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Tree recruitment in the Forest-tundra Ecotone

Limitation and facilitation processes in contrasting climatic Regions

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Biology

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ABSTRACT:

Aim: The aim of this study was to analyse how abiotic and biotic constraint and facilitation agents determine tree recruitment in the alpine zone in climatically different regions as well as across species; Birch, pine and spruce.

Location: The study was located to Grødalen, Haltdalen and Røros representing a coastal-inland gradient, where birch was included along the entire climatic gradient and all three species in one region (Haltdalen).

Methods: Variables collected for seedling/sapling (specimen <2m) locations and associated control locations were; surrounding vegetation layers at ground-, field- and shrub level, occurrence and type of shelter, soil samples, topography (land cover and slope position) and plant measurements (height, base diameter, crown area and age; Not recorded for control locations). Statistical analyses consisted of ANOVA and chi-squared tests were used to compare across regions and among variables.

Results: The occurrence of shelter (shrub, depression and boulder) and moist location characteristics such as dominance of bryophytes, facilitated seedling recruitment equally across all regions and species. Shrub shelters and high amounts of organic material in the soil facilitated birch height growth in the drier regions. Benefits from surrounding vegetation positively influenced the growth and survival of birch seedlings/saplings in drier regions. Dwarf shrub vegetation and shrub shelters increase moisture availability in the soil and provide shelter from wind scouring. Yet, dwarf shrub vegetation did not show any influence on height growth and survival for pine and spruce. In addition, pine recruitment was less affected by shelter presence and moist location characteristics than birch and spruce.

Conclusions: This study demonstrates that there is an interplay of regional and local facilitation agents effecting seedling recruitment and that these agents vary across species. This complicates production of general predictions regarding future response of tree recruitment to changing climate. Identifying relevant facilitation agents supplies the necessary building blocks for estimating the potential for further recruitment and growth of seedlings and saplings into the tundra environment.

SAMMENDRAG:

Mål: Hensikten med denne studien er å analysere hvordan abiotiske og biotiske begrensnings- og tilretteleggingsagenter bestemmer trerekrutteringen i alpine soner i klimatiske ulike regioner, så vel som mellom artene: bjørk, furu og gran.

Sted: Studien ble utført i Grødalen, Haltdalen og Røros og representerer en kyst-innland gradient, hvor bjørk er representert langs hele denne klimatiske gradienten, og alle tre arter (bjørk, furu og gran) er representert i en region (Haltdalen).

Metoder: Variablene som ble samlet for plantene og de tilhørende kontrollstedene er omgivende vegetasjonslag på bakke-, felt- og busknivå, forekomst og type av ly, jordprøver, topografi (arealdekke og hellingsstillinger) og plantemålinger (høyde, basediameter, kronediameter og alder; ikke registrert for kontrollsteder). Statistiske analyser består av ANOVA og Chi-kvadrat tester som sammenligner på tvers av regionene og mellom variablene.

Resultater: Forekomsten av ly (busk, depresjon og store steiner) og fuktige lokale egenskaper som dominans av moser, tilrettela frøplanterekrutteringen likt på tvers av alle regionene og artene. Ly i form av busker og store mengder organisk materiale i jorda hadde positiv påvirkning på høydeveksten hos bjørk i de tørre områdene. Naboliggende vegetasjon påvirket vekst og overlevelse hos frøplanter/unge individer av bjørk positivt i tørrere områder. Dvergbuskvegetasjon og busk-ly øke fuktigheten i jorda og gir beskyttelse mot vind. Dvergbuskvegetasjon ser ikke ut til å ha innflytelse på høydevekst og overlevelse for furu og gran. I tillegg ble fururekrutteringen mindre påvirket av nærvær av ly og fuktige lokale egenskaper enn bjørk og gran.

Konklusjon: Denne studien viser at det er et samspill av regionale og lokale tilretteleggingsagenter som påvirker frøplanterekrutteringen, og at disse faktorene varierer på tvers av arter. Dette kompliserer formuleringen av prediksjoner om framtidige responser av trerekrutteringen med hensyn til klimaforandringer. Studien identifiserer relevante tilretteleggingsagenter som er nødvendige byggesteinene for å estimere potensialet for videre rekruttering og vekst av frøplanter og unge trær i tundraen.

INTRODUCTION:

The topic of climate change in terms of current rising temperatures and its effects on tree encroachment in the tundra has been of great interest among scientists studying the dynamics of forest-tundra ecotone vegetation (Callaghan *et al*. 2002; ACIA 2005; Harsh *et al*. 2009). The encroachment is driven by a combination of increased height growth of previously established individuals and increased recruitment of new individuals beyond the current tree line (Kullman 2002; Hofgaard *et al*. 2009; Aune *et al*. 2011). Tree species represented in the forest-tundra ecotone have shown regional variation in their response to increasing temperatures, some regions showed tree line advancement whereas other regions remained stable over prolonged periods or showed signs of retreating (Lavoie and Payette 1994; Dalen and Hofgaard 2005; Batllori *et al.* 2009; Harsch *et al.* 2009). Higher temperatures, particularly winter warming, and increased precipitation are regional climatic characteristics that appear to have an enhancing effect on tree line encroachment (Hofgaard *et al*. 2009; Aune *et al*. 2011). There is an interplay of abiotic and biotic factors effecting recruitment in the forest tundra ecotone which drive the variation in forest-tundra ecotone responses seen at the different regions.

