



# Mountain birch seedlings above the sub-Arctic treeline:

How do abiotic and biotic factors affect the growth?

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## Abstract

Temperature is commonly suggested to be the most important regulating factor for the position of the treeline. But also other abiotic and biotic processes may influence. To understand treeline shifts, it is necessary to improve the knowledge about the treeline forming species and their establishment, growth and survival. What are the drivers behind the shifts? The abundance of other vegetation is previously reported to facilitate growth of seedlings above treeline and also warmer temperatures are commonly observed to improve growth.

This study observed growth of mountain birch seedlings during one growing season. The relative importance of environmental factors in relation to the amount of growth and abundance was investigated. The study was conducted in the area of Abisko, Northern Sweden, using 4 sites, where transects were established just above the treeline. The sites differed in the amount of mean precipitation and aspect of the slopes. The vegetation composition around the seedlings and at the average treeline was observed, soil temperatures measured and the aspect of the slope estimated

Seedling growth was observed at all sites, with the highest amount in the sites with most precipitation, Pålnoviken and Katterjåkk. The observed soil mean and maximum temperatures were consistently highest in the southern facing slopes of Jiebrenjåkk and Pålnoviken. The vegetation was mostly dominated by dwarf shrubs, herbaceous plant cover, mosses and bare ground, and did not differ between the seedlings and the average treeline. The best model for growth was found to be the combination of the factors site, herbaceous plant cover, litter and soil mean temperature. Herbaceous plant cover was observed to improve the amount of growth in the drier sites of Pålnoviken and Jiebrenjåkk.

The finding of mountain birch seedlings growing in all vegetation types along the treeline, indicates that they have no preference of vegetation type for establishment. However, the negative influence of bare ground on growth supports the theory that abundance of vegetation facilitates growth of seedlings. The highest amount of growth was found in the sites with most precipitation, suggesting this to be an important factor for growth. In contrast to the expectations, warmer soil temperatures and the south facing slopes did not affect growth positively. This could be explained by the extremely high temperatures of the summer that may have induced drought. Finally, the improved growth by herbaceous plant cover in the drier sites may be because of their preference of moisture and nutrient rich soils, that could also support the growth of mountain birch seedlings.

Key words: treeline, mountain birch, *Betula pubescens ssp. czerepanovii*

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# 1. Introduction

The rising temperatures are expected to cause an upward shift of the treeline position (Körner 2007, Danby & Hik 2007, Kullman & Öberg 2009). The treeline is the zone where forest turns into treeless vegetation, commonly defined as the elevation where trees with a height of 2 m are present (Holtmeier 2009, Öberg 2010). The environment above the treeline is harsh for new seedlings to germinate, establish and survive in, as it is characterized by environmental stress. Biotic and abiotic factors control the growth, e.g. air and soil temperature, wind, snow cover (distribution and duration), albedo, shading, shelters (rocks, pits, bushes), nutrient availability, precipitation, herbivory (e.g. reindeer, moose, rodents, insects) and vegetation composition (Kullman 2003, Alftine & Malanson 2004, Batllori et al. 2009, Grau et al. 2012). Some of the factors may affect the seedling establishment and growth above present altitudes positively, while others may affect it negatively.

To fully understand how temperature affects the treeline position, it is important to differentiate between air, soil and annual variation in temperature. The influence of warming might vary over seasons (Germino et al. 2002), and the soil temperature may be more important than previously observed (Körner & Hoch 2006). However, the actual effect of air temperature on the treeline position is still uncertain, since studies are discordant (Kullman & Öberg 2009, van Bogaert et al. 2011), though, a correlation between air temperature and the position of the treeline has been observed around the world (Körner 2007, Danby & Hik 2007). This is also found in Scandinavia, where the treeline across the mountain range has been expanding over the last decade, following the trend of rising temperatures (Truong et al. 2006, Kullman & Öberg 2009, Kullman 2014). Contrary, some studies observed no effect of warming on the treeline position (van Bogaert et al. 2011). On the other hand Grau et al. (2012) suggest that warming increase seedling growth, but that interaction of warming and vegetation could affect the treeline position more than the temperature itself. However, temperature may be especially important in the Arctic area, because there the warming is expected to become higher. Callaghan et al. (2010) have shown that the mean annual temperatures in Abisko, Northern Sweden rose 2.5°C over the last century and additionally the amount of extreme precipitation events rose during the same period. The predictions also include a higher level of precipitation (ACIA 2005, Callaghan et al. 2010, IPPC 2014).

Tundra vegetation can influence establishment of seedlings by facilitation and/or competition (Callaway & Walker 1997, Grau et al. 2012). At low altitudes the most common plant-plant interaction is competition, but with higher altitude (e.g. higher level of stress), it commonly turns into more facilitative relations (Callaway & Walker 1997). The interactions can also differ between stages of seedling establishment and survival, e.g. the abundance of dwarf shrubs can be positive in the first stage of establishment (protection from solar radiation and insect herbivory), but affect the long-term growth negatively (phenolic compounds released from leaves) (Grau et al. 2012). Other authors suggest that also abundance of herbaceous plants and mature trees facilitates seedling establishment above treeline (Germino et al. 2002, Maher et al. 2005). Wheeler et al. (2011) found that feathermoss (*Pleurozium shreberi*) facilitated growth of Black spruce seedlings above the treeline and suggest that this is due to the protective effect that mosses have for 1-3 year seedlings. Abundance of bare ground, litter and lichens are observed to affect growth positively (Ninot et al. 2008, Wang et al. 2012), contrary to negative observations of the effect of lichens by Tømmervik et al. (2008) and bare ground by Wheeler et al. (2011). However, most studies reports that long-term survival is favoured with vegetation present rather than without (Germino et al. 2002, Bader et al. 2007, Maher et al. 2009, Wheeler et al. 2011, Grau et al. 2013). Vegetation protects the seedlings from wind and solar radiation during summer, accumulates snow that protects the seedlings from frost damage in winter and provides it with moisture in the spring (Batllori et al. 2009).

