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Treeline Dynamics in Trillemarka-Rollagsfjell

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Abstract

The environmental effects that determine the altitude of the tree line have been discussed for a long time. Alpine ecosystems are known to be particularly sensitive to climate warming, and both biotic interactions as well as abiotic factors, such as temperature and precipitation, are important shapers of plant alpine communities.

Identifying the rate of response of the alpine tree line to changes in climate is crucial for understanding and predicting the future of alpine species as the world gets warmer. This study took place in the nature reserve of Trillemarka-Rollagsfjell, located in Buskerud County, south-eastern Norway. The goal was to see if there was an observable correlation between both summer temperature and precipitation, and the recruitment and growth of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens*) above the timberline in south-eastern Norway.

Both climatic data and physical samples were collected. The samples were all collected from two areas, between late July and early September 2015. For each area, ten different plots of 10x10 meters were established and sampled. The climate data was gathered from the Norwegian Meteorological Institute. The results showed no clear correlation, but depicted a large local variance in annual growth and recruitment, both for each site and in-between the species. In addition, an increase both in yearly growth and recruitment seemed to be evident, which could indicate that an increase in tree line altitude is happening.

The results appear to underline the importance of microhabitat and small-scale disturbances, such as grazing and snow-cover, in regard to individual establishment success and growth rate. As it stands, the results show that neither temperature nor precipitation alone are the most limiting for the trees in the tree line ecotone in Trillemarka-Rollagsfjell.

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1. Introduction

The alpine tree line - an abrupt change from tall, woody organisms to grass, lichen and small, crooked shrub-like plants as one ascends to a certain altitude. Trees give way to alpine plants, which are able to survive under harsh conditions where other plants would perish. The line is not globally fixed at one altitude, and the regional differences are significant; at its highest, the line is at about 5000 meters in the Andes mountains, but at its lowest it is only a few meters above sea level (Troll, 1973).

The environmental effects that determine the altitude of the tree line have been discussed for a long time. As far back as 1876, Hoffmann stated that the effect witnessed must be a result of temperature (Körner, 2012). Today it is believed to be a result of a varied combination of factors. These include altitude, latitude, temperature, precipitation, geographical orientation, soil composition, wind conditions and sun exposure. In lieu of climate change**,** and increasing unstable weather patterns and rising temperatures, it is reasonable to expect that one should be able to measure a change or response in the alpine tree line (Greenwood et al., 2015; Pachauri et al., 2015; Tingstad et al., 2015; Rigling et al., 2013; Milbau et al., 2009; Klanderud, 2005; McCarty, 2001; Walther et al., 2002).

For some species this change in climate might prove for the better, for others, the worse. Alpine ecosystems are known to be particularly sensitive to climate warming, and both biotic interactions as well as abiotic factors such as temperature and precipitation are important shapers of plant alpine communities (Klanderud, 2005; Huston and McBride, 2002). Thus, changes in these factors might also lead to a change in species composition. Identifying the rate of response of the alpine tree line to changes in climate is crucial for understanding and predicting the future of alpine species as the world gets warmer.

Climate change is predicted to lead to less snow cover during winter in northern ecosystems. This in turn decreases the amount of insulation plants get during winter, and might reduce winter survival (Erefur et al., 2008). While the increase in temperature happened fastest in the periods 1925-1944 and 1978-1997 (Jones et al., 1999), the process is still ongoing (Pachauri et al., 2015)**.** As summertime temperatures increase, it could prove beneficial for the plants' growth period, but combined with a worsening of wintertime conditions, the end result might be a negative one.

Recruitment is considered a key life history event dependent on a number of processes (Tingstad et al., 2015). However, predicting a recruitment rate based on temperature or precipitation alone is difficult, and the common view is that it is the culmination of multiple factors together that ensures the end result (Körner, 2012; Richardson and Friedland, 2007; Körner, 1998; Grace, 1989). In environments dominated by cold climates, abiotic conditions are especially recognized as the main limitations for plant recruitment (McCarty, 2001; Smith, 1994)

According to the stress-gradient hypothesis (Bertness and Callaway, 1994), the level at which biotic interactions impacts individuals in a habitat will vary depending on the rate of abiotic stress. At high levels of abiotic stress the amount of facilitation amongst plants increases, while competition increases when the stress levels are reduced (Callaway et al., 2002). At the alpine tree line where the climate is harsh and cold, abiotic conditions are often believed to be the greatest limiting factor for plant recruitment. Even so, a study done by Olsen and Klanderud (2014) on alpine plants showed that after successful germination has taken place, a switch occurs and biotic interactions, in a larger degree than abiotic conditions, become a main factor determining successful establishment.

After successful germination, microrelief might contribute to alleviate some of the abiotic stress (Hörnberg et al., 1997). It is also important to remember that a single year with preferable conditions will not be enough to ensure an individual prolonged survival, but rather a string of ‘good’ years are needed, where both abiotic and biotic factors allow for continued growth (Juntunen and Neuvonen 2006).

Taking this into account, it can be assumed that even though abiotic factors such as temperature and precipitation might be of most importance early on in an alpine plant’s life, they continue to have a major impact throughout the plant’s life history. It has been shown that precipitation and temperature in particular played a role regarding the rate of success for seedling establishment (McCarty, 2001; Smith, 1994). Therefore, we expect to see some correlation between recruitment and growth, and the climate variables chosen.

This study aims to see if there is an observable correlation between both summer temperature and precipitation, and the recruitment and growth of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens*) above the timberline in south-eastern Norway.

It is expected that an increase in both recruitment and growth will be observed – both of which could be considered indicators of a potential increase in tree line altitude. The term “tree line” will in this paper, where applied, be used as by Tingstad (2015), and refer to the area from the forest line up to the treeless alpine vegetation.

2. Methods and materials

2.1 Study area

The study was conducted in the nature reserve of Trillemarka-Rollagsfjell, located in Buskerud County, south-eastern Norway. The nature reserve as present was created in 2008, and it has an area of 147 km^2, and is a part of the natural geography region 33b - Buskerud and Oppland coniferous forest (Fylkesmannen, 2015). The reserve hosts a number of endangered species (Artsdatabanken, 2007; Hofton, 2003), and contains both old growth forest as well as old pastoral fields and cultural landscapes, all of which are characterized by high biological values. In addition, Trillemarka-Rollagsfjell is a popular area for recreational use all year round.

The reserve is a place of great contrasts with steep valleys and mountain peaks, ranging in height from 250 m a.s.l. to 1080 m a.s.l. at its highest (Hofton, 2003). There is a distinct annual variation in climate, ranging from relative warm summers to cold winters. The mineral soil found in the area is mainly moraine deposits. The soil coverage is most often thin and has a low pH. Podzol soil dominates the area, but there are yet pockets of rich brown soil on top of more nutrient-rich bedrock. The geology as a whole is dominated by quartzite, quartz slate, and the occasional occurrence of granite, granodiorite and granite gneiss (NGU, 2016; Hofton, 2003).

The forest in Trillemarka-Rollagsfjell reserve has a long history of human land-use, dating back to the 17th century (Blanck et al., 2013; Hofton, 2003), both for logging as well as pastures for livestock (Blanck et al., 2013; Kasin et al., 2013; Storaunet et al., 2013). Remnants like open grazing areas and old, crumbled cottages for herders can still be spotted throughout the area.