Assessment of recruitment in the forest-tundra ecotone needs consideration of not only broad-scale environmental impact factors but also influential factors acting at a local scale, both abiotic and biotic. In the forest-tundra ecotone factors influencing seed dispersal, recruitment and growth includes variables such as wind (Holtmeier and Broll 2010a), herbivory (Hofgaard 1997; Cairns and Moen 2004; Hofgaard *et al.* 2010), ground temperatures (Holtmeier 2009), parasites (Stöcklin and Körner 1999; Holtmeier and Broll 2010b) and snow cover (Sturm *et al.* 2001a; Holtmeier 2009). The variations in exposure to these environmental factors at different locations are associated with the variations seen among tree line responses to climate change (Hofgaard *et al.* 2009). In areas exposed to high wind velocities, snow abrasions can cause mortality or result in the inability to grow tall (Hadley and Smith 1983; Holtmeier and Broll 2010a). Snow cover is important in protecting tree seedlings and saplings from the winter desiccation as well as from winter browsers (Dalen and Hofgaard 2005; Hofgaard *et al*. 2009; Holtmeier and Broll 2010b). Snow cover also acts as a thermal insulator, increasing the soil surface temperature during the winter months as well as supplies the soil with moisture in the spring and early summer months benefiting seedling survival (Sturm *et al.* 2001a; Holtmeier and Broll 2010b). However, a snow cover persisting too long into the growing season inhibit seedling recruitment and survival through development of parasitic snow fungi (Stöcklin and Körner 1999) and shortening of the growing season (Hofgaard *et al.* 2009). Interactions between present tree species individuals and surrounding vegetation can facilitate further tree recruitment in terms of protection through enhanced snow-trapping, and earlier snow-melt as well as greater soil water content (Callaway 1995; Maher *et al*. 2005; Brooker *et al*. 2008). Sheltering in wind exposed areas is a fundamental aspect of tree seedling establishment which can include topographic features such as shallow depressions, terrace risers, boulders and sheltering vegetation such as krummholz and shrubs (Resler 2006; Batllori *et al*. 2009). These protective microsites become progressively more important for their survival as altitude increases due to wind velocities becoming more prominent (Brooker *et al*. 2008; Holtmeier and Broll 2010b). In addition, the establishment of seedlings into highly foraged areas can also greatly impair their success (Hofgaard *et al.* 2010).

Recruitment of the species depends on its requirements for survival and growth, and therefore the forest-tundra ecotone dynamics are mediated by species-specific traits in addition to the environmental conditions within and between regions. For this study three forest tundra ecotone regions representing a coast-inland gradient in central Norway (Sør-Trønderlag and Møre og Romsdal) are used as model areas. Birch (*Betula pubescens*), spruce (*Picea abies*) and pine (*Pinus sylvestris*) and since their life strategies vary, their response to changing climate may differ accordingly. By investigating what variables are affecting species-specific recruitment at the regional scale in terms of broad climatic differences as well as local variation within the region, predictions on the ecotone response to climate change can become more accurate.

For this MSc thesis my objective was to analyze how abiotic and biotic constraint and facilitation agents determine tree recruitment in the alpine zone in 1) climatically different regions and 2) among different tree species. For the comparison between regions, Grødalen, Haltdalen and Røros in central Norway were chosen with birch present in all three regions. For the comparison among species the climatically intermediate region, Haltdalen, where all three focal species are present, was used for analyses of species-specific responses. Questions I addressed in this thesis were; what environmental factors are influencing seedling recruitment above the tree line? Does the relative importance of these factors vary between climatic regions? Is there a species-specific recruitment pattern corresponding to these factors?

METHODS:

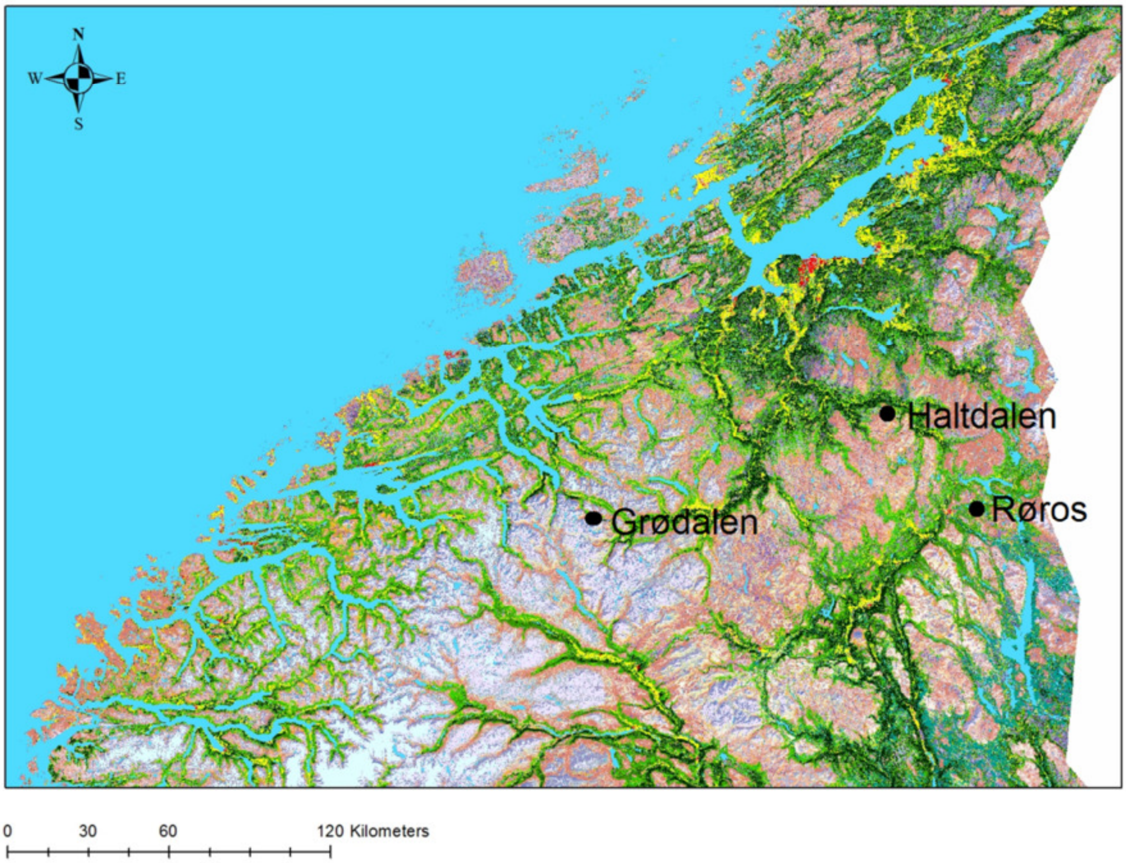

Figure 1: Map of study areas Grødalen, Haltdalen and Røros in Central Norway.

