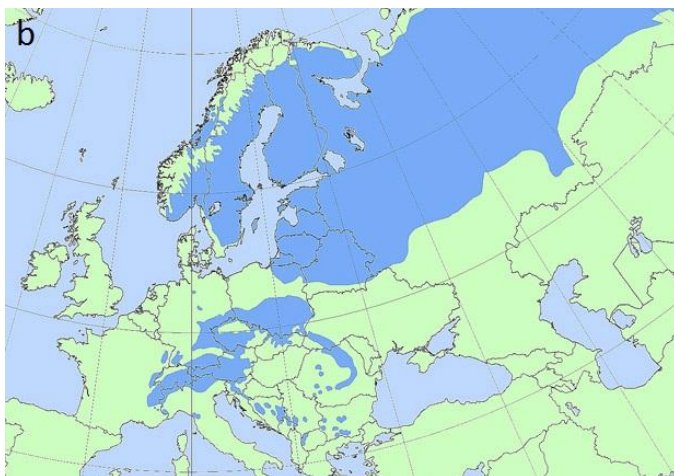
Three common Norwegian tree species, one deciduous and two conifers, were chosen for this study; birch (*Betula pendula*), Scots Pine (*Pinus sylvestris*) and Norway Spruce (*Picea abies*). Nomenclature follows Flora Nordica (2006).

Scots Pine is one of the dominant forest species within the boreal zone and it is well known for its wide ecological range (Ohlson & Zackrisson 1992; Ohlson 1995; White & More 2005). The genera *Pinus* is in fact one of the most widely distributed genera of trees in the Northern Hemisphere. Scots Pine is a species native to Norway, and can be found also at high elevations (Lid 1963; White & More 2005).

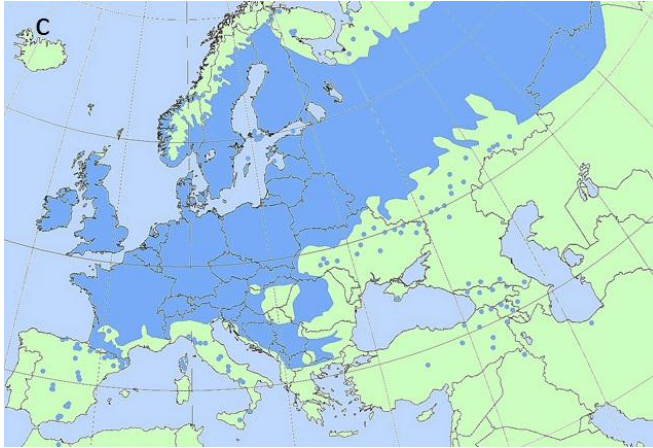
Norway Spruce is a very common conifer in eastern and northern Norway (Lid 1963; White & More 2005). It is native to Norway and an important economic species (Hanssen 2003). The genus is widely distributed over the cooler areas of the Northern Hemisphere, from the Arctic Circle to the more temperate latitudes (Hora 1986). It is known to be a shade-tolerant species.

Birch is native to the north temperate and Arctic regions (White & More 2005) . It is a deciduous tree which is known to be extremely hardy; some species in this genus reach even above the tree limit in the Northern Hemisphere. Seeds used in this study were from the species *Betula pendula*, one of the more characteristic lowland birch species (Jonsell et al. 2000).

All seeds were bought from “Skogfrøverket”, a public supplier of seeds. The seeds had been stored at -20 °C prior to sowing. The pine and spruce seeds used for the experiment had germination capacities of 93 and 92 % respectively. For birch it is normal to refer to the number of germinates per gram of seeds (Pers. comm. Heidi Røsok Bye at Skogfrøverket). For the seeds used in this study, the number was 905 germinates per gram of seeds. The seed quality is regarded as good if the number is above 800 germinates per gram of seeds.





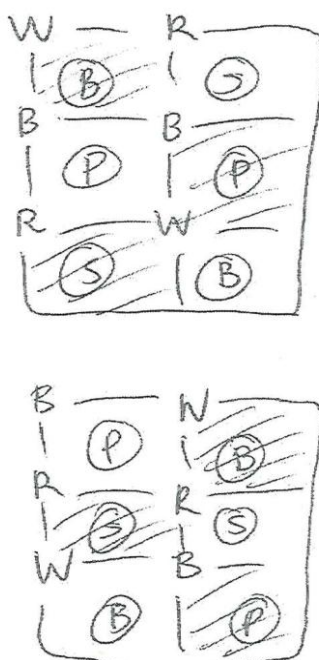


**Figure 2.3:** Distribution maps of a) *Pinus sylvestris*, b) *Picea abies*, c) *Betula pubescens*. Source: [http://www.euforgen.org/distribution\\_maps.html](http://www.euforgen.org/distribution_maps.html)), (compared with “Encyclopedia of trees” to check liability)

### 2.3 Experimental design

At each locality there were five blocks, and every block was split into two experimental main sites; one established in 2009 and another in 2010. Each of these experimental sites was made up of a rectangle which was divided into 6 smaller sub-plots (25 × 25 cm) (hereafter called plots); 2 for each of the study species. These plots were randomly divided into one gap plot and one plot with intact vegetation (Figure 2.4). The gaps were made by removing the upper soil layer with its vegetation, creating a bare soil plot where seeds could be sown.

This was done to minimize the competition from other species, and to see the impact this



**Figure 2.4:** Configuration of study plots. Shaded plots initiate gaps and white plots initiate intact vegetation. Letters in circle represent the species sown in the plot. Letters in the corner represent the colour of the sticks marking the plot. “B” in circle = Birch, “P” in circle = Pine, “S” in circle = Spruce. “B” in corner = blue stick, “R” in corner = red stick and “W” in

would have on tree seedling establishment. The intact vegetation plots had quite dense stands of graminoids and herbs, especially at lowland localities.

The sites were fenced to exclude large herbivores. The study sites were mowed to remove some of the biomass, but the plots were left undisturbed between sowing and harvest.

The first plots were established in 2009, and a new series of plots were made in 2010. In each plot, 50 seeds were sown (a total of 36 000 seeds). Coloured plastic sticks in the corners of the 25×25cm study plots marked which species were sown in which plots (Figure 2.4). The seeds were scattered on the bare soil of created gaps and in the intact vegetation. To prevent seeds from being blown or washed away, the seeds were carefully pressed down on the soil surface, but not covered. The work previous to the field season of 2011 was done by other persons engaged in the SeedClim project and the description of these methods is written from conversations with my supervisors.



**Figure 2.3:** Illustration photo from the locality of Fauske (LOW1). In front to the left near the red pole lies one of my experimental sites with six smaller plots marked with the red, blue and white plastic sticks.

In May and June 2011 I counted and registered all surviving seedlings in the plots. At the end of the growing season (late August and early September) all seedlings in each plot were registered again and harvested during twelve days of field work. Number of plants harvested

equalled the number of plants registered early in the season, except for a few seedlings accidentally trampled by animals. In gap plots with three or more plants present, three seedlings were randomly chosen and extracted from the soil, keeping as much as possible of the root system intact. For this work, a small spade was used to dig around the plant and care was taken not to damage the root system. If there were any remaining seedlings in the gap plots after the removal of three individuals with roots, these were harvested aboveground. This was done with a pair of small scissors and the plants were cut at their basis. Harvest with roots was only performed in gap plots, as it would be too time-consuming to extract the roots from the soil in the intact vegetation without damaging the root system or mixing the roots from the study plants with other plant roots. The seedlings were put in small plastic bags, marked and stored in a fridge with 4 °C and no light until further processing took place.

In the laboratory the seedlings harvested with roots were carefully rinsed in tap water to remove soil and other particles, and then divided into different plant components: roots, stem and needles. The different components were put in separate paper bags and dried in a kiln at 80°C for 24 hours until constant weight. The plants harvested aboveground were individually placed in paper bags and dried. The height and aboveground biomass weight of all seedlings were measured, and in addition measurements of roots, stem and needles were done separately for the subsample of seedlings harvested with roots. The height was measured as total length from the original “emerging” point to the apical meristem. The length of the roots was measured from the “emerging point” to the longest root tip.

Further, I weighed 20 frozen seeds from pine and spruce, and calculated mean seed weight for each species. The seeds were first soaked in water to release the seed coat, and the seed coat was removed before drying and weighing. This was done to be able to calculate total net growth.