The importance of other abiotic factors, e.g. precipitation, aspect of the slope and local topography should also be considered. Growth can be limited by water availability, and therefore the amount of precipitation and the presence of droughts may be important (Kullman & Öberg 2009). The local topography and aspect could also affect the exposure to wind and radiation (Kullman 2005, Kullman & Öberg 2009). High solar radiation has been found to inhibit growth above treeline (Bader et al. 2007).

To improve the understanding of the treeline structure and position, it is important to study the performance of seedlings of treeline forming species. How do they respond to different environmental factors and variations in them? The answers may help us predict what the structure and position of the future treelines will be. The aim of this study was to investigate the relative importance of different abiotic and biotic factors affecting growth of tree seedlings above the treeline. To address the aim, we set up a field study in the area of Abisko, northern Sweden, where the treeline forming species is mountain birch, *Betula pubescens ssp. czerepanovii*. Four sites were established just above the present treeline. They differed in the amount of precipitation, slope aspect and expected temperatures. During one summer we observed growth of mountain birch seedlings, studied the surrounding vegetation and coverage, measured soil temperatures and estimated the aspect of the slopes (referred to as *northernness*). We hypothesised that:

1. Birch seedlings will be found mostly in the presence of vegetation.
2. Seedling growth is limited by abundance of dwarf shrubs.
3. Warmer mean soil temperatures affect seedling growth positively.
4. Southern facing slopes will have higher seedling growth than northern facing slopes.
5. Sites with more precipitation will have higher seedling growth.

## 2. Material and methods

### 2.1. Study area

The study was performed in the area of Abisko (68°21' N, 18°49' E), Northern Sweden (fig. 1). Here the elevation of the treeline range between 600 and 800 meters above sea level and the species of tree that grow at the highest altitude and latitude is the mountain birch, *Betula pubescens ssp. czerepanovii*. The mountain birch grows slowly due to the environmental conditions, and reaches an age of about 100 years. The most common undergrowth is heath (dwarf shrubs dominated) or meadow (dominated by herbaceous plants and graminoids) vegetation (Väisänen 1998, Linkowski & Lennartsson 2005).

The study was carried out at four sites close to Abisko (fig. 1), Katterjåkk in west, Pålnoviken (fig. 3), Jiebrenjåkk (fig. 2) and the most eastern site of Stordalen. They were situated just above the treeline and were chosen to have different characteristics when it comes to the slope aspect (referred to as *northernness*) and amount of precipitation. The aspect of the slopes is mostly northern facing in Katterjåkk and Stordalen and southern facing in Jiebrenjåkk and Pålnoviken. Across the sites there is a gradient of precipitation, with the most, 848 mm, mean annual precipitation in Katterjåkk, followed by Pålnoviken, and the least, 304 mm, in Jiebrenjåkk and Stordalen (Åkerman & Johansson 2008).



**Figure 1** Map over the area with the four sites (Katterjåkk, Pålnoiviken, Jiebrenjåkk and Stordalen) marked with red and Abisko marked with orange.

In July 2014 the mean temperature in Abisko was 16.4°C and the precipitation was 57.5 mm. This is 4°C higher than the average temperature during the last century and also the amount of precipitation was higher than normal (42 - 54 mm) (Abisko naturvetenskapliga station A & B 2014). In August the mean temperature was 11.2°C, which is more than 1°C higher than average during the last century and the precipitation was 43.9 mm, which is similar to the previous century.

## 2.2. Fieldwork

In mid July 2014 transects were established at the four sites (fig. 1). Every site consisted of 3 transects of maximum 1 km each following the treeline at a parallel 20-50 m upslope. Along the transects 5 seedlings smaller or equal to 15 cm height were found, marked and measured. The transects were finished when 5 seedlings were found. In total 15 seedlings were thus measured at every site. To be able to measure the shoot- and width growth in the end of the season, the stem was marked with a permanent marker in the upper part of every seedling as a reference point for measuring shoot growth and at ground level for the width growth. At a distance of 10 cm from every seedling a soil temperature logger was placed at a depth of 5 cm to continuously measure the soil temperature every hour. The measurements that were conducted were; total plant height, shoot length, stem width (at ground level) and a visual estimation of the vegetation coverage (%) around the seedling.