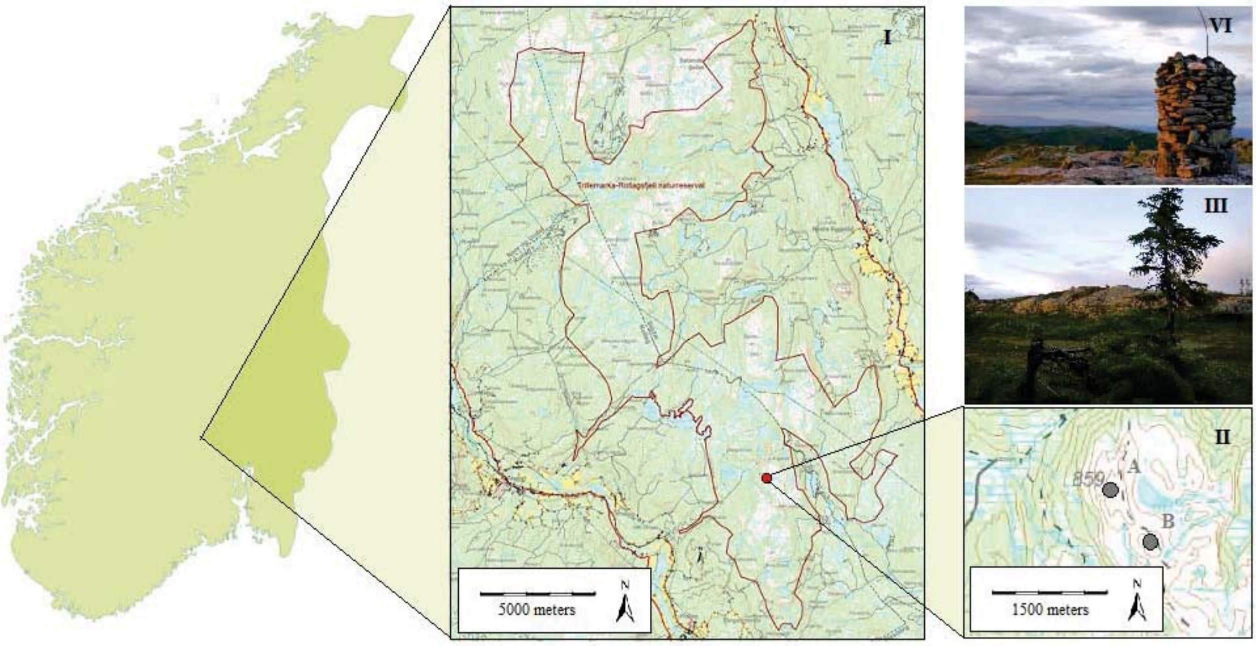


Figure 1 – I: Map showing Trillemarka-Rollagsfjell Nature Reserve. **II**: Locations of both sample sites, A and B. Approximately 1km between **III:** Mire with old trees below site A. **IV**: Cairn marking the highest point at site A.

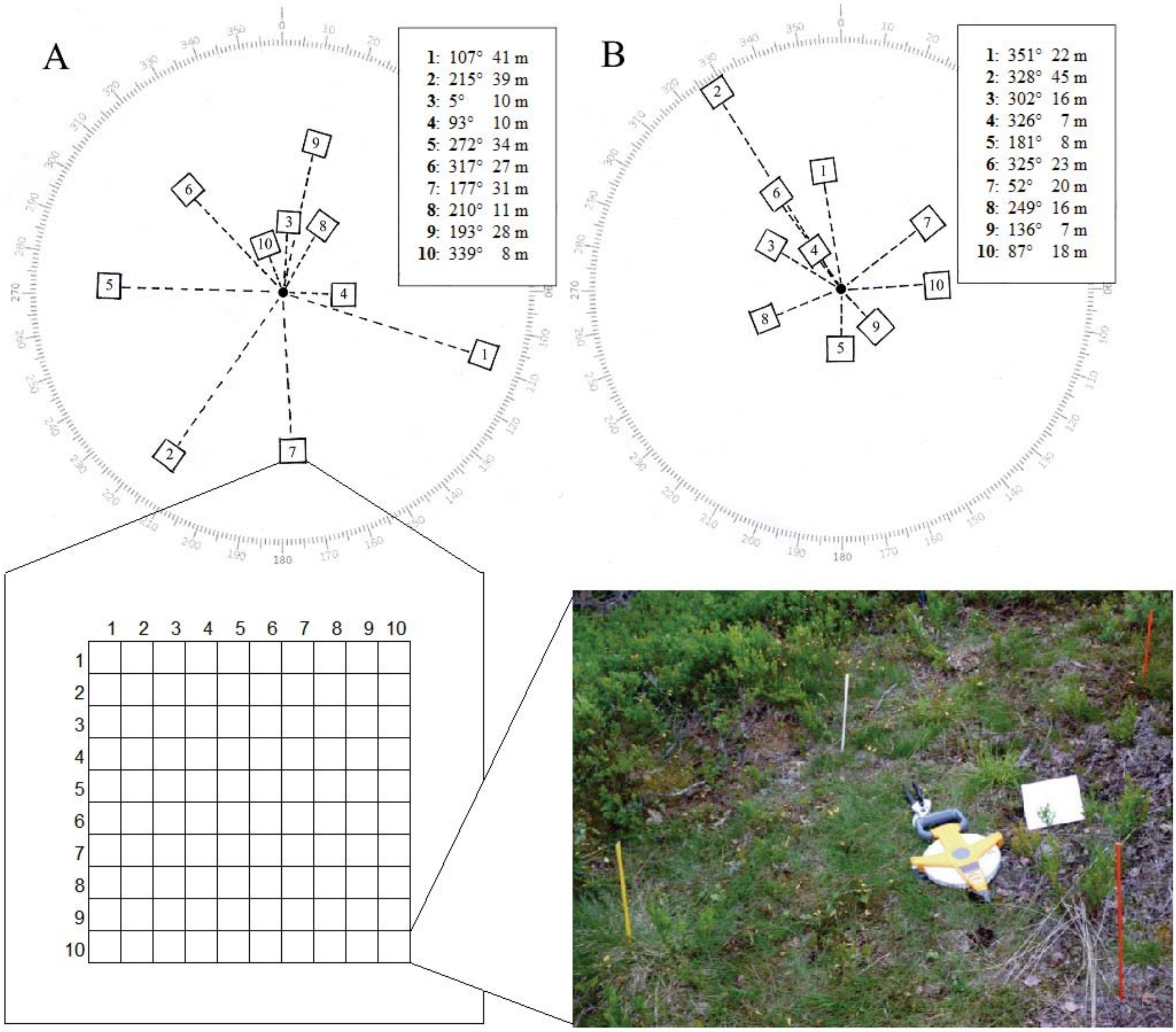
For this study two locations were selected on Langseterfjellet (Figure 1), located in the southern part of Trillemarka-Rollagsfjell nature reserve. Both locations had an exposed position – and similar exposure to both wind and sun. The terrain slope at location A is much steeper than at site B, at times almost a complete vertical drop. At location B, the incline at all sides was much lower, and rarely exceeded 20°**.** The sites were chosen based on the fact that while they were both similar in terms of location (~1 km between the areas) and altitude, they both had their distinct yet uniform shape. The expectation was that this difference would enable me to see to what extent microrelief and local conditions impact tree growth and recruitment.