## 2.4 Statistical analyses

Mean height, aboveground weight, root length, root weight, needle weight and stem weight were calculated for each plot and used in all statistics. Birch was omitted from the statistical analyses due to the very low number of established seedlings. In order to attain a normal distribution, some of the variables were log-transformed. For Pine the following values were log-transformed: aboveground weight (2009 and 2010), mean needle weight (2009 and 2010), mean stem weight (2009 and 2010) and mean root weight (2009).

To test the effect of precipitation, temperature, location and gap versus intact vegetation on the number of seedlings, a Kruskal-Wallis test was run for each of these factors. This was done separately for pine and spruce and for one cohort at the time.

To test the effect of treatment, temperature, precipitation and their interactions on the different plant morphology traits three-way analyses of variance (ANOVA) was conducted. One three-way ANOVA was run for each of the plant trait responses for pine and spruce separately. The factors were treatment (gap versus intact), precipitation (given as a categorical value of 1-4) and temperature (given as a category value of 1-3) (See table 2.1). This was done separately for the 2009 cohort and the 2010 cohort.

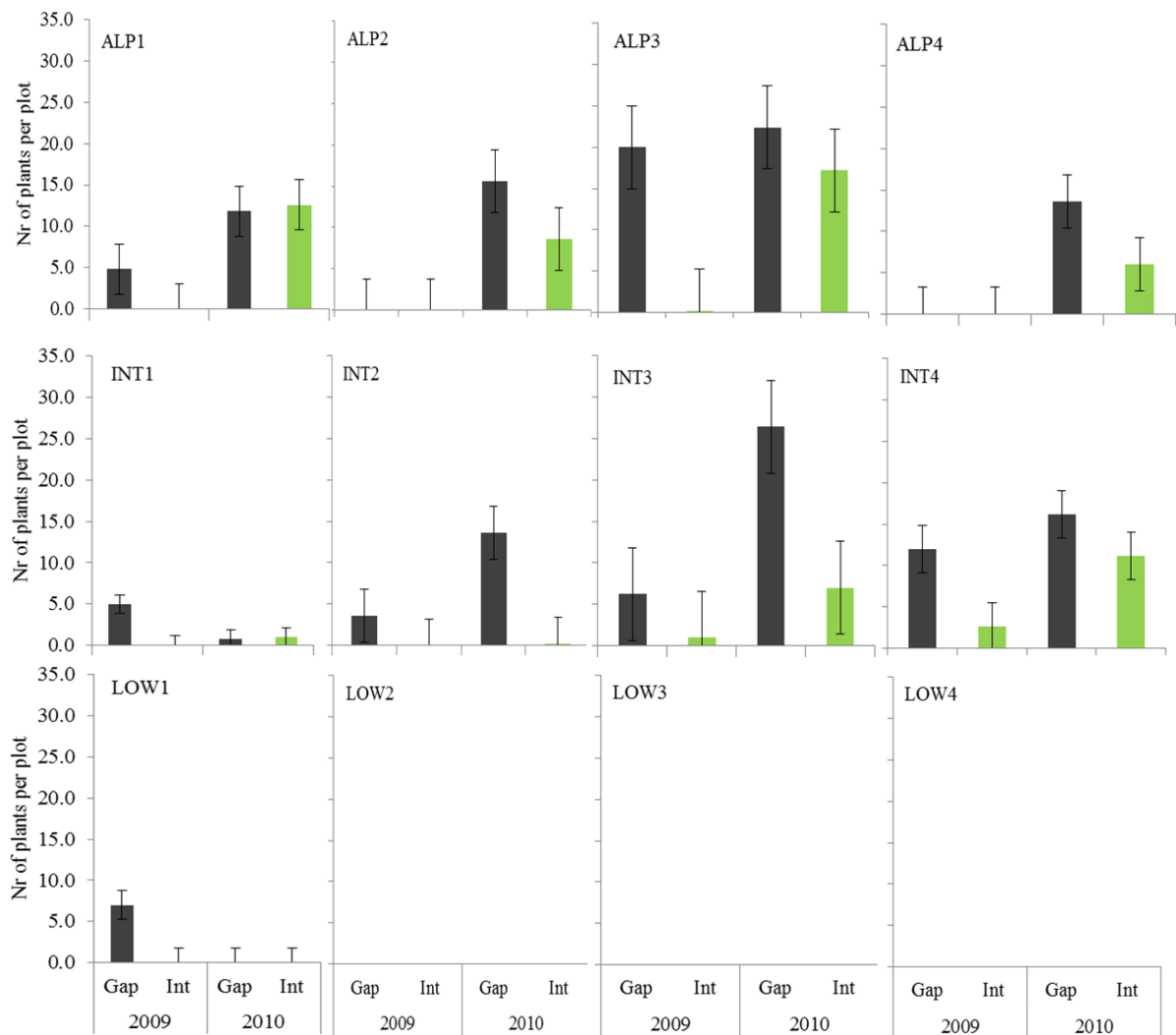
When testing height and aboveground weight, the full data set with all pine and spruce seedlings was used. Subsamples were used for analysing root weight, root length, stem weight and needle weight, as these data were obtained from the plants with roots, which were harvested in gaps with three or more plants present only. For the subsamples, tests were two-way ANOVAs with precipitation and temperature as explanatory variables.

The p-values were adjusted using “Holm”-method and the significance level was set to 0.05. Significant interactions were further investigated using Tukey’s post hoc test.

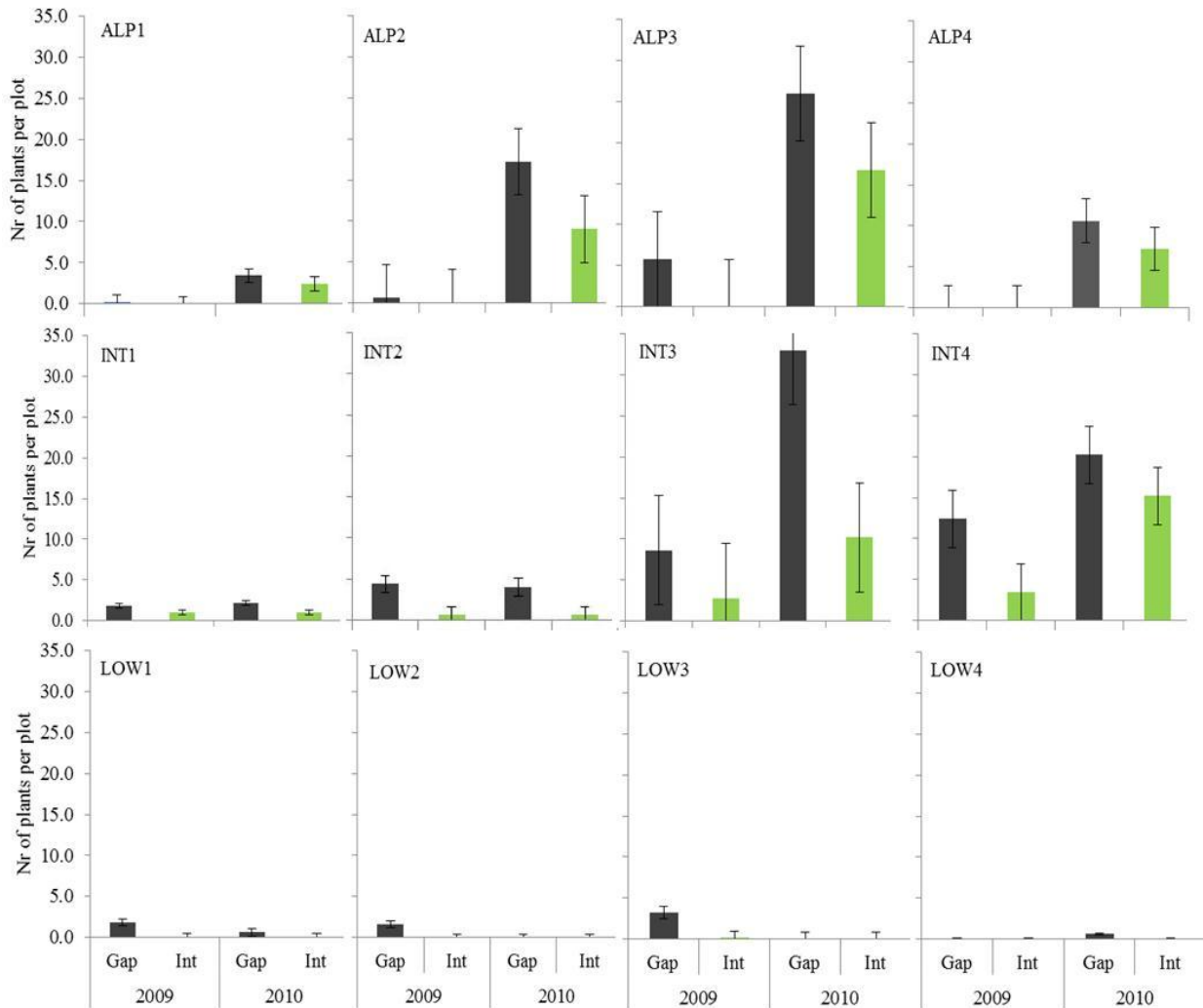
All statistical analyses were performed in R Studio, version 2.14.1 (R Development Core Team, 2009) and the graphic illustrations were made in R Studio or Excel 2010.