The vegetation in the direct area around the seedling was defined as the area of 20 cm \* 20 cm square around the seedling (fig. 4) and estimated in terms of its coverage (%) of the different growth forms (tree, bush, dwarf shrub, herbaceous, mosses, lichen) and other ground cover (litter, rock and bare ground). Also the aspect of the slope was estimated to get the indication of northerness according to:

$$\text{Northerness} = \cos(x),$$

where  $x$  is the angle of the downslope direction in degrees. Finally, to describe the average vegetation along the transects (referred to as “treeline”), a vegetation composition analysis was performed. Using 1 m<sup>2</sup> vegetation squares placed at even distances 10 times along every transect within the distance where the 5 seedling were found and coverage (%) of the different growth forms was estimated.



Figure 2 The treeline at Jiebrenjåkk, the treeline is marked with a white line.



Figure 3 The treeline at Pålnoviken, the treeline is marked with a white line.



Figure 1 Birch seedling with the 20\*20 cm square for vegetation analysis.

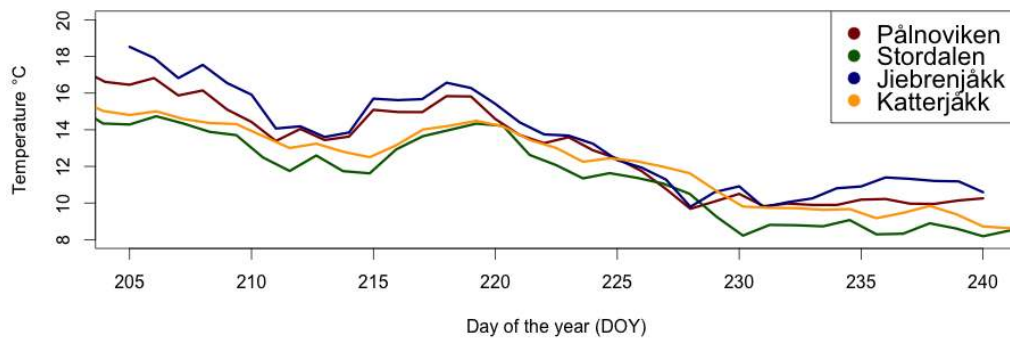
### 2.3. Data analysis and statistics

The data ( $n = 15$  per site) were statistically analysed using the software R (Development Core Team 2012). The response factors (Shoot growth, Shoot growth % and Width growth) were tested against the vegetation types and ground cover, soil temperature and northerness using *single linear regression analysis*. The importance of Site was analysed using *ANOVA*. To find out which of the environmental factors (soil temperature, slope aspect, vegetation types) that could explain seedling growth best *multiple linear regression analysis* was used. Backwards model selection based on F-value and  $R^2$  was used to optimize the model. To test if there was a selective preference of vegetation type where the seedlings manage to establish *non-metric multidimensional scaling* (NMDS) was used to compare vegetation squares with and without seedlings. Finally, the soil temperature data were used to calculate the daily mean, maximum and minimum temperatures at every seedling and the total mean temperature at the sites.

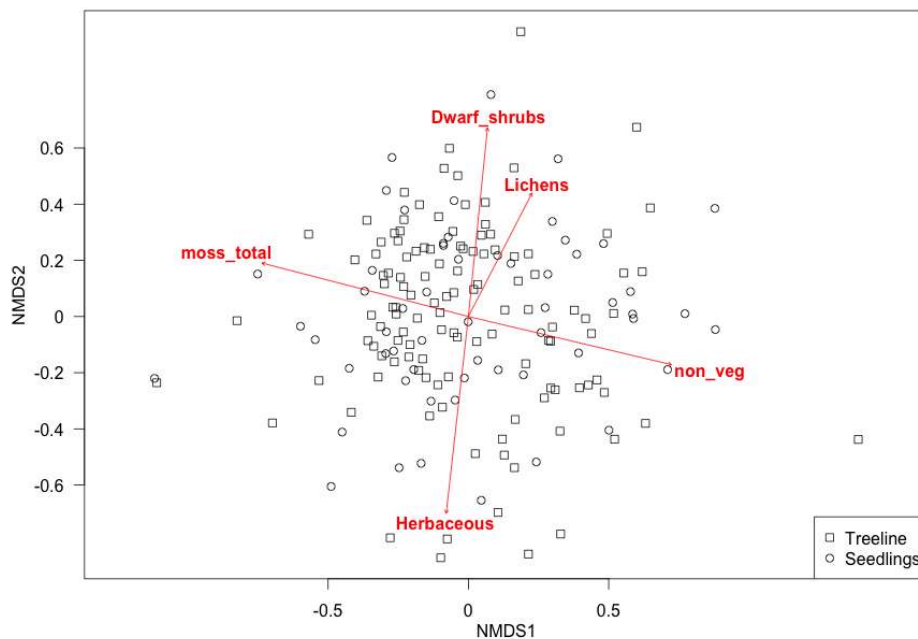
### 3. Results

#### 3.1. Soil temperature

The daily mean soil temperature at the sites differed consistently with the warmest in Jiebrenjåkk and the coldest in Stordalen (fig. 5). The temperatures of the southern facing slopes of Jiebrenjåkk and Pålnoviken followed each other very precisely. Similarly did the temperatures of the northern facing slopes of Stordalen and Katterjåkk. The maximum temperatures were also highest in the southern facing slopes of Pålnoviken and Jiebrenjåkk, while the coldest minimum temperatures differ less between the sites.



**Figure 5** Daily mean soil temperatures at the different sites, between the 23th of July (DOY=204) and the 28th of August (DOY=240), n=15 per site.