Study areas:

The three regions selected for this study reflect a moisture gradient or gradient in coastal influences (Moen 1999; Norwegian Meteorological Institute 2012). Grødalen (1100 m.a.s.l., N62° 32.572’, E8° 59.494’) signifies the oceanic region, Haltdalen (725 m.a.s.l., N62° 56.460’, E10° 55.662’) represents the intermediate climatic region, and Røros (850 m.a.s.l., N62° 33.191’, E11° 28.468’) which corresponds to the indifferent region (Moen 1999) was selected to represent continental/inland region (Figure 1).

Table 1: Characteristics for selected study areas. Mean temperature and total precipitation values (normal period 1961–1990) for each region is represented by its nearest meteorological station (Data source is the Norwegian Meteorological Institute, www.eklima.met.no).

Study areas	**Grødalen (G)**	**Haltdalen (H)**	**Røros (R)**
Altitude (m a.s.l.)	1100	725	850
Climate data and source			
Continentality class	O1 - slightly oceanic	O2 - markedly oceanic	OC - indifferent section
Meteorological station	Sunndal, Hafsås, Kongsvoll	Ålen	Røros
Direction and distance from study areas	6 km east, 3km south, 37 km southeast	16 km East	6km South-west
Altitude (m a.s.l.)	195, 698, 885	401	628
Temperature (°C) (annual average)	4.4, NA, -0.3	2.0	0.3
Warmest month (°C)	July (13.3), NA, July (9.9)	July (12.0)	July (11.4)
Coldest month (°C)	Jan. (-4.1), NA, Jan. (-9.8)	Jan. (-8.5)	Jan. (-11.2)
Precipitation, annual sum (mm)	740, 675, 445	800	504
Number of days with snow cover	200-225	175-199	175-199
Growing season (days with avg. temp. >5°)	140-150	130-140	130-140

The mean annual precipitation in the Grødalen region, as represented by the Hafsås meterological station (698 m a.s.l., 3 km to the south) is 675 mm. Temperature data was not available for this station, but mean annual temperature at the two closest stations with temperature recordings, Sunndal (195 m.a.s.l., 6 km to the east) and Kongsvoll (885 m.s.a.l., 37 km to the south-east) are 4.4°C and -0.3 °C, respectively. Monthly means for these stations are 13.3 °C and 9.9°C in July and -4.1 °C and -9.8°C in January, respectively. Out of the three regions, this area received the most days of snow cover, 200-225 days, and has a growing season between 140-150 days (Moen 1999). The growing season is defined as the number of days with an average temperature greater than 5 °C (Table 1). The Grødalen region is within the section “slightly oceanic” (Moen 1999).

For the intermediate region, Haltdalen, climate normals from the meteorological station Ålen (401 m.a.s.l, 16 km to the east) are used. The mean annual temperature for this station is 2.0 °C with a monthly average of 12.0 °C for July and a monthly average of -8.5°C for January. The mean annual precipitation is 800mm with snow cover present between

175-199 days of the year. The growing season for this region is 130-140 days (Moen 1999) (Table 1).

Røros represents the most continental region (Moen 1999). The nearest meteorological station is located close to the Røros village (628 m.a.s.l., 6 km to the south-west). At this station the mean annual temperature is 0.3°C with the highest monthly mean occurring during July at 11.4 °C and the lowest monthly mean of -11.2°C in January. The mean annual precipitation is 504mm with snow cover persisting for 175-199 days out of the year. The growing season in which temperatures were on average 5 °C or above was equivalent to 130-140 days (Moen 1999) (Table 1). All climate data refer to the normal period 1961-1990.

Study species:

The focal species for this study were two conifers and one deciduous; pine (*Pinus sylvestris*), spruce (*Picea abies)* and birch (*Betula pubescens*). Spruce and birch are commonly found in moist environments, although birch can be found in a greater range of climatic regions and is dominating in oceanic regions. Spruce are a more specialized species occupying moist landscape sections in inland regions. However, this species is plastic in its ability to survive and grow in very harsh environmental conditions, as illustrated by its ability to grow in clones through layering (Marr 1977). Pine, on the other hand, is often found in regions with relatively dry, warm and snow-poor climate conditions and in locations characterized by spars vegetation cover and bare soil (Kullman 2007).

Table 2: Characteristics for sampled specimens for the three regions by species.

Study areas	**Grødalen (G)**	**Haltdalen (H)**	**Røros (R)**
No. Sampling plots			
Birch	4	13	13
Pine		26	
Spruce		27	
No. Seedlings/saplings (subsample)	196 (50)	598 (150)	200 (50)
Birch	196	201	200
Pine		197	
Spruce		200	
Mean height (m)			
Birch	0.29	0.48	0.38
Pine		0.25	
Spruce		0.69	
Seedling/sapling age			
Birch	15.5	23.8	22.1
Pine		14.3	
Spruce		60	
Mean growth rate			
Birch	0.02	0.02	0.02
Pine		0.02	
Spruce		0.01	
Vitality (percent healthy)			
Birch	83.2	95.5	93.5
Pine		74.1	
Spruce		38	
Cones/catkins (%)			
Birch	0	6.0	2.5
Pine		2.0	
Spruce		0	
Average organic material (%)			
Birch	46.7	66.6	56.1
Pine		43.5	
Spruce		77.4	
No. per hectare			
Birch	560	155	154
Pine		76	
Spruce		76	