### 3.0 Results

In total, 2377 seedlings were registered and harvested in 71 intact plots and 136 gaps. In the remaining 513 plots no seedlings were found. Among the seedlings harvested were 1226 pines, 1138 spruces and 13 birches. Due to the low number of birches present this species was omitted from further analyses. In the gaps, the number of emerged seedlings ranged from 0 to 44 for spruce and from 0 to 41 for pine. In the intact vegetation plots the number ranged from 0 to 37 for spruce and from 0 to a maximum of 26 for pine.



**Figure 3.1:** Number of pine seedlings per plot at each of the 12 localities. The bar charts are arranged as they lie in the climate grid. Vertical axes goes from lowland to alpine and horizontal axes from dry to wet (left-right). Green bars show mean number of plants per plot in intact vegetation, and dark bars show the mean number of plants per plot in gaps where the vegetation was removed.



**Figure 3.2:** Number of spruce seedlings per plot at each of the 12 localities. The bar charts are arranged as they lie in the climate grid. Vertical axes goes from lowland to alpine and horizontal axes from dry to wet (left-right). Green bars show mean number of plants per plot in intact vegetation, and dark bars show the mean number of plants per plot in gaps where the vegetation was removed.

### 3.1 Number of plants

The numbers of established seedlings differed significantly among the localities (Figure 3.1 & 3.2) and there were significant effects of temperature, precipitation and treatment (Table 3.1 & 3.2). The overall pattern showed that there were more plants in the western part of the grid. A significantly higher rate of establishment of spruce and pine seedlings was found at intermediate and alpine localities compared to lowland localities; a result contrary to what I expected (Figure 3.1& 3.2; Table 3.1 & 3.2). The variation within each of the temperature categories was highest for the intermediate and alpine localities, while at the lowland

localities the within-category variation in number of plants per plot was relatively small (Figure 3.3). At intermediate and alpine localities the number of plants increased with increasing amounts of precipitation, while that was not the case for lowland localities (Figure 3.4).

More plants were found in gaps than in intact vegetation plots (Figure 3.1 & 3.2). Overall, 73 % of the pine seedlings and 69 % of the spruce seedlings were found in gap plots.

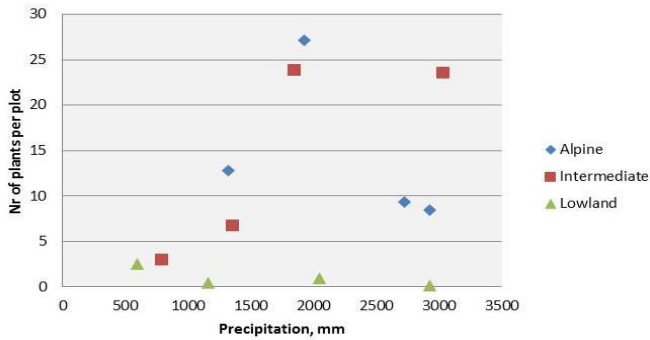
For both species the 2010 cohorts contained a significantly higher number of seedlings than 2009 cohorts, indicating that seedlings may suffer from mortality in their second growing season.

Table 3.1: Results from Kruskal-Wallis tests on the number of pine seedlings.

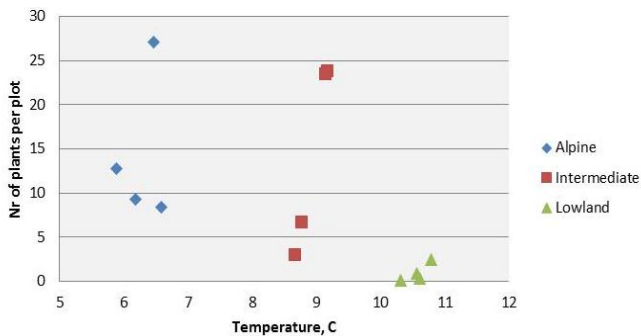
<b>PINE</b>	<b>2009</b>	<b>2010</b>
	<b>P - value (df)</b>	<b>P-value (df)</b>
<b>Factors</b>		
Temperature	<0.01 (11)	<0.01 (11)
Precipitation	<0.01 (10)	<0.01 (10)
Site	<0.01 (11)	<0.01 (11)
Gap vs intact	<0.01 (1)	<0.05 (1)

Table 3.2: Results from the Kruskal-Wallis test in the number of spruce seedlings.

<b>SPRUCE</b>	<b>2009</b>	<b>2010</b>
	<b>P - value (df)</b>	<b>P-value (df)</b>
<b>Factors</b>		
Temperature	<0.01 (11)	<0.01 (11)
Precipitation	<0.01 (10)	<0.01 (10)
Site	<0.01 (11)	<0.01 (11)
Gap vs intact	<0.01 (1)	0.076 (1)



**Figure 3.3:** Mean number of plants per plot at the different altitudes plotted against mean annual precipitation. The figure includes data from both the 2009 and 2010 cohort.



**Figure 3.4:** Mean number of plants per plot at the different altitudes plotted against temperature. The figure includes data from both the 2009 and 2010 cohort

### 3.2 Morphological traits

The results revealed that seedling growth patterns differed along both the precipitation-gradient and the temperature gradient.

#### *Height*

The tallest pine seedlings were found in intact vegetation plots of the westernmost alpine localities (Figure 3.5 & 3.6). The analysis of variance showed that temperature and gap vs. intact affected the height of pine seedlings significantly (Table 3.3). There was no significant effect of precipitation on the height growth of pine seedlings, but it was fairly close to significant for the 2009 cohort with a p-value of 0,075. The trends are however still rather similar both between years and species for the precipitation factor. In addition, the analyses revealed a significant interaction between temperatures and gap vs. intact for the 2009 cohort, suggesting that the effect of gap treatment on height growth differed between lowland, intermediate and alpine localities. Tukey's post hoc test showed that the height of plants in



gap plots at lowland and intermediate localities were significantly lower than that of the plants in alpine intact plots ( $P < 0.05$ ) (Figure 3.5).

The mean height of spruce seedlings was also significantly affected by temperature, precipitation (2009 cohort) and treatment (2010 cohort) (Table 3.4). In addition, there was a significant interaction between gap vs. intact and temperature, suggesting that the treatment effect differed along the altitudinal gradient. Tukey’s post hoc test showed that the height in the gap plots at the lowland and the intermediate localities were significantly different from the height of plants in gap plots at the alpine localities for the 2009 cohort which were taller ( $P < 0.05$ ). For 2010 cohort no pine seedlings were found at the lowland localities.