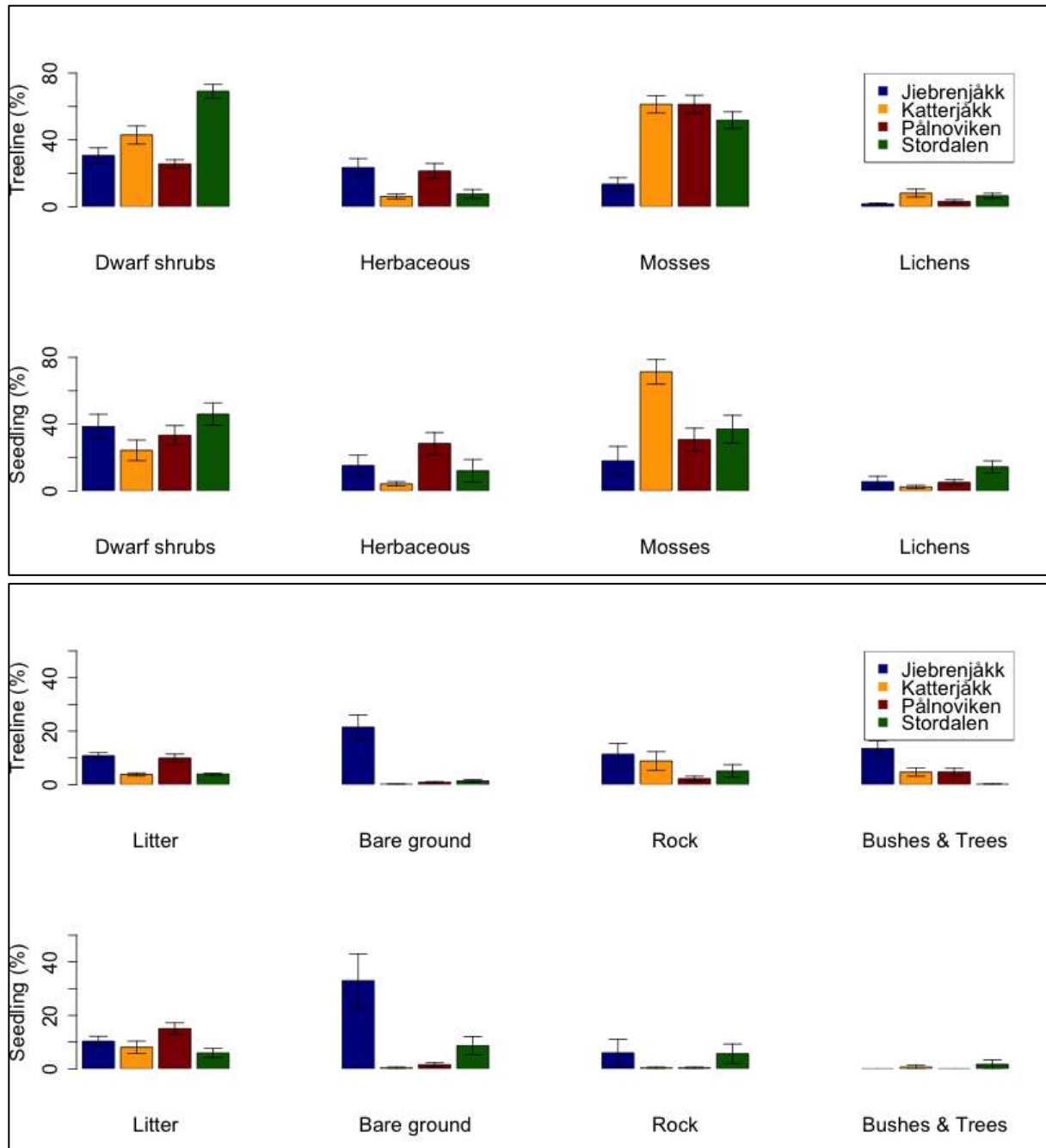
**Figure 6** The NMDS shows the vegetation around the seedlings (circles) compared with the vegetation at the treeline (squares).

#### 3.2. Vegetation analysis

The NMDS showed that the vegetation and ground cover around the seedlings and at the average treeline did not differ (fig. 6). Similarly, the relative abundance of different vegetation around the seedlings and at the treeline did not differ. There was a dominance of



mosses (45-75%) and dwarf shrubs (30-60%) at all sites except for Jiebrenjåkk that was dominated by dwarf shrubs (35%) followed by bare ground (25%), herbaceous (20%) and mosses (20-60%)(fig. 7).