Sampling design:

Data was collected from three climatically different regions to determine if there are any differences between them. Within each region 20x50m plots were positioned within a 50 meter wide altitudinal belt just above the tree line i.e. the highest limit of tree-sized (>2m) individuals of the tree species. These plots were not placed at wet, steep or rocky areas to increase data homogeneity and comparability between study areas, and to avoid complications during data collection. The number of plots were adjusted to fit the requirements of 200 seedling and sapling individuals (i.e. specimen <2m) per species (Table 2). Sampling took place in July, 2011. The following variables were recorded for all seedlings and saplings within the plots: GPS coordinates, living height, base diameter, crown diameter (consisting of two perpendicular measurements), vitality class (dead, reduced, and healthy; the reduced category was divided into reduced due to climate, herbivores or fungi if possible), presence of shelter and type of shelter (shrubs, boulders, depression and inter-specific tree species), local slope position (top /convex, slope, flat or bottom/concave), land cover type of the surrounding area and vegetation layer classification (ground-, field-, shrub-, and inter-specific tree layer) within a 20 cm radius of the specimens locations (See Table 3 and 4 for more detail). For shelters an object was considered a shelter depending on distance and size. Firstly, shelters were only considered when found within 2 meters of the sampled specimen and secondly within this distance more distant objects had to be larger (as a consequence of the distance).

A subsample of the sampled population consisting of 50 specimen per species for each region (every forth specimen) were sampled for age determination. The age samples

Table 3: Continuous variables used in this study and its units

Variables	Units
Living height	m
Base diameter	cm
Crown area	m
Age	yrs
Organic matter	%

were collected by taking core samples (5mm increment borer) when base diameters were larger than 5cm, or by cutting the specimen at ground level. Soil samples were also collected at these sample locations from directly below the surface as close as possible to the sampled individual.

For each sampled specimen one control location was randomly selected (rotating stick for direction choice) at a 5 meter distance from the specimen. The control locations were sampled according to the same protocol as for the specimen (except for variables recorded on the specimens and the GPS coordinates). This resulted in an equal amount of control locations as there were sampled specimens.

Data handling:

The two measurements collected for the crown diameter were combined to form the mean crown diameter of the sampled specimens. The crown area (Table 2) was calculated by using the following equation for ellipses:

$$\Pi \times (\text{diameter } a / 2) \times (\text{diameter } b / 2)$$

Soil samples collected in the field were brought to the laboratory and analysed for percent organic matter. The following processing steps were used: the samples were dried

Table 4: Categorical variables and their associated categories

Variables	Categories
Shrub layer	*Betula nana, Juniperus communis, Salix* spp. (Willow)
Field layer	evergreen dwarf shrubs, deciduous dwarf shrub, low herb with dwarf shrub, sedges (*Carex* spp./*Eriophorum* spp.*)*, tall herbs, low herbs, broad-leaved grass, thin leaved grasses, cloudberry (*Rubus chamaemorus)*
Bottom layer	lichen, bryophytes*, Sphagnum* spp., litter, stone/bare ground, water
Land cover	lee side, ridge, heath, stagnant water
Shelter	yes, no
Shelter type	shrub, boulder, depression, inter-specific tree
Slope position	top, bottom, slope, flat

at 105 °C for 24 hours, weighed, then heated at 600 °C for 30 minutes to remove all organic material and weighed again. The resulting weight data values were used to determine the percent organic matter, by applying the weight measurements to the following formula:

% Organic matter = 100 (Dry soil weight – burnt soil weight) / (dry soil weight)

Cored age samples were glued to wooden supports the day of sampling and brought to the laboratory for age determination. Samples were soaked prior to age determination and a scalpel was used to smoothen the surface allowing for better visualization of the annual rings. If further aid in visualization was needed, zinc ointment was applied to increase the contrast between early and late wood and thus ring visualization. Age determination was conducted using standard dendrochronological methods (Fritz 1976). A dissecting microscope with a magnification of 6-50x was used for the ring counting.

Statistical analyses:

Correlation was conducted between the response variables, height, base diameter, crown area and age to determine their predictive value regarding growth and survival of seedlings and saplings in the alpine zone. Height, base diameter and crown area were all highly correlated with each other (Table 5, 6). This relationship was also tested with PCA (Principle Component Analyses), revealing that height was also highly correlated to the first principle component, which accounts for much of the variability in the data. Therefore, only height

Table 5: Correlation of response variables for birch at the three regions, Grødalen, Haltdalen and Røros (bold font indicate significance).

		Base diameter	Areal	Age
Grødalen	Living height	**0.783**	**0.813**	**0.457**
	Base diameter	-	**0.858**	**0.623**
	Crown area		-	**0.468**
Haltdalen	Living height	**0.913**	**0.936**	**0.607**
	Base diameter	-	**0.905**	**0.751**
	Crown area		-	**0.568**
Røros	Living height	**0.926**	**0.928**	**0.870**
	Base diameter	-	**0.935**	**0.932**
	Crown area		-	**0.876**

and age was selected and used for further statistical analyses in response to the explanatory variables.

Chi-squared tests were used to determine whether the categorical, explanatory variables (Table 4) differed across regions and between birch, pine or spruce species. For the continuous explanatory variable, percent organic material (Table 3), a one-way ANOVA was used for these comparisons. Since this variable had a non-normal distribution, the values were converted into frequencies (a value between zero and one) and an ANOVA using generalized linear model (GLM) was applied.

Age structure for specimens were constructed for each region and species by the use of age sampled specimens and calculated age for non-age sampled specimens. For the samples without age data (3/4 of the data) linear regressions were used for each region (birch data) individually and for each species (Haltdalen data). The best linear regression was tested by determining R^2 for age against height as well as base diameter. The equation resulting from the regression with the highest R^2 was used for constructing age data for non-aged sampled specimens.