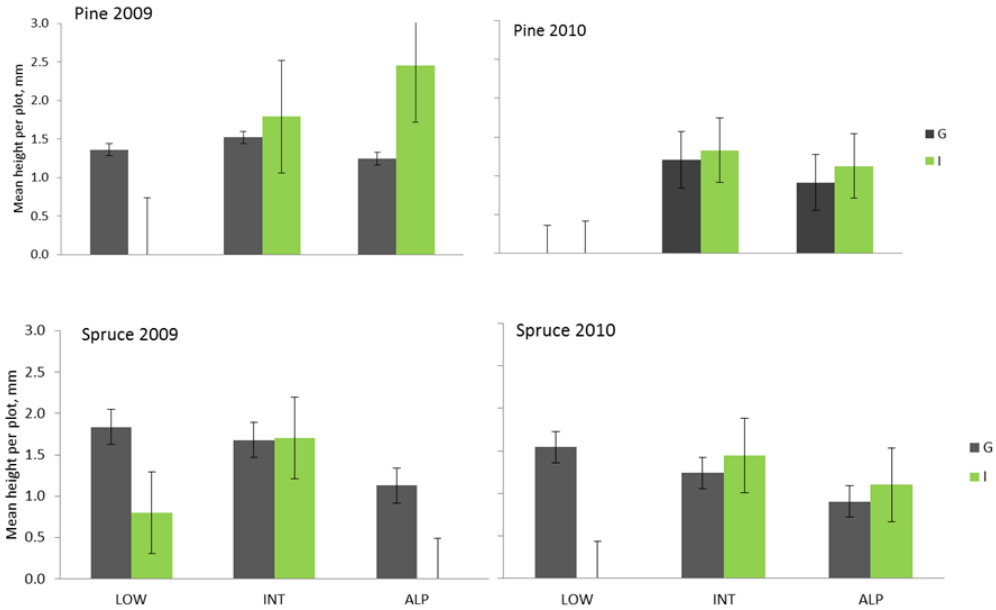


Figure 3.5: Mean height per plot (mm) for the different temperature categories; lowland, intermediate and alpine.

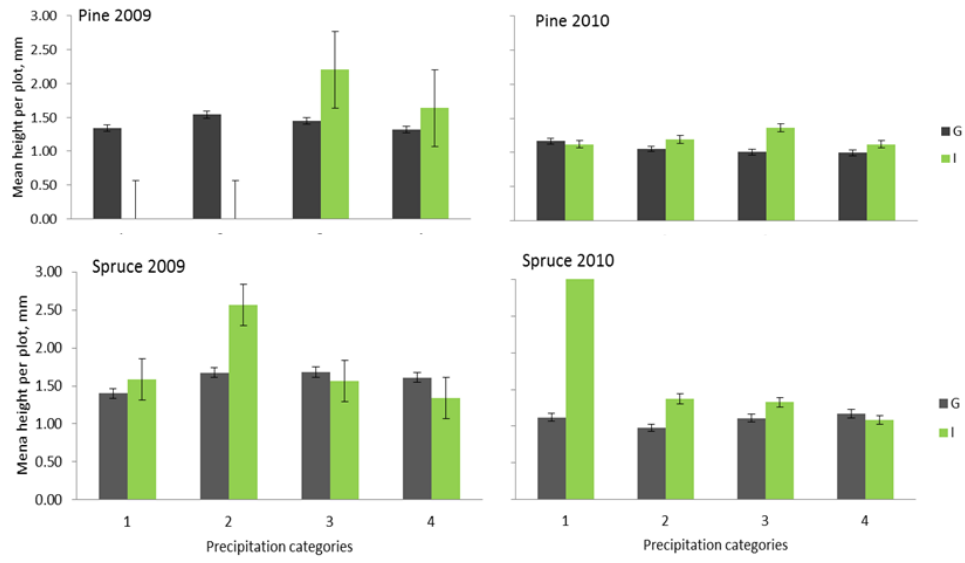


Figure 3.6: Mean height per plot (mm) for the different precipitation categories. 1= dry, 2= semidry, 3= wet and 4 = very wet.

**Table 3.3.** Summary of ANOVA for effects of climate and treatment (gap versus intact) on the morphological traits of pine seedlings. Data are based on mean values from plants sown in 2009 and 2010. Non-significant interactions are not shown

<b>PINE</b>		<u>2009</u>		<u>2010</u>	
Effects	<i>df</i>	F	P	F	P
<b>Response: mean height</b>					
<i>Temperature</i>	2	2.2	0.152	23.5	< <b>0.01</b>
<i>Precipitation</i>	3	2.8	0.075	1.6	0.201
<i>Treatment (gap.intact)</i>	1	14.8	< <b>0.001</b>	13.8	< <b>0.01</b>
<i>Temperature × gap.intact</i>	1	6.4	< <b>0.05</b>	-	-
<b>Response: mean aboveground biomass</b>					
<i>Temperature</i>	2	3.5	< <b>0.05</b>	35.6	< <b>0.001</b>
<i>Precipitation</i>	3	1.9	0.161	2.1	0.122
<i>Treatment (gap.intact)</i>	1	4.3	0.055	7.9	< <b>0.01</b>
<b>Response: mean root biomass</b>					
<i>Temperature</i>	2	5.3	< <b>0.05</b>	6.4	< <b>0.05</b>
<i>Precipitation</i>	3	1.7	0.216	1.6	0.211
<b>Response: mean root length</b>					
<i>Temperature</i>	2	5.6	< <b>0.05</b>	2.9	0.101
<i>Precipitation</i>	3	0.8	< <b>0.05</b>	1.7	0.192
<b>Response: mean needle biomass</b>					
<i>Temperature</i>	2	1.5	0.251	16.5	< <b>0.001</b>
<i>Precipitation</i>	3	2.8	0.085	1.6	0.229
<b>Response: mean stem biomass</b>					
<i>Temperature</i>	2	1.3	0.306	22.1	< <b>0.001</b>
<i>Precipitation</i>	3	1.3	0.320	0.5	0.684
<i>Temperature × precipitation</i>	3	-	-	3.9	< <b>0.05</b>

**Table 3.4.** Summary of ANOVA for effects of climate and treatment (gap versus intact) on the morphological traits of spruce seedlings. Data are based on mean values from plants sown in 2009 and 2010. Non-significant interactions are not shown.

<b>SPRUCE</b>		<u>2009</u>		<u>2010</u>	
Effects	<i>df</i>	F	P	F	P
<b>Response: mean height</b>					
<i>Temperature</i>	2	9.4	< <b>0.001</b>	10.1	< <b>0.001</b>
<i>Precipitation</i>	3	4.2	< <b>0.05</b>	0.7	0.546
<i>Treatment (gap.intact)</i>	1	1.1	0.308	5.9	< <b>0.05</b>
<i>Temperature × treatment</i>	1	9.5	< <b>0.05</b>	-	-
<b>Response: mean aboveground biomass</b>					
<i>Temperature</i>	2	5.3	< <b>0.05</b>	6.4	< <b>0.01</b>
<i>Precipitation</i>	3	0.7	0.542	1.1	0.578
<i>Treatment (gap.intact)</i>	1	3.1	0.090	2.6	0.116
<b>Response: mean root biomass</b>					
<i>Temperature</i>	2	2.6	0.117	8.9	< <b>0.01</b>
<i>Precipitation</i>	3	2.1	0.175	0.6	0.629
<i>Temperature × precipitation</i>	3	-	-	4.5	< <b>0.05</b>
<b>Response: mean root length</b>					
<i>Temperature</i>	2	11.1	< <b>0.01</b>	1.1	0.387
<i>Precipitation</i>	3	1.7	0.206	0.9	0.446
<b>Response: mean needle biomass</b>					
<i>Temperature</i>	2	1.2	0.350	6.5	< <b>0.01</b>
<i>Precipitation</i>	3	2.9	0.09	2.5	0.091
<b>Response: mean stem biomass</b>					
<i>Temperature</i>	2	2.2	0.154	4.1	< <b>0.05</b>
<i>Precipitation</i>	3	0.7	0.550	0.6	0.637

## Aboveground Biomass

Seedlings of both species had a higher biomass in gap plots than in intact vegetation plots. The direct effect of this treatment was, on the other hand, only clearly significant for the 2010 cohort and close to significant for the 2009 cohort of pine seedlings (Figure 3.7 & Table 3.3). The effect of treatment was not proven significant for the spruce seedlings (Table 3.4). The aboveground biomass was significantly affected by temperature. There was no significant effect of precipitation on the mean aboveground biomass for neither spruce nor pine (Table 3.3 & 3.4).

The aboveground biomass for pine was highest at lowland localities (cohort 2009) and decreased with decreasing temperature (Figure 3.7). Pines sown in 2009 had a larger biomass in gap plots, while the difference between biomass in gap and intact plots was smaller for the 2010 cohort (Figure 3.7). Pines showed larger variation in dry weight biomass than spruce. Spruce seedlings at the intermediate localities had the highest aboveground biomass (Figure 3.7). Spruce seedlings in lowland gaps were tall, but had a comparably low biomass. The same trend could be found for spruce seedlings in intact vegetation at intermediate and alpine localities for the 2010 cohort (Figure 3.7). This indicates climate-specific trends in the seedlings allocation patterns.