The study area is situated at roughly 860 m a.s.l. Site A is located at the top of Langsetervarden (859 m a.s.l., N°60.02665 E°09.21388), while site B (842 m a.s.l., N°60.02458 E°9.21752) lies approximately 1km south east of site A (Figure 1). The area is above the timberline, and has an open, sparsely vegetated appearance. The vegetation has a heath-like outlook in places and is dominated by low-growing shrubs such as European blueberry (*Vaccinium myrtillus*) and dwarf birch (*Betula nana*), intermixed with small stands of trees which rarely reach a height of more than 1.5 meters. Langsetervarden (the cairn in Figure 1) lies on top of a long ridge that stretches from south to north, and the wind exposure caused by the openness of the area is clearly visible in the growth form of the trees that manage to take root. A popular trekking path meanders along the entirety of the ridge.

2.2 Data collection

Both climatic data and physical samples were needed. The samples were all collected from two areas, A and B, between late July and early September 2015.

For each area, ten different plots of 10x10 meters were established and sampled (Figure 2). The exact locations for each plot were chosen before arrival by first randomly generating ten different compass courses (between 0 and 360). Likewise a distance between 5 and 45 meters were then randomly generated for each course. In order to acquire these numbers a random number generator provided by random.org ("Random.org," 2016), was used. The generator utilizes atmospheric noise when a number is produced, in order to achieve true randomness.



A

1:	107°	41 m
2:	215°	39 m
3:	5°	10 m
4:	93°	10 m
5:	272°	34 m
6:	317°	27 m
7:	177°	31 m
8:	210°	11 m
9:	193°	28 m
10:	339°	8 m

B

1:	351°	22 m
2:	328°	45 m
3:	302°	16 m
4:	326°	7 m
5:	181°	8 m
6:	325°	23 m
7:	52°	20 m
8:	249°	16 m
9:	136°	7 m
10:	87°	18 m

Figure 2 – Sampling design, sampling plot locations, final courses and distance for site A and B.

Using the highest point of each area as the origin, the plots were then mapped out (established) utilizing the generated numbers.

A couple of factors that might invalidate a plot should they occur were determined beforehand. These were as follows:

1) Soil coverage < 50% (due to e.g. bare rock or boulders)

2) Overlap with other plots

Should either or both factors occur one would take one of two actions. If, for instance, the plot was located on a bare rock surface, one could simply change the compass-course by 180 degrees, and then check if the plot was now valid. If the problem was one of overlap with another plot, the plot could be moved sideways while still maintaining the same distance from the origin until there was no longer an overlap.

Each plot was then divided into sub-plots measuring a square meter each, a hundred in total for each plot. Within each sub-plot all trees of the species Scots pine, Norway spruce and birch were counted and sampled.

2.2.1 Field work

Most of the trees found were of a small size, and the samples could primarily be collected using common pruning shears. For the trees of some size (i.e. diameter of trunk > 10cm) a standard 5 mm increment borer (Haglöf AB, Sweden) was used (Figure 3).

All samples were collected as close to the root-neck as circumstances allowed, in order for the sample to contain as many tree rings as possible. The samples were then put in separate paper envelopes and labelled with a unique ID, before being stored in a dry space. A total number of 277 samples were collected.

Figure 3 – Sample being taken with increment borer.

2.2.2 Climate data

The climate data needed was collected from the Norwegian Meteorological Institute ("eKlima," 2016), asking for homogenized temperature values and total monthly precipitation for the months of May, June, July and August. A continuous series of temperature and precipitation data from 1945 to 2015 was collected from a weather station in Nissedal (Stnr.: 37230, 252 m a.s.l.. N°59.0257 E°8.5187).The series was correlated with data from a station in Geilo (Stnr.: 25590, 810 m a.s.l.., N°60.5173 E°8.2015; Data series: 1967-2005)**.** The station at Geilo was deemed as representative of the climate one would observe at the sample site, being located at an altitude of 850 meters and inland. The Pearson correlation gave a coefficient of 0.88 for temperature and 0.77 for precipitation, and was deemed significant given as only the general trend was needed and not the specific temperature.

2.3 Analysis

While Scots pine and Norway spruce are both conifers, birch is a deciduous tree. The rings of deciduous trees are in general notoriously more difficult to read than those of conifers**.** The ring pattern develops due to annual differences in growth speed, and the appertaining cell-size of the wood. In high altitude or alpine areas, the growth period, or window, for all species is much shorter than for their lowland relatives**.** This slow annual growth makes for rings that are closer together, and often harder to distinguish.

2.3.1 Lab work

The samples of Scots pine and Norway spruce were prepared using fine sanding paper on the cutting surface, before being measured and read using a Lintab 6 Tree-ring station with a Leica M50 microscope. The sanding paper helped clear up the surface, as well as add contrast to the rings. All measurements where collected and saved with the program TSAPWin Professional 4.58e.

The samples from the birch trees were not possible to read using sanding paper. Instead, a fine scalpel was used to cut a clear surface, which was read and measured on the Lintab Tree-ring station.

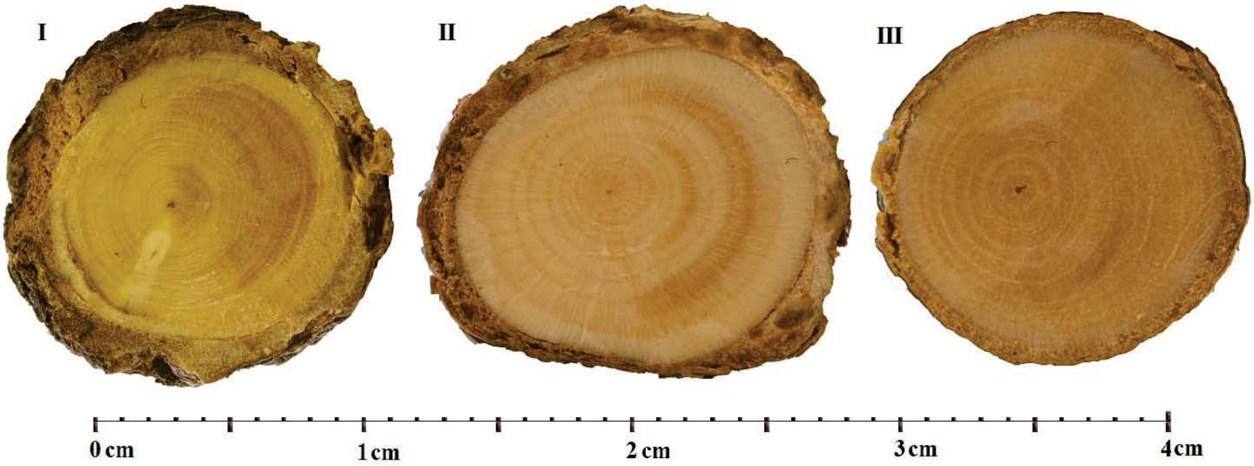


Figure 4 – Picture illustrating the difference in ring growth for each species. All pictures were taken with identical lighting and camera settings. Approximate scale bar for reference. **I:** Norway spruce. **II:** Scots pine **III:** Birch

2.3.2 Oil treatment

Eleven of the birch samples were in particular hard to read, even after a scalpel had been used. After being soaked in MP52 furniture oil overnight all eleven samples could be read. Another 23 birch samples that had proven difficult to read were then also treated with oil and given an additional reading to see if there was an improvement in readability. I ran a paired samples t-test on the last 23 samples to see if the difference was significant, using the data from pre- and post-oil treatment.