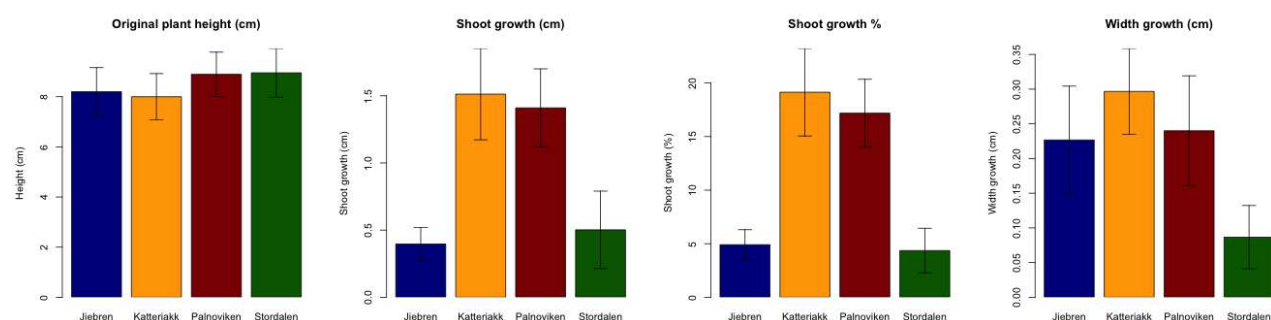


**Figure 7** Relative cover distributions (%) of vegetation types and ground cover at the treeline and around the seedlings at the sites, Jiebrenjåkk, Katterjåkk, Pålnoiviken and Stordalen. Errorbars are standard error (SE) of mean (n=60).

### 3.3. Seedling growth

Growth of shoot length and width were observed at all the sites, with an average of 11 % in addition to the original height. Across the sites the seedlings were of similar initial size and using single linear regression analysis, a positive correlation was found between total initial seedling height and shoot growth ( $p=0.004$  \*\*). The Shoot growth-% was most pronounced

in the sites with highest mean annual precipitation, Katterjåkk and Pålnoiviken (fig. 8). The longest mean shoot growth was found in Katterjåkk (1.5 cm) and Pålnoiviken (1.4 cm), followed by the driest sites of Stordalen (0.5 cm) and Jiebrenjåkk (0.4 cm).



**Figure 8** Original plant height (cm), absolute shoot length growth (cm), relative shoot length growth (%) and absolute width growth (cm) at the different sites.

### 3.4. Multiple linear regression and correlation with individual factors

In the multiple linear regression model where the response factor was Shoot growth- % the best predictor variables were: Site ( $p=0.0004$  \*\*\*), Herbaceous cover ( $p=0.042$  \*) Litter ( $p=0.098$ ) and Mean soil temp ( $p=0.392$ ) (table 1). Of the total variation in seedling growth this model explained 30 % ( $p<0.001$ ).

**Table 1** Results of multiple linear regression describing the relationship between proportional shoot growth (Shoot growth- %) and the environmental variables measured.

<b>Response factor:</b> <b>Shoot growth-%</b>		<b>R<sup>2</sup>=0.30</b>
<b>Factor</b>	<b>F-value</b>	<b>P-value</b>
Site	7.2	0.0004 ***
Herbaceous	4.4	0.042 *
Litter	2.9	0.098 .
Mean soil temperature	0.7	0.392

**Table 2** Test statistics of interaction of site and herbaceous plant cover with response factor Shoot growth-%.

<b>Response factor:</b> <b>Shoot growth-%</b>		<b>R<sup>2</sup>=0.37</b>
<b>Herbaceous</b>	<b>F-value</b>	<b>P-value</b>
Pålnoiviken	0.4	0.523
Jiebrenjåkk	12.6	0.004 **
Katterjåkk	3.6	0.081 .
Stordalen	20.6	0.0006 ***

Using single linear regression analysis when analysing the factors individually with response factor Shoot growth-%, a positive significance with the factor site was found (appendix 1). Two of the vegetation types, dwarf shrubs ( $p=0.049$  \*) and bare ground ( $p=0.067$  .), affected Shoot growth-% negatively. The other factors did not show any significance.

The interaction of Herbaceous plant cover and Site resulted in significant effect on the Shoot growth-%. It was strongest in Stordalen ( $p=0.0006$  \*\*\*) and Jiebrenjåkk ( $0.004$  \*\*). This model explained 37 % ( $p < 0.0001$ ) (tab. 2) of the variation in seedling growth.

## 4. Discussion

### 4.1. Importance of vegetation

The occurrence of birch seedlings seemed not to be determined by particular vegetation types, since they were found in the same vegetation composition as the treeline overall, including bare ground. The observed negative correlation of growth by bare ground could support the theory that vegetation facilitates growth (Germino et al. 2002, Bader et al. 2007, Grau et al. 2013), which support our hypothesis no. 1 (Birch seedlings will be found mostly in the presence of vegetation). Even though the seedlings are not found in a certain vegetation type, they can be influenced via amount of growth. For example the herbaceous cover appeared to facilitate growth, but interestingly it was most important in the drier sites of Jiebrenjåkk and Stordalen. This might be because of herbaceous plants preference of moist and nutrient rich soils (Väisänen 1998), which is influencing growth of mountain birch positively (Weih & Karlsson 2001). And also here the facilitative relation of shading and protection may be important. The result of dwarf shrubs inhibiting growth is supporting hypothesis no. 2, and is in accordance to previous studies (Grau et al. 2012). The positive influence of litter on growth is also in accordance with previous observations that observed litter improve growth (Ninot et al. 2008, Wang et al. 2012), as this could both protect the seedling and provide the soil with nutrients.