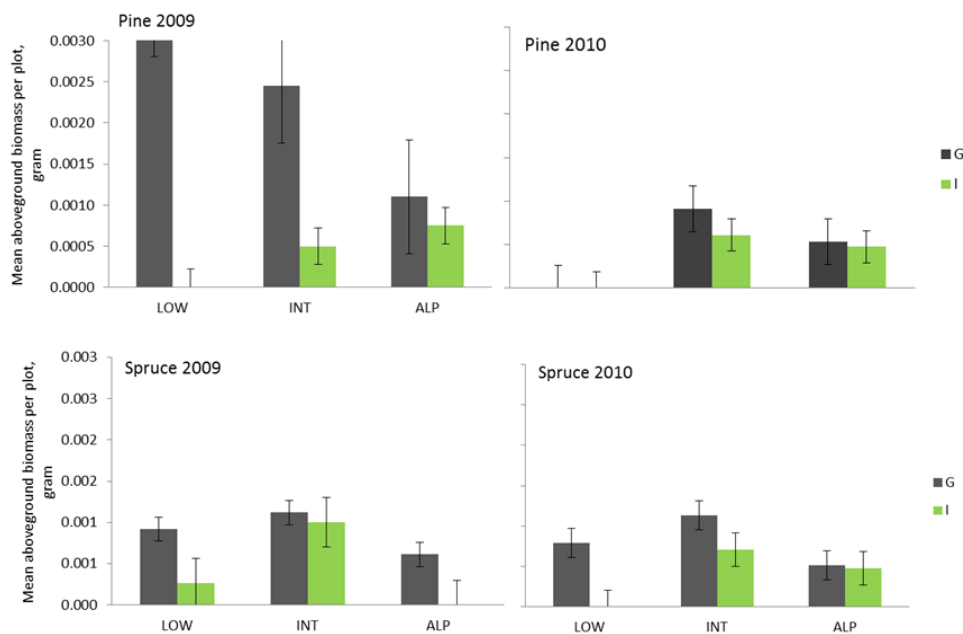


Figure 3.7: Mean aboveground biomass (gram) per plot for the different temperature categories; lowland, intermediate and alpine.

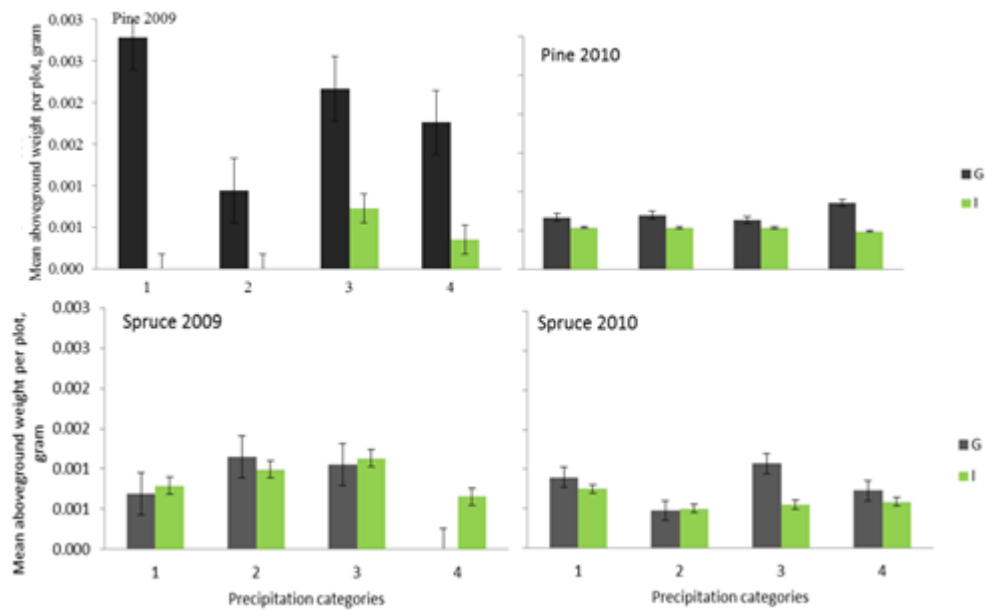


Figure 3.8: Mean aboveground biomass (gram) per plot for the different precipitation categories. 1 = dry, 2 = semidry, 3 = wet and 4 = very wet.

### *Allocation*

Roots of both species were longer at intermediate and alpine localities for both cohorts, and the root: shoot length ratio was larger for intermediate and alpine localities compared to lowland localities (Figure 3.9).

The pine seedlings in lowland localities from the 2009 cohort had a large root and needle biomass (Table 3.5). This result might be biased due to few pine seedlings found at the lowland localities in the plots from 2009, and due to one extreme individual with values well above the mean for both weight and length.

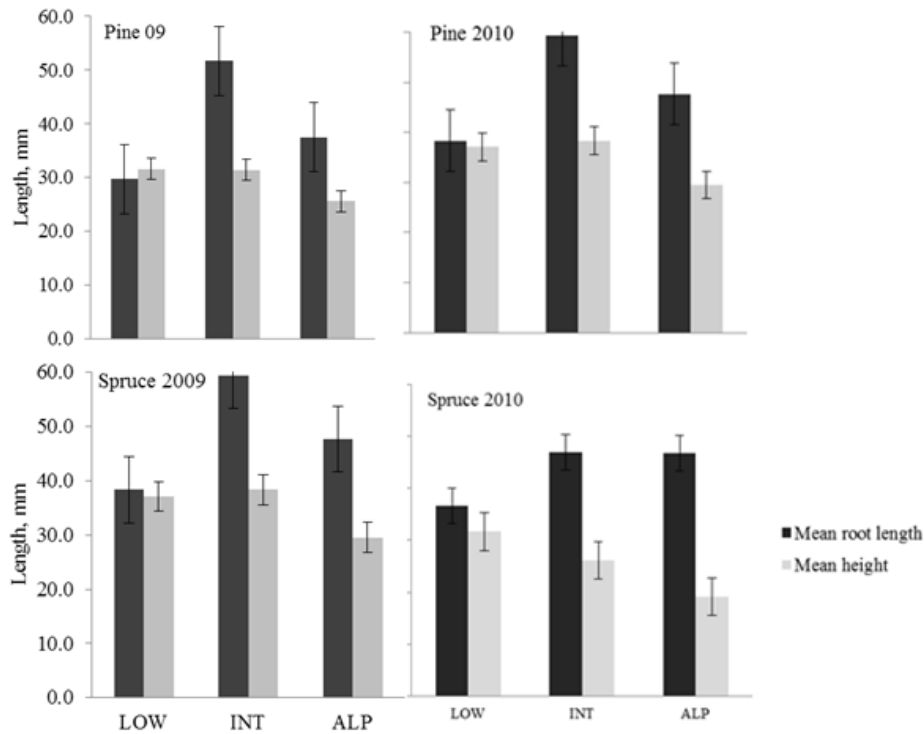


Figure 3.9: Root length (mm) and plant height (mm) of pine and spruce seedlings for the different temperature categories: lowland, intermediate and alpine.

Table 3.5: Biomass allocation for pine and spruce. Numbers are based on mean values. Standard errors are shown.