2.4 Crossdating and Chronology

There existed at the time of writing no master chronology with which to crossdate the samples. Due to this lack, the samples, as well as the climate data, were grouped into matching three year intervals. It has been taken into account that the samples might have rings missing, and that the age calculated might not be entirely correct. It was decided to use three-year intervals to ‘even out’ any discrepancies connected to any potential misdating of the samples, and the belief that the general trends would still be visible in spite of this, thereby making the dataset more robust.

3. Results

Out of the 277 collected samples 167 came from site **A** (density 0.17 trees per m^2) and 110 from site **B** (density of 0.1 trees per m^2). Norway spruce was the least common species at either site, despite appearing to have the longest history of establishment at both locations (Figure 6). Birch was the most common species at site **A** with more than 50%, followed by Scots pine with ~38%. At site **B** the division is a bit more even, and Scots pine was the most numerous with ~45%.

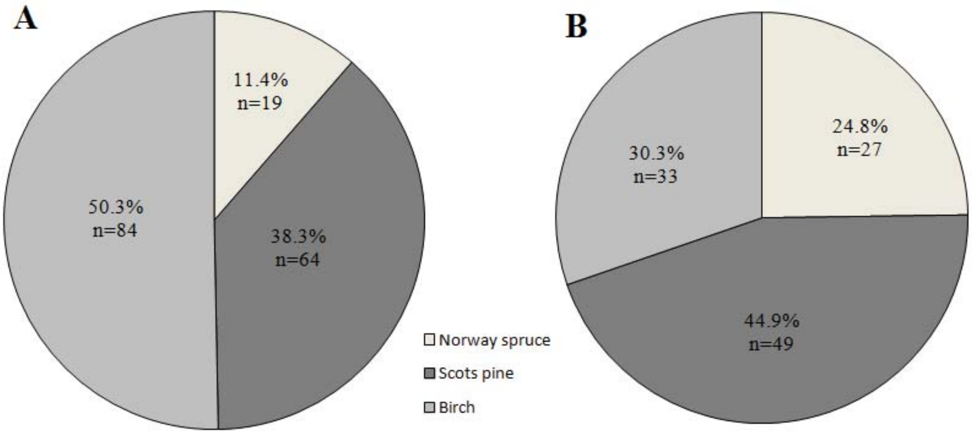


Figure 5 – Distribution of species, site A and B.

3.1 Recruitment

3.1.1 Norway Spruce

Of the three species sampled, Norway spruce had the longest living individual (69 years), but overall the smallest population size. The graph (Figure 6) depicts a steady but slow increase in individuals from the seventies and onwards. The pattern is mostly the same for both sites, with slightly more individuals at site **B**. The total number of Norway spruce sampled was 46 - 19 at site **A** and 27 at site **B**.

3.1.2 Scots pine

At both sites there seemed to be a rapid increase in Scots pine individuals from the nineties to present date. The earliest spotted recruitment at both sites dates from the late seventies. The total number of Scots pine samples came to 113 - 64 at site **A** and 49 at site **B**.

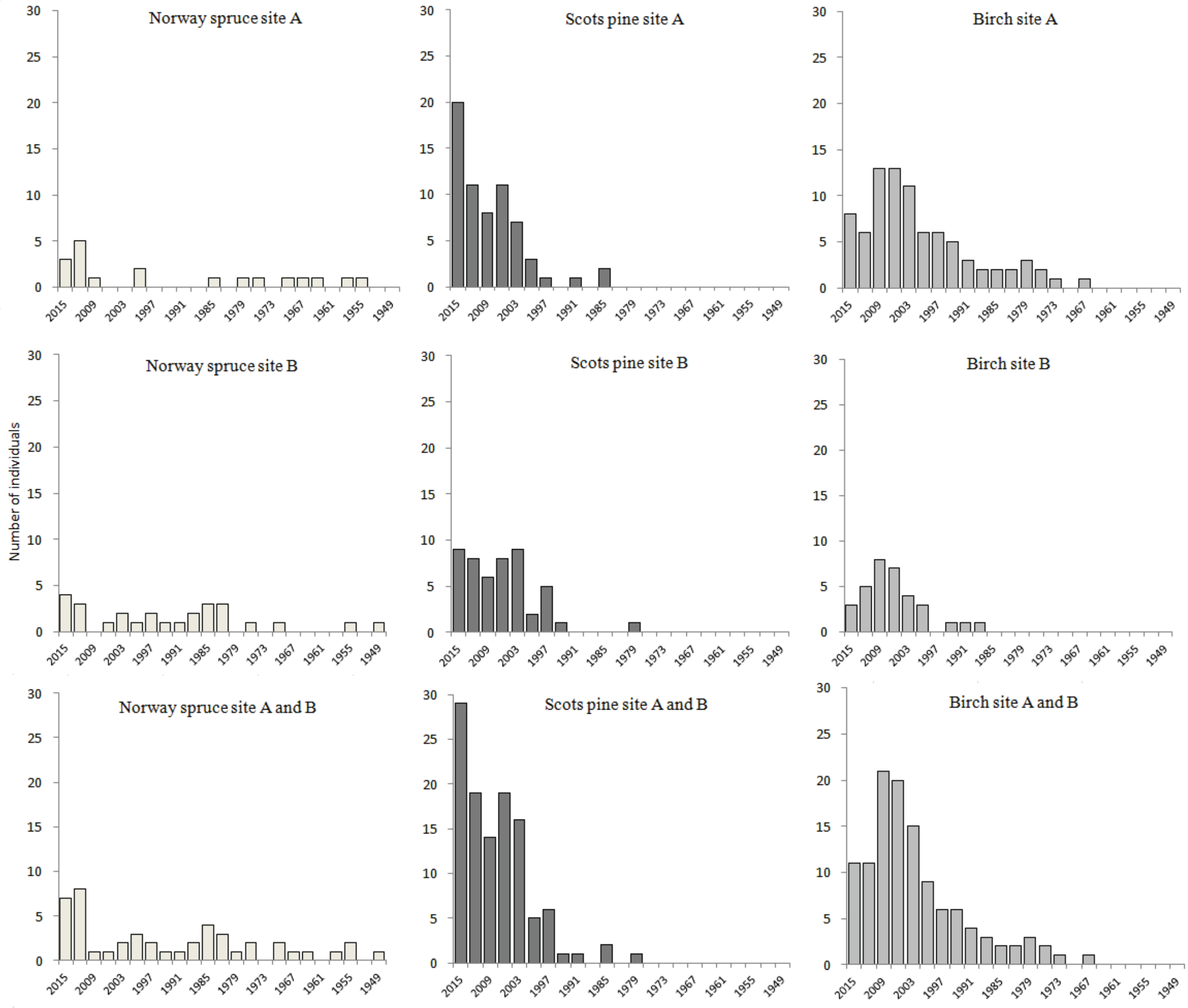


Figure 6 – Individual three-year interval recruitment for all three species and both sample sites