When determining what factors were affecting seedling and sapling recruitment the data was first analysed for whether recorded environmental factors (Table 4) were significantly associated with the specimen locations. Further, to test for significant

Table 6: Correlation of response variables for the three species in Haltdalen (bold font indicate significance).

		Base diameter	**Areal**	**Age**
Birch	Living height	**0.913**	**0.936**	**0.607**
	Base diameter	-	**0.905**	**0.751**
	Crown area		-	**0.568**
Pine	Living height	**0.885**	**0.914**	**0.889**
	Base diameter	-	**0.884**	**0.832**
	Crown area		-	**0.865**
Spruce	Living height	**0.875**	**0.920**	**0.731**
	Base diameter	-	**0.846**	**0.837**
	Crown area		-	**0.782**

differences between the control data and the specimen data chi-squared tests were used for categorical data and the Mann-Whitney test was used for the continuous variable (percent organic matter). These tests were conducted for each region using only birch data and for each species using only data from Haltdalen, separately. To determine significant effects of explanatory variables on height growth and age of the specimens within the three regions (only birch data) and for each species (only data from Haltdalen), a one-way ANOVA was conducted. If there was significance the analyses was followed by Tukey's honest significant difference (HSD) test for each region and species to determine what categories within the categorical variables had mean values for height and age that differed significantly from each other. Categories (Table 4) with sample sizes less than 5 were not included in the results due to their low statistical power and low conclusion values. The age data used in this analysis included both the collected and calculated age data. To support the assumption of normality in used statistical models, the response variables, height and age, were log transformed. A two-way ANCOVA was used when determining significant differences in the relationship between height and percent organic matter. This relationship between height and organic matter content in the soil was also tested for correlation to compare any differences in significance among species or regions. All statistical analyses were performed in the R-package (R Development Core Team 2007).

Table 7: Chi-squared test showing significant differences (p), degrees of freedom (df) and test statistic (X^2) between the three climatic regions; Grødalen, Haltdalen and Røros.

	p	**df**	**X^2**
Shrub	< 0.001	6	100.2
Field	< 0.001	14	137.7
Bottom	< 0.001	10	86.7
Growth substrate	0.299	2	2.4
Land cover	< 0.001	6	25.5
Shelter	0.069	2	5.4
Shelter type	< 0.001	8	56.9
Slope	< 0.001	6	29.3

Table 8: Results from ANOVA (z) determining significant differences (p) in amount organic material (%) in the soil within the control locations between the three regions Grødalen, Haltdalen and Røros.

		p	**z**
Organic material (%)	Haltdalen-Grødalen	0.270	1.1
	Røros-Grødalen	0.436	0.8
	Røros-Haltdalen	0.735	0.3

RESULTS:

Analysis across climatically different regions:

General comparison among regions:

When determining differences among the three study areas (using control data), shrub-, field-, bottom-layer, land cover, shelter type and slope, were found to be greatly significant ($p < 0.001$) with only growth substrate, shelter and percent organic material being non significant (Table 7, 8). Of the three regions, Grødalen showed greatest deviation from the other two with more *Betula nana*, evergreen dwarf shrub and litter (Figure 2). Boulders were also more abundant at this region.

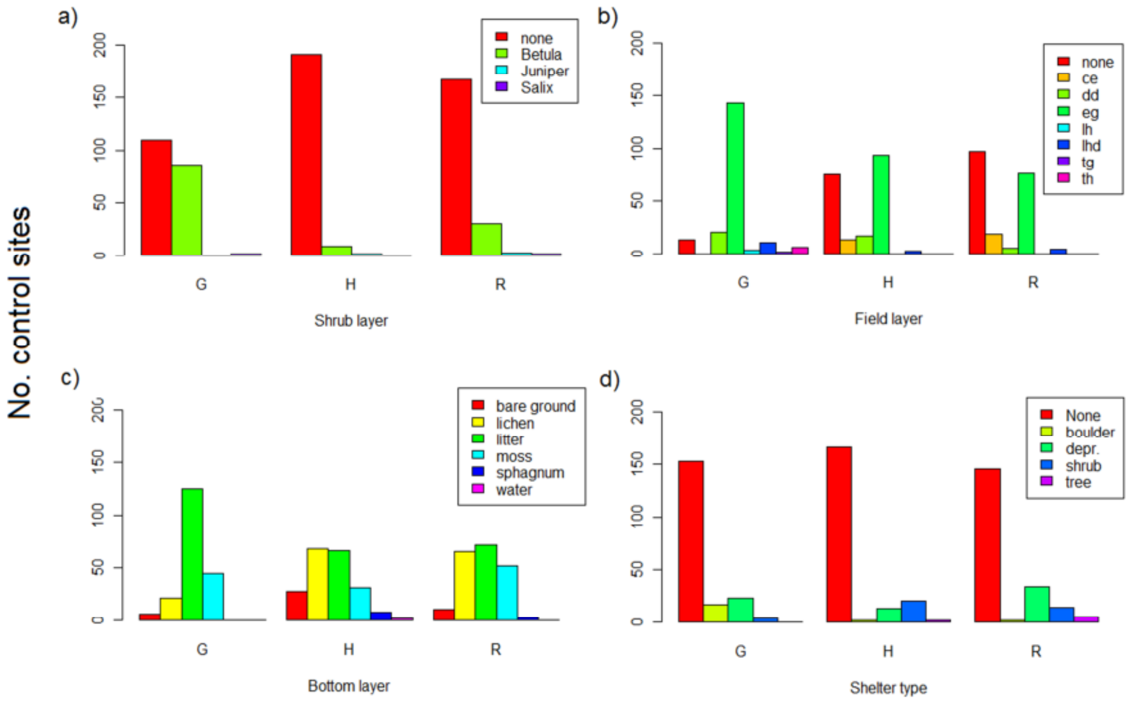

Figure 2: Number of control locations/sites containing a dominant characteristic associated to one of the categories within the different explanatory variables; a) Shrub layer, b) field layer, c) bottom layer and c) shelter type for Grødalen (G), Haltdalen (H) and Røros (R).