	Root biomass $\pm$ SE	Needle biomass $\pm$ SE	Stem biomass $\pm$ SE
Pine 09			
<i>Low</i>	0.0532 $\pm$ 0.049	0.0625 $\pm$ 0.0523	0.0077 $\pm$ 0.0021
<i>Int</i>	0.0104 $\pm$ 0.001	0.0209 $\pm$ 0.003	0.0122 $\pm$ 0.0025
<i>Alp</i>	0.0054 $\pm$ 0.0006	0.0132 $\pm$ 0.002	0.007 $\pm$ 0.0006
Pine 10			
<i>Low</i>			
<i>Int</i>	0.0087 $\pm$ 0.0009	0.0148 $\pm$ 0.0015	0.0058 $\pm$ 0.0004
<i>Alp</i>	0.0053 $\pm$ 0.0008	0.0082 $\pm$ 0.0005	0.0036 $\pm$ 0.0002
Spruce 09			
<i>Low</i>	0.0048 $\pm$ 0.0007	0.0061 $\pm$ 0.0008	0.0061 $\pm$ 0.0005
<i>Int</i>	0.0139 $\pm$ 0.0013	0.0193 $\pm$ 0.003	0.0144 $\pm$ 0.0028
<i>Alp</i>	0.0065 $\pm$ 0.0009	0.0123 $\pm$ 0.0022	0.0069 $\pm$ 0.001
Spruce 10			
<i>Low</i>	0.0034 $\pm$ 0.002	0.0069 $\pm$ 0.0016	0.0052 $\pm$ 0.0017
<i>Int</i>	0.0097 $\pm$ 0.0009	0.0127 $\pm$ 0.0011	0.0073 $\pm$ 0.0013
<i>Alp</i>	0.0053 $\pm$ 0.0003	0.0076 $\pm$ 0.0004	0.0033 $\pm$ 0.0002

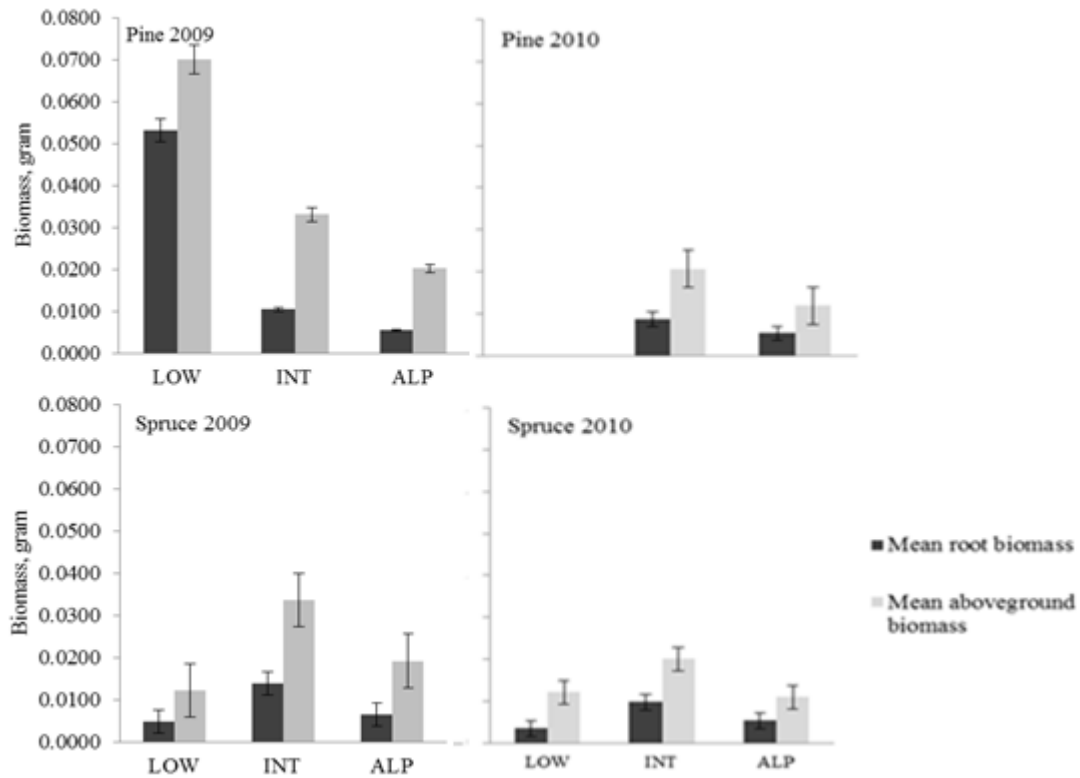


Figure 3.10: Root biomass and aboveground biomass for the different temperature categories; lowland, intermediate and alpine.

Temperature had a significant impact on both the length and biomass of roots of pine seedlings from the 2009 cohort ( $P < 0.05$ ). For the 2010 cohort, only the root length was significantly affected by temperature. Precipitation was only significant for the mean root length of the 2009 cohort of pine seedlings (Table 3.3), and it is therefore not shown in the figures. For spruce seedlings, significant values were found for the root weight of the 2010 cohort and the root length of the 2009 cohort (Table 3.4). Precipitation had no significant impact on the root growth of spruce seedlings.

The ANOVA showed one significant interaction between temperature and precipitation for root weight of spruce in the 2010 cohort ( $P < 0.05$ ) (Table 3.4). Tukey's test revealed that in the wettest sites (precipitation category 4), the root biomass was significantly larger at the intermediate localities compared to the alpine localities. The aboveground biomass was larger than the root biomass for all groups (Figure 3.10). The difference between root and aboveground biomass seemed to be larger at the intermediate and the alpine localities,

compared to at the lowland localities. This may say something about the allocation patterns of spruce and pine seedlings and how it relates to climatic factors.

Needle biomass for both spruce and pine seedlings from the 2010 cohort were significantly affected by the temperature ( $P < 0.001$ ) (Table 3.5). The highest values for needle biomass were found at lowland localities for pine, and decreased with increasing altitude. The highest values for needle biomass for spruce were found at intermediate localities. Both spruce and pine followed the same trends at intermediate and alpine localities.

### *Seed weight*

When dry seed biomass was subtracted from the biomass of the plant, the results revealed that the average seedling had gained weight during the study period. The mean dry seed biomass for pine was 0.031 grams and 0.039 grams for spruce, numbers which are much lower than the mean total dry biomass of 0.271 and 0.296 for pine and spruce, respectively. There were also examples of a few seedlings that had almost no net growth, i.e. the dry biomass of the seedling nearly equalled the dry seed biomass.



Figure 8: Illustration photos. a) a pine stem collected at Vikesland (Low2). This stem was from a seedling sown in a gap plot in 2009. At the time of harvest it had fulfilled its third growing season, and the growth nodes are clearly visible, as is the apical meristem at the top. b) a pine seedling from a gap plot at Fauske (Low1) sowed in 2010. This seedling had a very short root with few branches. c) A pine seedling collected at Gudmedalen (ALP3), in the more western, alpine part of the grid. This seedling was sown in 2009, and it looked viable and healthy at the time of harvest. The picture shows the needles from the first year, and the length growth during the second season with the new set of needles in an upper crown (light green needles). The roots on this seedling were short, but they were more branched compared with the roots on the seedling in b). All photos: Lise Tingstad.



## 4.0 Discussion

This study reveals that the establishment success of pine and spruce seedlings is clearly affected by climatic attributes like precipitation and temperature. The dominant role of temperature for successful reproduction among trees has been found in several previous studies (Grace et al. 2002; Juntunen & Neuvonen 2006; Kullman & Engelmark 1990; Kullman 2001; Payette & Fillion 1985; Tranquillini 1979). However, the results contradict my hypothesis regarding temperature, as the establishment rates were higher at the colder localities. This may suggest that different biotic interactions override the temperature factor as determinant of establishment success.

### 4.1 Number of plants

My hypothesis was that in general more seedlings would be found at the warmer and wetter localities. The latter was confirmed, as the number of pine and spruce was higher in the western part of the grid. The western part had the highest precipitation, which could favour seedling establishment. According to the expectations and previous studies mentioned (e.g. (Körner & Paulsen 2004) most plants should have been found localities like Arhelleren (Low3) and Øvstedalen (Low4), but this was certainly not the case, and there can be several possible explanations for this. There was a positive relationship between number of seedlings and increasing precipitation, but at intermediate and alpine localities only. For the lowland localities there was almost no difference in number of plants observed along the precipitation gradient. For the temperature gradient the results revealed an opposite trend than expected, since lower temperatures did not seem to restrict establishment. The establishment rate for pine and spruce was significantly higher at the intermediate and alpine localities, and in comparison very few plants were found at the warmer lowland localities. The competition from other plants might have been the general inhibiting factor at lowland localities, neutralizing the potential positive effects of increased precipitation along the east-west gradient and a generally higher temperature at lower elevation. Increased establishment rate at western localities could also be due to increased snow cover through winter precipitation, which may function as insulation and reduce the risk of frost damage. Frost heaving has been

reported to be one of the most common causes of seedling damage and mortality during the 1<sup>st</sup> winter (Erefur et al. 2008), stressing the importance of an insulating snow cover.