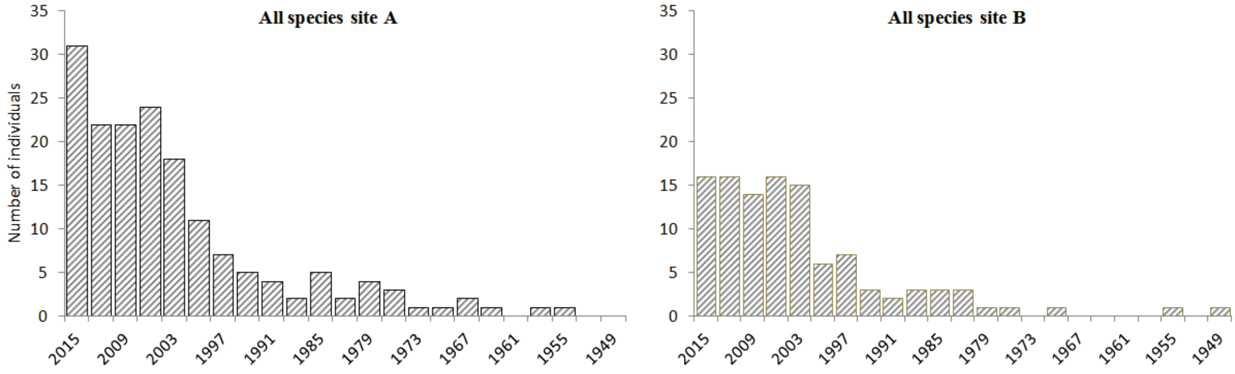


Figure 7 – Three-year interval recruitment for all three species at both sites.

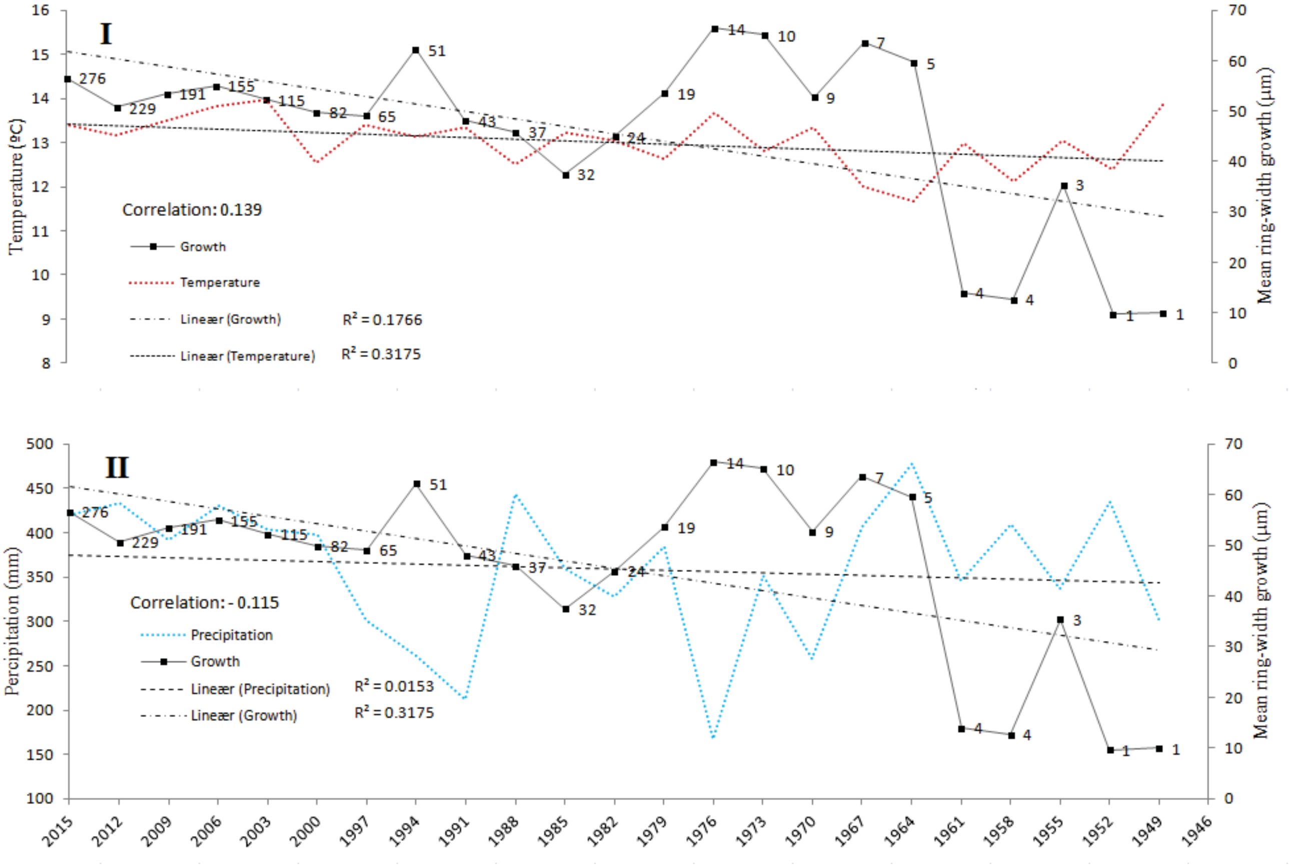
3.1.3 Birch

The oldest individual of birch was sampled at site **A** and dated from 1966. At site **B** the oldest sample dated from 1987. If we look at both sites together, there seems to be a rapid increase in the total number of individuals from the nineties onward (Figure 5). There was however a distinct difference between the sites when they were inspected separately, more so than for Norway spruce and Scots pine. Between the two sites, site **A** had both the largest number of individuals and the longest history of establishment. The recruitment seems to have increased steadily since the eighties, with a distinct peak in the period 2003 – 2009. The numbers of birch samples found at site **A** was 84, while site **B** had a much lower total number – 34. The general trend for both sites is an increase over the last 20 years with a similar peak in recruitment in the years 2003 – 2015.

For all three species there appears to be an increase in the number of successful recruitments, but there are clear local variations, most noticeable for Scots pine and birch.

3.2 Growth

There does not appear to be any clear correlation between temperature and growth, nor between precipitation and growth. A multiple variable regression analysis using both factors showed no significance.



Figur 8 – The graphs show mean three-year interval growth for all samples. Number of samples indicated at each point. **I:** Mean three-year summer temperature (May, June, July and August) with trend line. **II:** Mean three year summer precipitation (May, June, July and August) with trend line.

3.2.1 Norway spruce

While the pattern for recruitment concerning Norway spruce looked relatively similar for both locations (Figure 6), the variety in growth did not (Figure 9). At site **B** the amount seems to be mostly stable, and noticeably lower than at site **A**. Site **A** on the other hand varies much more, all the while being higher. There is for both sites a dip in growth around the late eighties lasting out through the nineties.