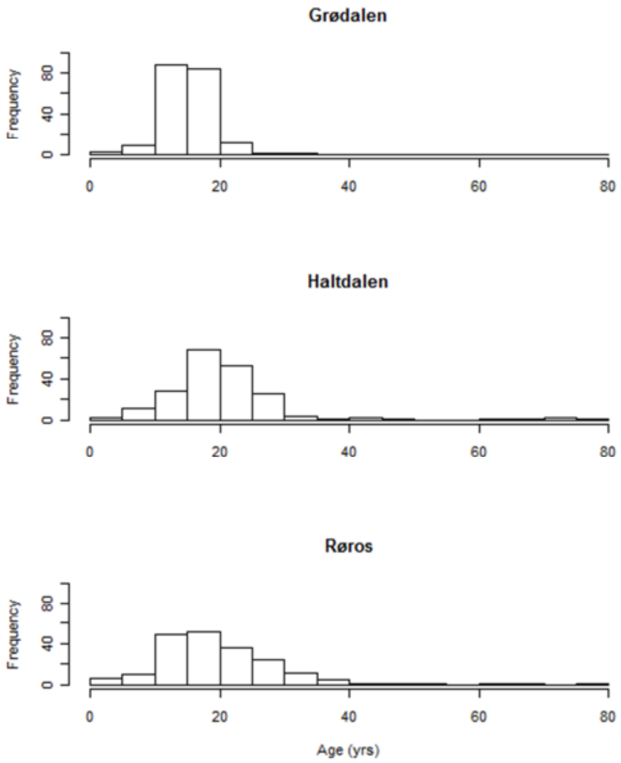

Figure 3: Frequency of birch across age categories with 5 year intervals for the three regions, Grødalen, Haltdalen and Røros.

Birch showed a more narrow age distribution in Grødalen than in the two other regions with maximum ages of 30 years and with highest frequency between 10-20 years. Haltdalen and Røros had similar distributions reaching up to 80 years and with the highest frequency in age classes 10-20 years (Figure 3).

In Grødalen 17% of sampled birch specimens had reduced vitality (Figure 4), and 97% of these appeared to be a result of herbivory. Plants with reduced vitality made up 4.5% of the specimens both in Haltdalen and Røros (Figure 4). In Haltdalen fungi (67%) and climate damages (33%) were the main reasons for reduction while in Røros (4.5% reduced) climate damages, fungi and herbivory were equally responsible for the damages. Røros was also recorded with some dead birch specimen (2%) (Figure 4).

When comparing control locations with specimen locations for Grødalen, Haltdalen and Røros, shelter ($p<0.001$, df=1, $X^2=46.7$; $p<0.001$, df=1, $X^2=27.5$; $p=0.042$, df=1, $X^2=4.1$, respectively) and shelter type (p<0.001, df=3, X^2=50.2; p<0.001, df=4, X^2=29.1; p=0.003, df=4, X^2=16.3; respectively) were significantly more frequent in the specimen locations than in the control locations for all three regions (Table 9). In Haltdalen there were also significant differences between the control and specimen locations for bottom layer (p=0.005, df=5, X^2=17.0) as well as land cover type (p=0.001, df=2, X^2=13.4) (Table 9). Bottom layers dominated by bare ground were less frequent in the specimen data and for land cover there was more specimen data associated with lees side locations. In addition,

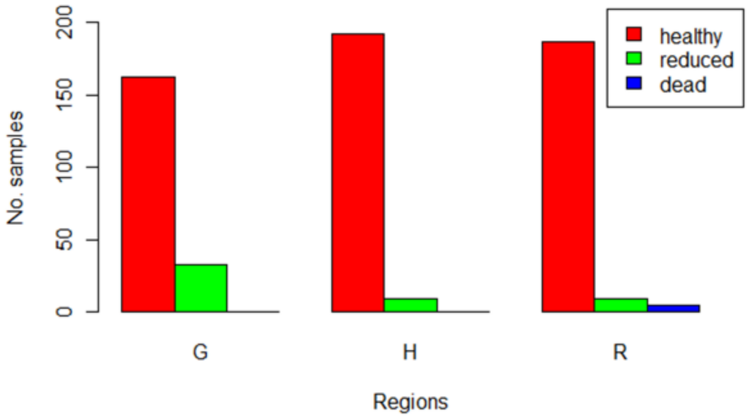

Figure 4: Number of birch specimen within the vitality class healthy, reduced or dead, for birch at three regions, Grødalen (G), Haltdalen (H) and Røros (R).

Table 9: P-values resulting from chi-squared tests and Mann-Whitney tests of the explanatory variables, comparing control data with specimen data for each climatic region, Grødalen, Haltdalen and Røros (Significance indicated in bold).

	GRØDALEN	HALTDALEN	RØROS
Chi-sq.			
Field	0.067	0.673	0.691
Bottom	0.226	**0.005**	0.373
Land cover	0.142	**0.001**	0.600
Shelter	**<<0.001**	**<0.001**	**0.042**
Shelter type	**<<0.001**	**<0.001**	**0.003**
Slope	0.067	0.279	**0.037**
Mann-Whitney test			
Organic material (%)	0.225	0.571	0.122

Røros, control and specimen locations were significantly different in the locations slope position ($p=0.037$, $df=3$, $X^2=8.5$) (Table 9) and the specimen locations were found more at the bottom of slopes and less on flat surfaces than the control locations.

Height response of Betula pubescens

Comparing different categories within recorded categorical variables (Table 4) for the three regions showed that field layer, bottom layer, shelter and shelter type all differed significantly between the categories (Figure 5).