One of the most parsimonious explanations for the low number of seedlings found at lowland localities is competition. Plants growing in the same locality compete for many resources; e.g. light, space, water and nutrients. Interspecific competition rates are higher at lowland localities both due to higher species diversity, a generally higher growth rate which leads to more biomass and denser vegetation compared to the intermediate and the alpine localities. There are many fast-growing species of herbs and graminoids in the lowland that easily outperform small tree seedlings with a slower growth rate. Many of the lowland plots were quite overgrown at the time of harvest (e.g. Vikesland). The competing plants probably came from the soil seed bank or the seeds had landed on the bare soil of a gap plot shortly after the gap was made. The thick humus layer, as found in several of the lowland localities in this study, may be considered negative for regeneration of spruce seedlings because it takes the seedlings too long to grow roots into the mineral soil which provides more stable moisture conditions (Hanssen 2003). This factor may be part of what is limiting the conifer seedlings at the otherwise suitable lowland localities. In the alpine zone, the native plant species are slower growing and most of them do not get very tall, suggesting they are not as good competitor species (Krebs 2001). Interspecific competition is lower at the more marginal and colder alpine localities, which the results in this study also indicate. The intermediate localities seem to be the most suitable for conifer seedling establishment in this study. These localities do not have the high competition rates of the lowland, and not the harsh climatic conditions of the alpine area.

The effect of competition was experimentally tested by comparing gaps and intact vegetation plots. The gap plots were created manually, but the natural equivalent of gap plots is often found as clearings, small disturbed areas or canopy gaps in forests (Gray & Spies 1996). In my study, there were a significantly higher number of seedlings found in gap plots compared to intact vegetation plots, and this trend was consistent across the whole grid. Previous studies also show higher emergence and establishment of seedlings in gaps (Gray & Spies 1996; Munier et al. 2010). Despite the slight differences in the two conifer species' requirements, both will most likely benefit from a canopy gap (de Chantal et al. 2003), as the lower competition rate for seedlings is positive for establishment and growth. Still, at the lowland localities very few seedlings were found even in the gap plots. Seedlings in gap plots are generally more exposed and hence more vulnerable to injuries and damage (Munier et al.

2010). However, the low number of seedlings in the lowland gaps in my study is probably due to the higher level of competition, as many of the lowland gaps were invaded by surrounding vegetation.

Microsite facilitation might lie behind some of the local results. Establishment of tree seedlings might in general be facilitated by inanimate objects (e.g. rocks, logs) or intra- or interspecific associations (Smith et al. 2003). A local factor facilitating seedling establishment could for example be the presence of a tree stand, or a small hill nearby the study plots providing conditions better than expected from the altitudinal position of the plot. Germino et al. (2002) found that young seedlings had a higher survival rate closer to tree islands, or when they had overhead structures such as fallen stems. Rambæra (locality INT 3), which had the highest establishment rate among the intermediate localities, is situated right in front of a small cliff that may have had a sheltering effect and could potentially have improved conditions for establishment. In the near vicinity of the study site at Rambæra, saplings and small trees of all three study species were observed, confirming the area as generally suitable for natural tree germination and establishment, and it is likely to be so also in an experimental setting. Structural self-facilitation (e.g. cotyledon orientation, needle clustering) may also enhance seedlings carbon gain and seedling survival (Smith et al. 2003). Increased seedling establishment could on one hand be followed by even greater facilitation, leading to greater seedling and sapling growth, creating a positive feedback mechanism. On the other hand, too many seedlings in one area can result in increased competition and self-thinning.

Gaps can also have different microclimatic conditions, and gaps probably facilitate establishment and growth more at the intermediate and alpine localities compared to the lowland localities. In gap plots, the sun radiance is stronger during the day, possibly raising daytime mean temperature and increasing the evaporation of water from the soil. The night time temperature will most likely be utterly lowered in gap plots due to the direct exposure to the cold night sky. Hence, seedlings in gap may experience more drought - and temperature-related stress (Smith et al. 2003). Another study found that seedling growth of Ponderosa Pine (*Pinus ponderosa*) increased with increasing night time mean temperatures (Coop & Givnish 2008), proposing that the direct exposure in gaps might have a negative influence on seedling survival. However, since the gaps created for this study are relatively small (25×25 cm), drought stress from increased evaporation or temperature stress is not thought to be a major problem, as the higher establishment rate in gap plots suggests. In this study, there is probably a benefit of gaps. The increased irradiance in gap plots can be positive for photosynthesis and

carbon gain. The light environment is by some said to be even more important for plant establishment than other factors like nutritional status (Erefur et al. 2008), suggesting that high light levels can compensate for lower nutritional levels in the soil and the potentially higher drought and temperature-related stress in gap plots. Erefur (2008) found that light was the limiting factor for growth. Altitude (and hence temperature) was not directly a part of her study, but if the conifer seedling establishment in this study was not temperature-limited, Erefur's results might be of interest. Light might be one important factor determining establishment success, and could potentially explain the low establishment rates at the lowland localities.

However, tree seedlings are small, and all though they have established and survived for two and three growing seasons at several of the localities in this study, it is not given that these seedlings would have become mature trees if they had not been harvested. The microclimatic conditions are different for a small seedling reaching only 2-6 centimetres above ground than for a sapling or a taller tree. As the plant grows, it loses the thermal advantage of being short. The apical meristem will experience a temperature different from that near the ground, and the whole plant will be more prone to abiotic factors like wind exposure (Smith et al. 2003). This architectural disadvantage of trees is probably one important factor limiting the development from seedlings and saplings to full-grown trees in the alpine ecotone. Further, neighbouring plants will not provide the same shelter for a tree as for a small seedling. According to Körner and Paulsen (2004), tree seedlings are commonly found above the tree line, nested into the low stature alpine vegetation, but few of them become mature trees. There may therefore develop an extensive zone of short and stunted seedlings or saplings above the tree line which fail to develop into trees, or they display climatically shaped growth forms (often referred to as *krummholz*) (Grace et al. 2002). Further studies should be conducted in order to find out if seedlings emerging and surviving the first season(s) in fact have a real chance of maturing and producing new generations of trees. Juntunen and Neuvonen (2006) found that small seedlings of both pine and spruce showed higher mortality than larger trees. Thus the seedling stage might be the most critical of life stages.

In the statistical analysis there was an overall significant effect of what I called "temperature" on the number of seedlings. The different temperatures derive from the three levels of altitude, and therefore, in the interpretation of these results, it must be considered whether the significance originally derives from the temperature factor alone. Altitude is a complex gradient consisting of more than just temperature. Lowland, intermediate and alpine localities

also differ in nutrient availability, soil/humus depth, seed-bed substrate and other abiotic factors like wind exposure (Smith et al. 2003). The number of plants at a given locality will be impacted by all of these factors and in addition by seasonal differences and local variation in topography and microclimate. These effects might locally overrule the broad scale climatic conditions (Holtmeier & Broll 2007). In some cases, tree line rise might be the result of phenotypic responses of individual trees to more favourable local conditions rather than a real advance of tree growth to higher elevation (Holtmeier & Broll 2005). It is not known for sure which factor(s) that have been the most protruding in defining the conditions for seedlings in this study. In Synnfjell mountain area in Southern Norway there was also found significant effect of different altitudes on the establishment and growth of spruce seedlings (Christensen 1999).

Spruce and pine have partly different requirements for growth, the former being a shade-intolerant and the latter a more shade-tolerant species (Ohlson & Zackrisson 1992). This can be seen in the results; in fact pine did better than spruce at most localities, but to a lower extent in intact plots compared to gap plots. The more shade-tolerant spruce seedlings were closer to match the number of pines in the intact plots, a result which is in line with the theory of growth requirements for both species. However, in general the two conifer species showed very similar trends in this study for both cohorts.

Seed predation could possibly be a limiting factor for establishment of trees. Common post-dispersal predators on pine and spruce seeds are various birds, rodents and many insects such as ground beetles (Smit et al. 2006). If seeds are uncovered they will be easily detected by visually searching seed-predators, but covered seeds will still be detectable for predators using olfaction (Nilson & Hjältén 2003). On northern Scandinavian clear-cuts, birds are thought to be the most important seed predators on pine, and a study indicated that covering of the seeds reduced predation, but at the same time lowered germination frequency (Nilson & Hjältén 2003). Seeds were not covered in our study, and seed-predation might have had an influence on the establishment rate, maybe especially at the lowland localities. Nilson (2003) showed that seed removal by various predators was highest in intact vegetation (Nilson & Hjältén 2003). Another study found lower seed predation levels on *Pinus*-seeds on clear-cuts compared to sheltered sites (Nystrand & Granstrom 2000).