3.2.2 Scots pine

Scots pine has noticeable differences in growth for the two locations during the late eighties up through the nineties (Figure 9). There was a prolonged peak of growth at site **A** (>100µm) in the period 1982-1997, while site **B** only had minimal growth. From around year 2000 both areas show the same level of annual growth, with a slow but steady increase up to present date.

3.2.3 Birch

Birch seems to have an overall decline in annual growth, most noticeable at site **A** (Figure 9). Since the first detected establishment at site **B** in the mid eighties, both areas seems to have approximately the same pattern of growth, albeit a bit lower at site **B**.

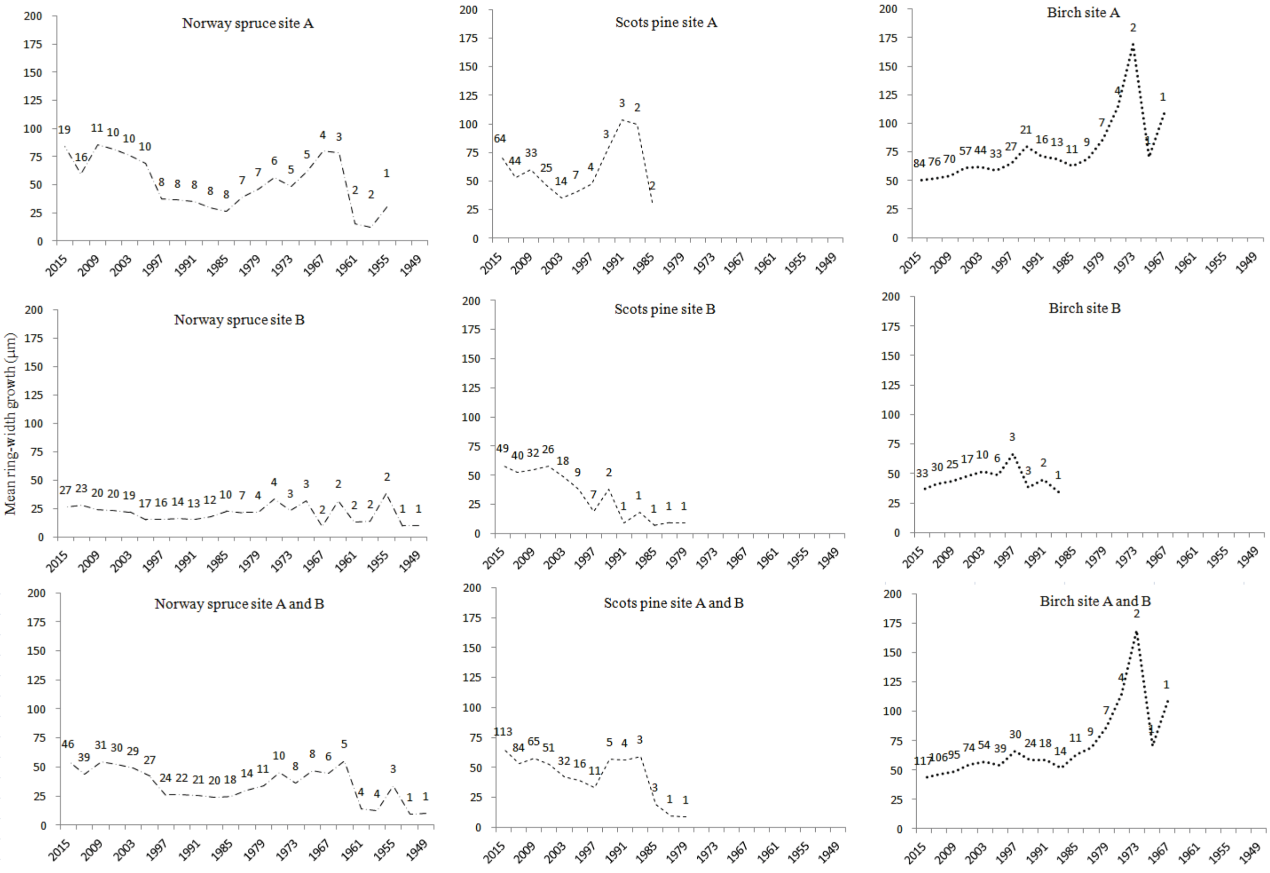


Figure 9 – Mean three year interval growth (µm) for each species at both sites, total n at a given time for each datapoint.

Looking at the growth pattern for all three species at once, but separately for each site, the overall level of growth is noticeably higher at site **A** than **B** (Figure 10).

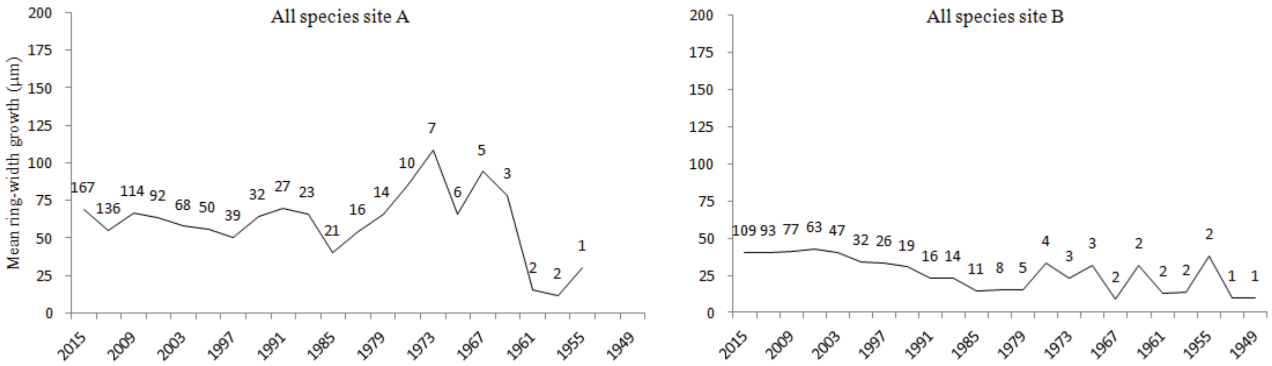


Figure 10 – Mean three year interval growth for all three species at each site.

3.3 Samples treated with oil

In all, 23 samples were treated with oil before being read a second time. Four of the samples ended up with a lower dating than previous, while the rest all got a higher one. A paired sample T-test showed the treatment to be significant (Table 1).

Table 1 – Summary of paired t-test for samples before and after treatment with oil

SUMMARY			Alpha	0,05				
Groups	*Count*	*Mean*	*Std Dev*	*Std Err*	*t*	*df*	*Cohen d*	*Effect r*
Before	23	13.39	9.11					
After	23	19.04	12.30					
Difference	23	-5.65	8.77	1.83	-3.09	22	0.64	0.55

T TEST					
	p-value	*t-crit*	*lower*	*upper*	*sig*
One Tail	0.0027	1.72			yes
Two Tail	0.0053	2.07	-9.44	-1.86	yes

4. Discussion

The initial assumption was that tree recruitment and growth would be correlated with variations in temperature and precipitation, but the results show that this was not the case, as I did not find any clear correlations. However, the presence of a large and site-specific variation among the studied tree species was clear. Nonetheless, the predicted increase in both yearly growth and recruitment seems to be evident, albeit without a clear explanation. As stated in the introduction, this could indicate that the tree line altitude is actually increasing.