### 4.2. Precipitation, temperature and aspect of slope

The difference in growth between the sites showed better conditions for the seedlings in Pålnoviken and Katterjåkk (fig. 7). Those sites also have the highest mean yearly precipitation according to the gradient from west to east (Åkerman & Johansson 2008), supporting my hypothesis no. 5. It is also in accordance with results from Germino et al. (2002), which found greatest establishment and survival of seedlings (*Picea engelmannii* and *Abies lasiocarpa*) above the treeline (Snowy range, Wyoming, USA) with low temperatures and high precipitation. Surprisingly no significant correlation was found between any of the measured abiotic factors, soil temperatures and aspect of slope and growth (against hypothesis no. 3 and 4). As earlier mentioned, the actual effect of air- and soil temperature on growth of seedlings is still uncertain (van Bogaert et al. 2011, Kullman & Öberg 2009). However, there is a series of studies that observed higher level of growth with warming, e.g. Grau et al. (2012) showed more growth with experimental warming than without when using open top chambers. Additionally, Weih and Karlsson (2001) suggest that a higher air temperature may enhance the leaf expansion rate and shoot growth rate of mountain birch, whereas a higher soil temperature may increase root growth and nutrient uptake. The summer of this study (2014) had extremely high air temperatures in July and August. In July the temperature was 4°C higher than normal. Also the soil temperatures followed this pattern and exceeded the normal. This could affect the growth of seedlings, since the combination of high temperatures, high solar radiation and water stress (evaporative demand), are found to inhibit the growth and survival of seedlings (Cui & Smith 1991), though, this study did not observe any significant correlation to growth by high maximum temperatures. Finally, the high temperatures could increase the demand for water and add on to the pattern of a high level of growth at wet sites.

The inter annual variations in temperature may be of importance, since seedlings could suffer from frost damage in warmer autumns (Germino et al. 2002), when the period without

snow is getting longer, the seedlings stay exposed for radiation and frost temperatures a longer time. And similarly, warmer spring temperatures may cause more frost damage.

The lack of correlation between growth and aspect was surprising, since previous research suggest that growth above the treeline is inhibited by larger amount of solar radiation (Germino et al. 2002, Bader et al. 2007), and the southern aspect get more solar radiation than the northern facing slopes. However, we found the lowest growth in Jiebrenjåkk, the site with most southern aspect and exposure for sun, warmest temperatures and also one of the least mean precipitations, indicating that the importance of factors that differs between the sites (e.g. precipitation, temperatures and aspect) in combination may be important for growth. Even though temperature and aspect in the current study was not observed to affect growth above the treeline significantly, there could be indirect effects on other factors that are affecting growth, e.g. vegetation composition, height and coverage.

Another factor related to the sites is the abundance of shelters. Vegetation being one, but also other structures like stones, pits and hills could protect by accumulating snow on leeward side (Batllori et al. 2009) and reduce the exposure of solar radiation (Germino et al. 2002). Batllori et al. (2009) suggest that krummholz mats may be especially protective since snow accumulates on their leeward side and Munier et al. (2010) found that open canopy forest influence growth positively. Finally, the growth of seedlings may be improved by tree islands or fallen stems sheltering and protecting them (Germino et al. 2002).

### **4.3. Other factors**

The complexity of treeline-position shifts is a challenge to study; in this study we have observed one summer season looking at the effect of vegetation composition, aspect, soil temperature and precipitation, but to completely understand the dynamics also other factors should be included:

Firstly, grazing has been observed to control the growth and survival of seedlings (Hofgaard et al. 2010, Rundqvist et al. 2011). It may be both larger herbivores (e.g. moose, reindeer), but also rodents (e.g. lemmings) and insects (e.g. autumnal moths). Also human-induced changes of reindeers grazing patterns could affect the treeline to expand upwards, when the reindeers are not grazing any more, allowing bushes and trees to expand upward. It may be followed by consequences of changed albedo (e.g. more thermal radiation absorbance with bushes and trees than tundra) (Rundqvist et al. 2011) and changed vegetation in their preference of lichens (Tømmervik et al. 2008). Additionally, it is observed that grazing reduce the amount of new seedling shoots above treeline and affect the seedlings to produce larger leaves (Hofgaard et al. 2010). Secondly, outbreaks of autumnal moths could also cause a lot of birch trees to die (van Bogaert et al. 2011), especially in areas dominant of monocorm mountain birch (only one stem), contrary to areas of polycorm birch (many stems), since monocorm trees are more depending on dispersal by seeds to survive as a population. Thirdly, the importance of winter conditions is by Batllori et al. (2009) suggested to be the most regulating factor for seedling survival. This is highly depending on snow cover depth, distribution and duration, and also observed to be important by other authors (Kullman & Öberg 2009).

## **5. Conclusions**

The future treeline position and structure depends on a range of biotic and abiotic factors. The mountain birch was in this study found all over the treeline, in all vegetation types that characterized the different sites, including bare ground. This suggests that the seedlings had no preference of vegetation type. However, the abundance of vegetation improved growth in

contrast to the negative influence by bare ground. The highest growth was found in the sites with most precipitation, suggesting this to be an important factor for growth. In contrast to the hypothesis warmer soil temperatures and southern facing slopes did not affect growth. The combination of the factors site, herbaceous plants cover, litter and mean soil temperature, was found to favour growth most. Abundance of herbaceous plants cover improved growth most in the drier sites of Jiebrenjåkk and Stordalen, this might be explained by herbaceous plants preference of moist- and nutrient rich soils.