In Grødalen, there were significant differences within the field layer ($p<0.001$, $df=6$, $F=4.3$) (Figure 5a), bottom layer ($p<0.001$, $df=3$, $F=20.7$) (Figure 5b), shelter type ($p=0.023$, $df=4$, $F=3.256$) (Figure 5d) and land cover ($p<0.001$, $df=2$, $F=21.9$) categories. Within the field-layer vegetation specimens were significantly taller when associated with deciduous

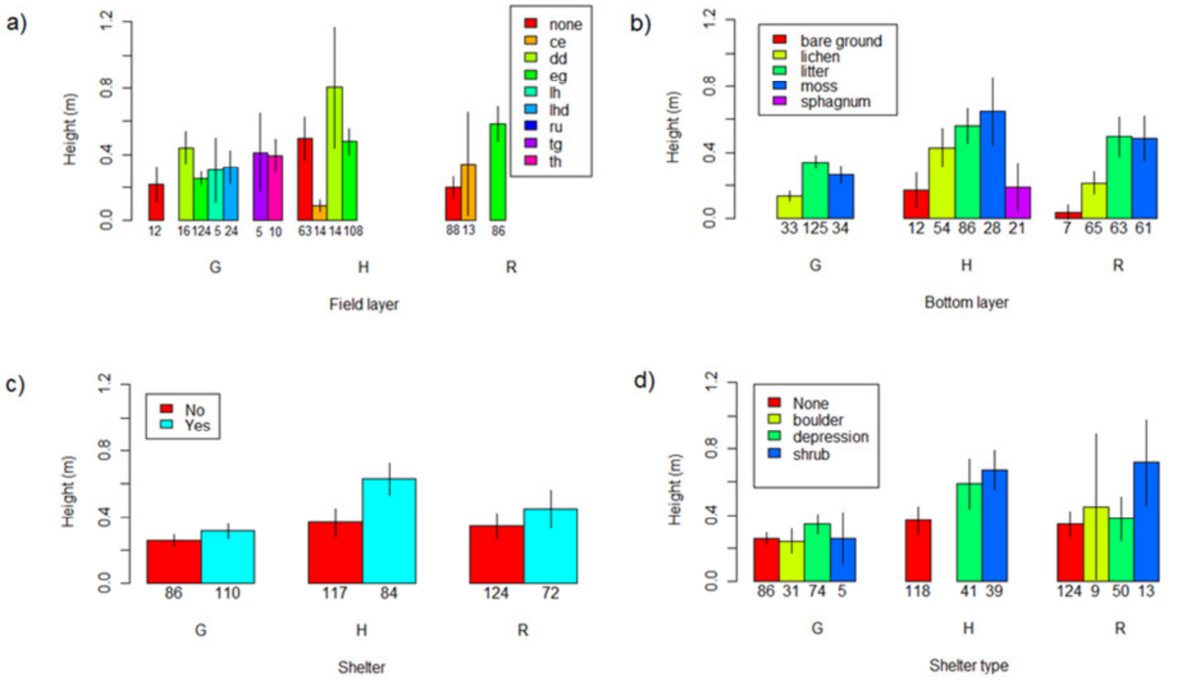

Figure 5: Histograms showing average specimen height (m), with the 95 percent confidence interval, for each category of a) field layer, b) bottom layer, c) shelter and d) shelter type for Grødalen (G), Haltdalen (H) and Røros (R). Field layer vegetation consist of sedges (ce), deciduous dwarf shrubs (dd), evergreen dwarf shrubs (eg), low herbs (lh), low herb with dwarf shrubs (lhd), cloudberry (ru), thin leaved grass (tg) and tall herbs (th). Sample sizes (n) for each category are indicated below each bar.

dwarf shrubs than with evergreen dwarf shrubs (p=0.005) or locations without field layer vegetation (p=0.022). Within bottom layer vegetation, specimens were significantly taller when associated with litter (p<0.001) and bryophytes (p<0.001) than lichen. The only shelter type that showed significantly taller birch was depression type shelters (p=0.032). Lastly for land cover there were taller specimens in heath (p<0.001) and lee side (p<0.001) locations than on ridges.

In Haltdalen, there were significant differences within field layer (p<0.001, df=4, F=6.5) (Figure 5a), bottom layer (p<0.001, df=4, F=10.6) (Figure 5b), land cover (p<0.001, df=2, F=21.857), shelter (p<0.001, df=1, F=27.238) (Figure 5c), shelter type (p<0.001, df=4, F=10.050) (Figure 5d) and slope (p=0.004, df=2, F=5.714). This region also had taller specimens associated with deciduous dwarf shrubs (p<0.001) than with sedges which was also true for evergreen dwarf shrubs (p<0.001) and when associated with no field layer (p=0.002). In terms of the bottom layer vegetation, bare ground or *Sphagnum* were associated with significantly shorter specimens than locations with litter (p=0.001, p<0.001, respectively), lichen (p=0.008, p<0.001, respectively), and bryophytes (p<0.001, p<0.001, respectively). Specimens located on lee sides were significantly taller than specimens located in heath environments (p<0.001). There were also significantly taller specimens

Table 10: Correlation of percent organic material with height (m) and age (yrs) at each region.

		Grødalen	**Haltdalen**	**Røros**
% organic material vs.	Height (m)	0.844	0.001	< 0.001
	Age (yrs)	0.109	0.674	< 0.001

Table 11: Two-way ANOVA determining differences between regions in regards to percent organic material in response to height and age.

		Height (m)	**Age (yrs)**
% organic material	Haltdalen – Grødalen	0.047	0.207
	Røros – Grødalen	< 0.001	0.127
	Haltdalen - Røros	0.087	0.006

when shelter was present and of the shelter types, shrub vegetation was the only type with a significant difference from no shelter (p<0.001). There were also significantly taller specimens on slopes than on flat surfaces (p=0.003).