Even though my results show no clear correlations between tree performance and the climatic variables, it is widely accepted that temperature and precipitation is of great importance to the forming of alpine communities (Greenwood et al., 2015; McCarty, 2001; Milbau et al., 2009; Aitken et al., 2008; Klanderud, 2005; Luckman and Kavanagh, 2000; Körner, 1998). However, in addition to climatic factors, several other factors have also been identified as potentially important in shaping alpine plant communities. For example, rodents has been shown to greatly influence seedling recruitment through predation, with a clear correlation between rodent cycles and seedling establishment (Nystuen et al., 2014). Baier (2006) also showed that the specific substrate a Norway spruce seedling had, greatly impacted growth and success. The study depicted the possibility of large local variations on a small scale, which has also been shown to be the case for the establishment success of Norway spruce in boreal forests (Hörnberg et al., 1997). Overall, it is for each location a question of what specific conglomerate of factors limits growth, and to what extent each individual factor contributes in the limitation (Brang, 1998).

The precise mechanics that define the tree line have been much discussed in the past, and continue to be so to this day, resulting in several different theories that seek to explain the phenomenon (Körner, 2012; Richardson and Friedland, 2007; Chapin and Körner, 1994; Körner, 1998; Grace, 1989). The problem according to Körner (2012) is that none of the theories proposed are globally applicable. There will always be local differences that cause species in one area to react to certain conditions while the same conditions might have no perceivable effect in another area. The question then, for each location, is what the exact composition of limiting factors are, and to which extent a factor plays a role.

As temperatures rise, the predicted reduction in wintertime snow cover will lead to reduced soil temperature, which in turn slows down both plant cell division and any further development into functional tissue, and would therefore, at a given point, stump tree growth (Körner and Paulsen, 2004).

My results show a general increase in annual growth, both for Norway spruce and Scots pine, but a slight decrease for birch at both location **A** and **B** (Figure 8). Looking at this alone, if reduced winter snow cover is an issue, it could seem to be a species-specific response to reduced soil temperature. In its extension, this could imply that birch suffers more from low soil temperatures than Norway spruce and Scots pine. At the same time, the graphs picturing annual recruitment (Figure 5) draw a different picture. Here, it seems like both Scots pine and birch are doing increasingly well, while Norway spruce barely shows any change. However, should low soil temperatures as a result of unstable winter snow cover be a significant issue, it is unlikely there would have been this increase in successful recruitment.

Of the three species, only Scots pine seems to show a positive increase both for recruitment and growth. This could imply a future change in species composition to a more Scots pine dominated plant community at the tree line in the study area.

Several authors have shown that the role of microhabitat, microrelief and facilitation is of great importance (Callaway et al., 2002; Gottfried et al., 1999; Hörnberg et al., 1997, 1997; Klug-Pümpel, 1982). Both recruitment and growth appears to be lower at site **B** for all species, but the trends are the same. The difference in overall topography between the sites might be the cause of this. The spatial and temporal response to climate in alpine ecotones has also been shown to vary, (Kullman, 2002; Luckman and Kavanagh, 2000) and positive feedback or facilitation from older, already established trees, could be important (Bekker, 2005). Site **A** has much steeper sides, but also a much more rugged terrain – with gorges, cracks and large stones permeating the landscape. Site **B** is much more open and exposed and has few naturally occurring shelters. Kimball and Weihrauch (2000) postulated that wind abrasion and mechanic stress to a large degree contributed in shaping the alpine-tree line ecotone. Site B could therefore, to a greater extent than **A,** be limited by mechanic stress caused by wind, but it is also reasonable to expect that both snow-cover and time of thawing, and to that extent, growth season, will be different.

The age distribution shown by the results suggests an increase in successful recruitment for Scots pine and birch. The factors that stress a plant change in severity throughout the different life stages, and even if conditions for seedling establishment overall are favourable, it could be that a switch occurs as the seedling reaches a certain stage, triggering an abrupt die-off. As shown by Olsen and Klanderud (2014), such a switch in biotic competition and stress is possible. To determine whether this applies here would require continued study of the site over consecutive years, to see if the age- and population distribution stays constant.

Grazing, both by wild and domesticated creatures, regulates both species composition and spatial distribution (Chapin and Körner, 2013; Hofgaard, 1997a, 1997b; Kullman, 1995). The old dairy summer farm Tråen langseter lies approximately one kilometre north of site **A.** The summer farm burned down in 1912 (Sigdal kommune, 2016), and has since then not been in use. Even though the amount of livestock grazing in the area has abated greatly the last hundred years, there are still some sheep that are kept out on pasture in the area during summertime. The continued grazing pressure from both wild animals and the sheep kept there might be enough to continue suppressing tree recruitment. Site **B,** being much more accessible, would conceivably be much more impacted by such grazing than site **A**. This could account for the differences in both growth and recruitment for site **A** and **B**, but further research would be needed in order to verify that.

Regarding future predictions on climate warming, differences in snow cover and thawing might induce a greater state of inter species competition at each site (Klug-Pümpel, 1982). A recent study done by Lett et al. (2014) shows snow cover above the tree line as the dominant control for seedling survival. In milder climates the effect of snow cover depends on the degree to which there is a bryophyte cover present.

If my working hypotheses were correct, we should have witnessed a corresponding climb and drop in recruitment and growth as temperatures and precipitation changed. As it stands, my results seem to show that neither of these factors alone are the most limiting for the alpine trees here investigated. A non-invasive, multi-year, multi-season follow-up study could provide some of the answers**.** It would have to include information about nearby topography such as rocks, hollows, other trees or stumps when plotting the seedlings, and where each tree-seedling was plotted and marked in relation to the others. In addition, it would be very helpful to do on-site recordings of climatic variables, rather than depend on 'off-site' data from distant weather stations. Cordoning off some areas to prevent grazing, and monitoring them over time whilst having a control area, could also shed light on the degree to which grazing impacts on-site recruitment.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. Evolutionary Applications, vol.1, 95–111. doi:10.1111/j.1752-4571.2007.00013.x

Artsdatabanken (2007). Rødlista og Trillemarka. Nationen.

Baier, R., Ettl, R., Hahn, C., Göttlein, A. (2006). Early development and nutrition of Norway spruce (*Picea abies* (L.) Karst.) seedlings on different seedbeds in the Bavarian limestone Alps – a bioassay. Annals of Forest Science, vol.63, 339–348. doi:10.1051/forest:2006014

Bekker, M.F. (2005). Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. Arctic, Antarctic and Alpine Research, vol.37, 97–107.

Bertness, M.D., Callaway, R. (1994). Positive interactions in communities. Trends in ecology and evolution, vol. 9, 191–193. doi:10.1016/0169-5347(94)90088-4

Blanck, Y.-L., Rolstad, J., Storaunet, K.O. (2013). Low- to moderate-severity historical fires promoted high tree growth in a boreal Scots pine forest of Norway. Scandinavian Journal of Forest Research, vol. 28, 126–135. doi:10.1080/02827581.2012.706635

Brang, P. (1998). Early seedling establishment of Picea abies in small forest gaps in the Swiss Alps. Canadian Journal of Forest Research, vol 28, 626–639.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J. (2002). Positive Interactions Among Alpine Plants Increase With Stress. Nature. vol.417, 841–844. doi:10.1038/nature00805

Chapin, F.S.I., Körner, C. (2013). Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Springer Science & Business Media.