We can now accept the hypothesis 1 (Birch seedlings will be found mostly in the presence of vegetation), partly accept no. 2 (Seedling growth is limited by abundance of dwarf shrubs), but reject no. 3 (Warmer mean soil temperatures affect seedling growth positively) and no. 4 (Southern facing slopes have more growth than northern). Finally, we accept no. 5 (Sites with more precipitation will have higher seedling growth).

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## 7. References

Abisko naturvetenskapliga station (A). 2014. Temperatur 2014.

Abisko naturvetenskapliga station (B). 2014. Nederbörd 2014.

ACIA. 2005. Arctic Climate Impact Assessment. Cambridge University Press, 1042p.

Alftine, K.J. and Malanson, G.P. 2004. Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science* 15: 3-12.

Bader, M.Y. van Geloof, I. Rietkerk, M. 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecology* 191: 33-45.

Batllori, E. Camarero, J.J. Ninot, J.M. Gutiérrez, E. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* 18: 460-472.

Callaghan, T.V. Bergholm, F. Christensen, T.R. Jonasson, C. Kokfelt, U. Johansson, M. 2010. A new climate era in the sub-Arctic: Accelerating climate changes and multiple impacts. *Geophysical research letters*. Vol. 37.

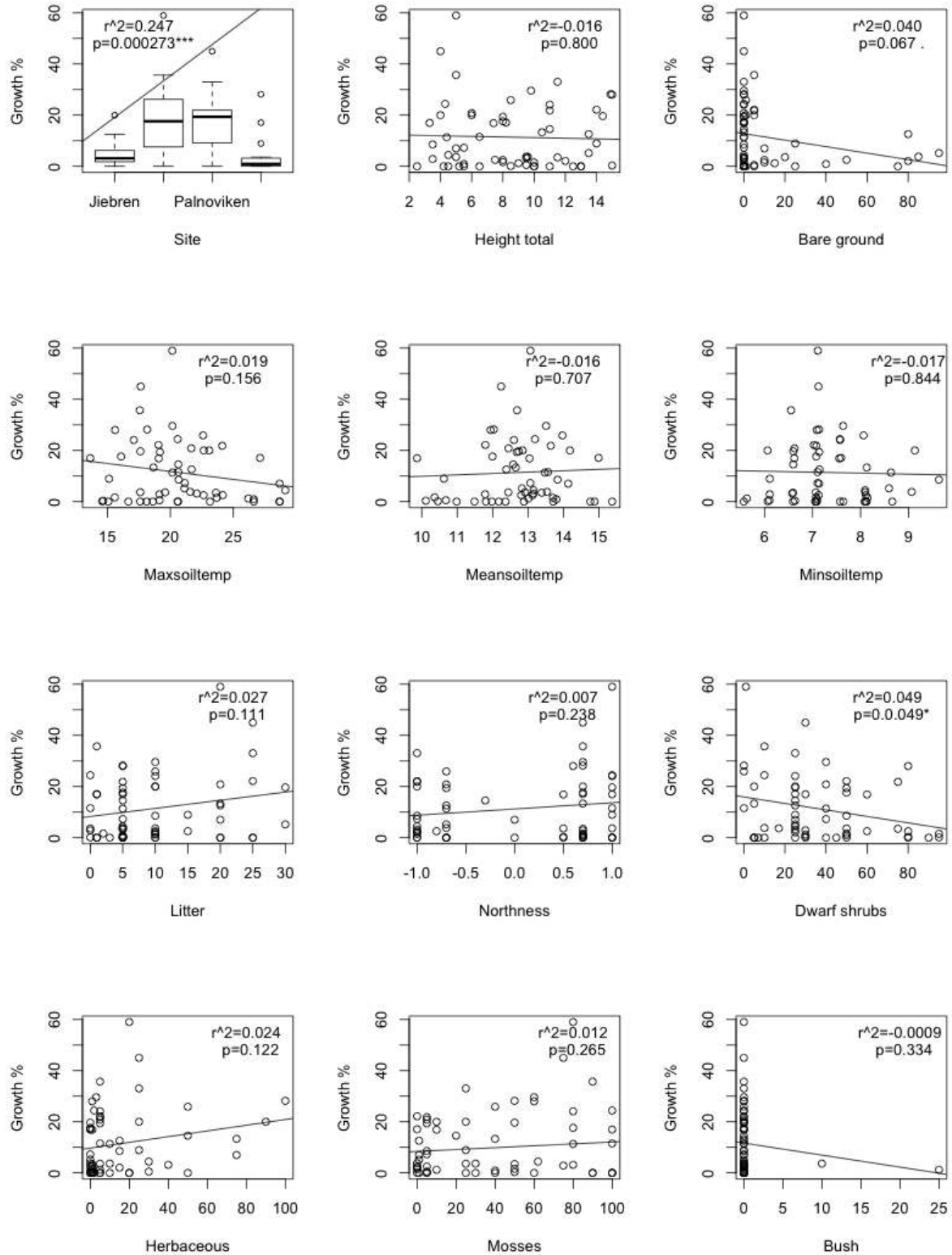
Callaway, R. M. Walker, L. R. 1997. Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology*. Vol. 78. No. 7: 1958-1965.