Large-seeded species often have an establishment advantage over small-seeded species (Turnbull et al. 1999), and both spruce and pine have relatively large seeds (Jonsell et al. 2000). Production of large seeds is more resource demanding and large-seeded species often

produce a lower quantity of high-fecundity seeds (Turnbull et al. 1999). Spruce and pine seeds might have a competitive advantage when introduced to the alpine environment because of their relatively larger seed size. In comparison, birch seeds are very small and might have experienced a competitive disadvantage.

Birch was omitted from all analyses due to a very low number of registered seedlings. The low number of birch in the plots could seem surprising, since birch normally is one of the most common tree species found in the alpine ecotone in Norway (Larsson 2004; White & More 2005). Observations of mature birch trees were made in the vicinity of several of the lowland and intermediate localities, but the observed trees were most likely from either *B. pubescens* or *B. tortuosa*, two birch species with a wide distribution in Norway (Jonsell et al. 2000). *B. tortuosa* is normally one of the most common tree species at high elevations in Norway (Jonsell et al. 2000). Seeds used in this study were from *B. pendula*. I believe this seed source was not optimal, and the results from the birch plots may not be representative for birch establishment at tree line ecotones. *B. pendula* is common in the southern lowland, but is normally not found above 900 meters (Jonsell et al. 2000; Lid 1963). Hence, the seeds sown in this experiment probably did not have the best prerequisites for establishment at high elevations. Future seed sowing experiments might benefit from choosing a different seed source if possible. In addition, birch seeds are very small and light, and could be blown away or washed away by heavy rainfalls. This might have happened at some of the localities, but it cannot explain the low number of seedlings in the entire climate grid. Birch trees normally produce a huge amount of wind dispersed seeds. Many thousands of seeds might land within a small area, and in this experiment only 50 seeds were added to each plot. For spruce and pine this number is more equal to the natural seed rain, while for birch, 50 seeds is a very small amount. Hence, according to the per cent emergence rates, pine and spruce had better chances for a successful establishment within our plots. It would have been a good idea to adjust for the seed number according to the species' normal seed rain and number in order to avoid this source of error. Birch tree line is thought to have a migrating potential (Hofgaard 1997), unfortunately not visible in this study.

## 4.2 Morphological traits

Few seedlings were found in lowland gap plots, but the ones who had established there seemed viable at the time of harvest. The pine seedlings were tallest in the intact vegetation plots at the intermediate and alpine localities for both cohorts. The clear benefit from gap plots had diminished as the elevation increased, probably due to the lower temperature and the lower competition. The pine seedlings in intact vegetation plots at intermediate and alpine localities had allocated more resources to height growth, most likely to reach above the competing vegetation for light. In the harsher climate in the alpine, the intact vegetation's positive shelter effects may be of greater importance for growth, which also could explain why the pine seedlings were taller in the intact vegetation.

The spruce seedlings were tallest in lowland gap plots for both cohorts, and the difference between gap and intact vegetation plots became smaller with increasing altitude. The differences in height growth between gap and intact plots were best seen on the seedlings in the lowland localities from 2009, as these had fulfilled three growing seasons before harvest. Due to increased competition for light, the spruce seedlings at the lowland localities may have allocated more resources to height growth. Since even the gap plots were overgrown at some of the lowland localities, the competition factor could also explain the extended height growth in these plots.

When it comes to biomass, the benefit of the gaps was very clear. The difference in aboveground biomass between gap and intact vegetation plots was largest for the lowland and smallest for the alpine localities. The mean biomass of seedlings was found to be highest at intermediate localities, except for pines from 2009 which clearly had a higher biomass in the lowland localities. The results for pine 2009 in the lowland localities may be biased due to few observations and one extreme individual which was well above the mean for both size and weight.

Plants growing in intact plots were tall, but had a proportionately lower aboveground biomass. In the intact plots, seedlings had to compete with other plants and could be forced to allocate more resources to height growth. Before a seedling can build up "stability" tissue like thicker stem and roots, it needs to obtain the building materials for this purpose from the activity of photosynthetic tissue (Norgren 1996). The allocation is then in favour of the

photosynthetically active tissue, as seen from the dry weight of the needles, which made up a high part of the aboveground biomass of the harvested seedlings in this study.

Seedlings from lowland localities were found to invest less in root growth compared to the seedlings from intermediate and alpine localities. This same result was found to be true also for grassland plants at the same localities (Skarpaas et al. 2012). The humus layer is thicker at the lowland localities, which could have been expected to trigger root growth because of the plant's need to reach the mineral soil. However, there may be a trade-off between aboveground length growth to get enough light, and root growth in order to attain nutrients and water resources. Water and nutrients might be harder to obtain at the more marginal habitats, meaning a greater need for a more developed root system (Körner 1999). It could also be that longer roots are needed at higher altitudes because of less mycorrhization (Körner 1999). At the alpine locations the need for extensive height growth aboveground is also reduced due to the less competitive, low neighbouring vegetation and better light conditions. It was also seen in Körner's (1999) study that aboveground allocation decreased with altitude. My results is in consistence with the "optimal partitioning theory", which states that plants should allocate biomass to the organ that acquires the most limiting resource (McCarthy & Enquist 2007), and allocation is then optimized in relation to environmental conditions (Skarpaas et al. 2012).

The relations with precipitation were not shown to be significant in the statistical analyses, and are therefore not further commented here.

#### 4.3 Perspectives

Based on Holocene history, future tree line performance given a continued human induced climate warming can be predicted, and Kullman (2006) expects a pine tree line rise of 400 metres within a century as a likely outcome for the tree line in the Swedish Scandes. He also reported that seedlings of *B. pubescens*, *P. sylvestris* and *P. abies* in the Scandinavian mountains had established 500-700 metres above their former limits (Kullman 2004). The tree line in southern Norway has risen during the last decades and can be expected to continue to do so also for the years to come (Juntunen & Neuvonen 2006). My results seem to be in line with these projections, since the pine seedlings were numeral at the alpine localities of the



climate grid. If tree seedlings are able to tolerate the harsher climate and poorer soil at intermediate and alpine localities, it is reasonable to believe that the tree line has a potential for an upward migration, especially with the increasing global mean temperatures. In Norway, the mean temperature has increased significantly since 1876 (Larsson 2004) and is likely to continue doing so. Pine trees has a zero growth threshold for extension growth of shoots between 6 and 7.5 °C (Körner & Paulsen 2004). The lowest temperature registered in our study was 5.87 °C, meaning that with the predicted temperature rise this threshold might not be limiting growth of pine trees in the near future. Maybe, as results from this study could be inducing, we already are at a level where the limitations are not caused by temperature.

However, the tree line is not determined by the temperature factor alone. Pine range expansion have been found to be driven by exceptionally favourable years for recruitment, the frequency of which may increase with climate warming (Dullinger et al. 2004). Despite a lot of research on the topic, it is not clear how the tree line could be determined by climatic variables in the future (Grace et al. 2002). This could considerably accelerate range expansion driven by climate change.

In Scandinavia, there are fewer and fewer undisturbed areas left (Hofgaard 1997), and therefore further studies should include anthropogenic factors in order to develop even more reliable and realistic models. One factor traditionally said to impact the regeneration of trees at the tree line ecotone is the amount of grazing (Hofgaard 1997). The tree line seen in many areas in Norway can be defined more by anthropogenic impact through the historical land use than through climatic limitations (Larsson 2004). If previous land use has affected the tree line position, the tree line will be expected to change with further changes in land use. It would be very interesting to gain more knowledge of tree regeneration and tree line dynamics in accordance with such issues.

#### 4.4 Conclusion

This study reveals that the two conifer species *Pinus sylvestris* and *Picea abies* do not seem to be limited by temperature for seedling germination and early growth along an east-west gradient in southern Norway. The establishment rate and successive growth was significantly higher in gap versus intact vegetation plots, clearly showing a positive response from reduced competition. In some areas, we might see an upward migration of trees that is not related to climate change directly. If temperature is not a limiting factor, the alpine ecotone might turn into a suitable habitat for conifer establishment. This study is a rather short-term study and more knowledge of the long-term responses would be interesting. To my knowledge, not many such long-term studies have been conducted. As it stands today, it looks like we can expect a more forested future in the alpine ecotone.

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