Chapin, F.S., Körner, C. (1994). Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Trends in Ecology and Evolution, vol.9, 45–47.

eKlima (2016) . EKlima - Gratis tilgang til meteorologisk institutts vær- og klimadata fra historiske data til sanntidsobservasjoner. URL: http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39049&_dad=portal&_schema=PORTAL (accessed 4.24.16).

Erefur, C., Bergsten, U., de Chantal, M. (2008). Establishment of direct seeded seedlings of Norway spruce and Scots pine: Effects of stand conditions, orientation and distance with respect to shelter tree, and fertilisation. Forest Ecology and Management, vol.255, 1186–1195. doi:10.1016/j.foreco.2007.10.024

Fylkesmannen (2015). Trillemarka-Rollagsfjell Naturreservat - Årsmelding 2015. Forvaltningsstyret for Trillemarka-Rollagsfjell Naturreservat.

Gottfried, M., Pauli, H., Reiter, K., Grabherr, G. (1999). A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. Diversity and Distributions, vol.5, 241–251.

Grace, J. (1989). Tree lines. Philosophical Transasctions of the Royal Society of London, vol.B 324, 233–245.

Greenwood, S., Chen, J.-C., Chen, C.-T., Jump, A.S. (2015). Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. Journal of Vegetation Science, vol.26, 711–721. doi:10.1111/jvs.12269

Hofgaard, A. (1997a). Inter-Relationships between Treeline Position, Species Diversity, Land Use and Climate Change in the Central Scandes Mountains of Norway. Global Ecology and Biogeography Letters, vol.6, 419–429. doi:10.2307/2997351

Hofgaard, A. (1997b). Structural changes in the forest-tundra ecotone: a dynamic process, in: Past and Future Rapid Environmental Changes. Springer, pp. 255–263.

Hofton, T.H. (2003). Trillemarka-Rollagsfjell: en sammenstilling av registreringer med hovedvekt på biologiske verdier. Siste Sjanse-Rapport. vol.5, 151.

Hörnberg, G., Ohlson, M., Zackrisson, O. (1997). Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research, vol.27, 1015–1023. doi:10.1139/x97-045

Huston, M.A., McBride, A.C. (2002). Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford. 47–60.

Jones, P.D., New, M., Parker, D.E., Martin, S., Rigor, I.G. (1999). Surface air temperature and its changes over the past 150 years. Reviews of Geophysics, vol.37, 173–199. doi:10.1029/1999RG900002

Kasin, I., Blanck, Y. -l., Storaunet, K.O., Rolstad, J., Ohlson, M. (2013). The charcoal record in peat and mineral soil across a boreal landscape and possible linkages to climate change and recent fire history. The Holocene, vol.23, 1052–1065. doi:10.1177/0959683613479678

Kimball, K.D., Weihrauch, D.M. (2000). Alpine vegetation communities and the alpine-treeline ecotone boundary in New England as biomonitors for climate change.

Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. Journal of Ecology, vol.93, 127–137. doi:10.1111/j.1365-2745.2004.00944.x

Klug-Pümpel, B. (1982). Effects of microrelief on species distribution and phytomass variations in a Caricetum curvulae stand. Vegetatio, vol.48, 249–254.

Körner, C.(2012). Alpine Treelines - Functional Ecology of the Global High Elevation Tree Limits, 1st ed. Springer Basel.

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. Oecologia, vol.115, 445–459.

Kullman, L., 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of ecology, vol.90, 68–77.

Kullman, L. (1995). New and Firm Evidence for Mid-Holocene Appearance of Picea Abies in the Scandes Mountains, Sweden. Journal of ecology, vol.83, 439. doi:10.2307/2261597

Lett, S., Wardle, D., Nilsson, M.C., Dorrepaal, E. (2014). Seedling establishment at the alpine tree line - Can there be too much winter protection? Am. Geophys. Union Fall Meet. 2014 Abstr. GC22E-05.

Luckman, B., Kavanagh, T. (2000). Impact of Climate Fluctuations on Mountain Environments in the Canadian Rockies. American Geophysical Union, Fall Meeting 2014, abstract #GC22E-05, vol.29, 371–380. doi:10.1579/0044-7447-29.7.371

McCarty, J.P. (2001). Ecological Consequences of Recent Climate Change. Conservation Biology , vol.15, 230 – 331.

Milbau, A., Graae, B.J., Shevtsova, A., Nijs, I. (2009). Effects of a warmer climate on seed germination in the subarctic. Annals of Botany, vol.104, 287–296. doi:10.1093/aob/mcp117

NGU (2016). Berggrunn - Nasjonal berggrunnsdatabase. URL http://geo.ngu.no/kart/berggrunn/ (accessed 4.22.16).

Nystuen, K.O., Evju, M., Rusch, G.M., Graae, B.J., Eide, N.E. (2014). Rodent population dynamics affect seedling recruitment in alpine habitats. Journal of Vegetation Science, vol.25, 1004–1014. doi:10.1111/jvs.12163

Olsen, S.L., Klanderud, K. (2014). Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. Oikos, vol.123, 71–78. doi:10.1111/j.1600-0706.2013.00336.x

Pachauri, R.K., Mayer, L., Intergovernmental Panel on Climate Change (Eds.) (2015). Climate change 2014: synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Random.org (2016). URL https://www.random.org/ (accessed 4.24.16).

Richardson, A.D., Friedland, A.J. (2007). A review of the theories to explain Arctic and alpine treelines around the world. Journal of Sustainable Forestry, vol.25.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M. (2013). Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests.

Global Change Biology, vol.19, 229–240. doi:10.1111/gcb.12038

Sigdal kommune (2016). Langsetervarden (859 m.o.h.) og Store Øytjønn (701 m.o.h.) - UT.no. http://www.ut.no/. URL http://www.ut.no/tur/2.8824/ (accessed 5.4.16).

Smith, R.I.L. (1994). Vascular plants as bioindicators of regional warming in Antarctica. Oecologia, vol.99, 322–328. doi:10.1007/BF00627745

Storaunet, K.O., Rolstad, J., Toeneiet, M., Blanck, Y. (2013). Strong anthropogenic signals in historic forest fire regime: a detailed spatiotemporal case study from south-central Norway. Canadian Journal of Forest Research, vol.43, 836–845. doi:10.1139/cjfr-2012-0462

Tingstad, L., Olsen, S.L., Klanderud, K., Vandvik, V., Ohlson, M. (2015). Temperature, precipitation and biotic interactions as determinants of tree seedling recruitment across the tree line ecotone. Oecologia, vol.179, 599–608. doi:10.1007/s00442-015-3360-0

Troll, C. (1973). The Upper Timberlines in Different Climatic Zones. Arctic and Alpine Research, vol.5, A3–A18.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F. (2002). Ecological responses to recent climate change. Nature, vol.416, 389–395.

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