- Cui, M. and Smith, W. K. 1991. Photosynthesis, water relations and mortality in *Abies Zasiocarpa* seedlings during natural establishment. *Tree Physiology*. No. 8: 37-46.
- Danby, R.K and Hik, D.S . 2007. Variability, Contingency and Rapid Change in Recent Subarctic Alpine Tree Line Dynamics. *Journal of Ecology*. Vol. 95. No. 2: 352-363.
- Grau, O. Ninot, J. M. Blanco-Moreno, J. M. van Logtestijn, R. S. P. Cornelissen, J. H. C. Callaghan, T. V. 2012 Shrub–tree interactions and environmental changes drive treeline dynamics in the Subarctic. *Oikos*.
- Grau, O. Ninot, J. M. Cornelissen, J. H. C. Callaghan, T. V. 2013. Similar tree seedling responses to shrubs and to simulated environmental changes at Pyrenean and subarctic treelines. *Plant Ecology & Diversity*. 6:3-4, 329-342.
- Holtmeier, F-K. 2009. *Timberlines- Ecology, Patchiness, and Dynamics*. Springer.
- Hofgaard, A. Lökken, J. O. Dalen, L. Hytteborn, H. 2010. Comparing warming and grazing effects on birch growth in an alpine environment- a 10-year experiment. *Plant ecology & Diversity*. Vol. 3. No. 1: 19-27.
- IPCC. 2014. Summary for policymakers. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 1-32.
- Kullman, L. 2003. Förändringar i fjällens växtvärld – effekter av ett varmare klimat. *Svensk Botanisk tidskrift*, 97: 210-221.  
(<http://svenskbotanik.se/wp-content/uploads/2013/10/Kullman.pdf>)
- Kullman, L. 2005. Wind-Conditioned 20th Century Decline of Birch Treeline Vegetation in the Swedish Scandes. *Arctic Institute of North America*, Vol. 58, No. 3.
- Kullman, L. Öberg, L. 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology*. Vol. 97: 415-429.
- Kullman, L. 2013. Ecological tree line history and palaeoclimate – review of megafossil evidence from the Swedish Scandes. *Boreas*, Vol. 42: 555–567.
- Kullman, L. 2014. Treeline (*Pinus sylvestris*) landscape evolution in the Swedish Scandes – a 40-year demographic effort viewed in a broader temporal context. *Norsk Geografisk Tidsskrift–Norwegian Journal of Geography* Vol. 68: 155–167.
- Körner, C. Hoch, G. 2006. A Test of Treeline Theory on a Montane Permafrost Island. *Arctic, Antarctic, and Alpine Research*. 38:113–119.
- Körner, C. 2007. Climatic Treelines: Conventions, Global Patterns, Causes. *Erdkunde*, Bd. 61, H. 4 (Oct. - Dec.): 316-324.

- Lett, S. 2014. Climate- warming induced forest expansion- Factors determining seedling establishment at the tree line. (Intro essay)
- Linkowski, W. Lennartsson, T. 2005. Biologisk mångfald i fjällbjörkskog – en kunskapssammanställning. Centrum för biologisk mångfald, SLU.
- Ninot, J. M, Batllori, E, Carrillo, E, Carreras, J, Ferré, A, Gutiérrez, E. 2008. Timberline structure and limited tree recruitment in the Catalan Pyrenees. *Plant Ecology & Diversity*. 1:1: 47-57.
- R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- Rundqvist, S. Hedenås, H. Sandström, A. Emanuelsson, U. Eriksson, H. Jonasson, C. Callaghan, T.V. 2011. Tree and Shrub Expansion Over the Past 34 Years at the Tree-Line Near Abisko, Sweden. *AMBIO*, 40:683–692.
- Truong, C. Palmé, A. E. Felber, F. 2006. Recent invasion of the mountain birch *Betula pubescens* ssp. *tortuosa* above the treeline due to climate change: genetic and ecological study in northern Sweden. *Journal compilation. European society for evolutionary biology*.
- Tømmervik, H. Johansen, B. Riseth, J. A. Karlsen, S. R. Solberg, B. Högda, K. A. 2008. Above ground biomass changes in the mountain birch forests and mountain heaths of Finnmarksvidda, northern Norway, in the period 1957–2006. *Forest ecology and management*.
- van Bogaert, R. Haneca, H. Hoogesteger, J. Jonasson, C. de Dapper, M. Callaghan, T.V. 2011. A century of tree line changes in sub- Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*. 38: 907-921.
- Wang, Y. Camarero, J.J. Luo, T. Liang, E. 2012. Spatial patterns of Smith fir alpine treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive recent treeline patterns. *Plant Ecology & Diversity*, 5:3, 311-321.
- Weih, M. Karlsson, P.S. 2001. Growth response of Mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist*. 150: 147-155.
- Wheeler, J. A. Hermanutz, L. Marino, P. M. 2011. Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest–tundra ecotone (Labrador, Canada). *Oikos* 120: 1263–1271.
- Väisänen, R. 1998. Current research trends in mountain biodiversity in nw europe. *Pirineos*. 151-152: 131 a 156.
- Åkerman, H.J. Johansson, M. 2008. Thawing Permafrost and Thicker Active Layers in Sub-arctic Sweden.
- Öberg, L. 2010. Treeline dynamics in short and long term perspectives – observational and historical evidence from the southern swedish scandes.

# Appendix 1

## Individual correlations of Shoot growth-% and different environmental factors.







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