In Røros there were significant differences within the field layer (p<0.001, df=5, F=11.7) (Figure 5a), bottom layer (p<0.001, df=3, F=13.8) (Figure 5b) and shelter type(p=0.027, df=3, F =3.1) (Figure 5d). Røros had taller specimens associated with evergreen dwarf shrubs, which were significantly taller than locations without any field layer vegetation (p<0.001). Specimens associated with bare ground and lichens were significantly shorter than those associated with litter (p<0.001, p<0.001) and bryphytes (p<0.001, p=0.002). The type of shelter present also showed a significant height difference between shrubs and no shelter (p=0.016) as in Haltdalen.

Amount of organic material in the soil at specimen locations showed correlation with specimen height (increasing height with increasing amount of organic material) in Haltdalen (p=0.001, df=48, t=3.463) and in Røros (p<0.001, df=46, t=4.749) but not in Grødalen (p=0.844, df=47, t=0.120) (Table 10) (Figure 6). When comparing the relationship between height and organic material across regions, Grødalen differed significantly from Haltdalen (p=0.047, df=1, t=2.0) and Røros (p<0.001, df=1, t=3.8) (Table 11).

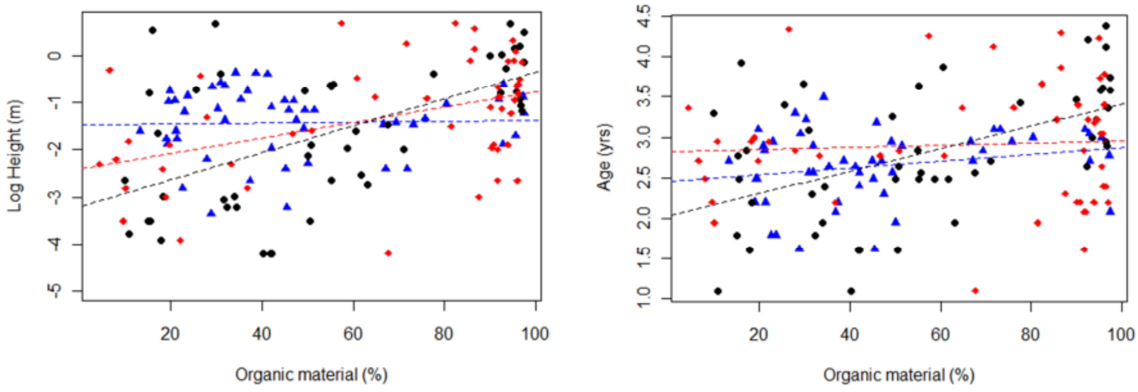

Figure 6: Percent organic material versus height (m) and age (yrs) for Grødalen (blue, rectangles), Haltdalen (red, squares) and Røros (black, circles)

Age response of Betula pubescens

The average age was significantly different in Grødalen for bottom layer vegetation (p=0.013, df=3, F=3.7) (Figure 7b), land cover type (p<0.001, df=2, F=10.9), shelter (p=0.003, df=1, F=9.1) (Figure 7c) and shelter type (p=0.013, df=3, F=3.7) (Figure 7d). Litter-dominated bottom-layer vegetation had significantly older specimen than when associated with lichen dominated vegetation (p=0.008). Lee side (p<0.001) and heath type land cover environments (p<0.001) also showed significantly older specimens than when located on ridges. Presence of shelter had a positive effect on age with depressions having significantly older specimens than locations without shelter (p=0.012).

The average age was significantly different in Haltdalen for the field layer (p=0.001, df=4, F=4.5) (Figure 7a), bottom layer (p<0.001, df=4, F=6.3) (Figure 7b), shelter (p=0.012, df=1, F=6.5) (Figure 7c) and slope (p=0.013, df=2, F=4.4). Effects of field layer on age were the same as with height where older specimens were associated with evergreen dwarf shrubs (p<0.001), deciduous dwarf shrubs (p=0.007) and no field layer vegetation (p=0.001) than in locations dominates by sedges. Also bottom layer vegetation showed similar response as for height where specimen locations dominated by lichens (p<0.001), litter (p<0.001) and bryophytes (p=0.005) had older specimens than when dominated by *Sphagnum*. Shelter (p=0.012) as well as locations on slopes (p=0.010) also resulted in significantly older specimens.

The average age was significantly different in Røros for the field layer (p<0.001, df=5, F=7.0) (Figure 7a) and bottom layer (p<0.001, df=3, F =10.9) (Figure 7b). Specimens were significantly older when associated with evergreen dwarf shrubs than without field layer vegetation (p<0.001). Specimens in litter and bryophyte dominated locations were significantly older than when associated with bare ground (p=0.002, p<0.001, respectively) and lichen (p=0.002, p<0.001, respectively).

Amount of organic material in the soil at specimen locations was correlation with specimen age (increasing age with increasing amount of organic material) in Røros (p<0.001, df=46, t=4.0) but not in Grødalen (p=0.109, df=47, t=1.6) and Haltdalen (p=0.674, df=48, t=0.4) (Table 10) (Figure 6). When comparing the relationship between height and organic material across regions, Haltdalen and Røros differed significantly from one another (p=0.006, df=2, t=2.8) (Table 11).

Table 12: Chi-squared test showing significant differences (p) degrees of freedom (df) and the test statistic (X^2) between sample populations belonging to the different species, birch, spruce and pine at Haltdalen.

	p	**df**	**X^2**
Shrub	0.006	4	14.4
Field	< 0.001	12	59.5
Bottom	< 0.001	10	96.4
Growth substrate	< 0.001	2	23.9
Land cover	< 0.001	4	36.2
Shelter	0.038	2	6.5
Shelter type	0.008	8	20.8
Slope	< 0.001	6	25.8

Table 13: Results from ANOVA (z) determining significant differences (p) in percent organic material in the soil between control locations associated with birch, pine or spruce.

		p	**z**
Organic material (%)	Birch-Pine	0.099	1.7
	Birch-Spruce	0.914	0.1
	Spruce-Pine	0.112	1.6

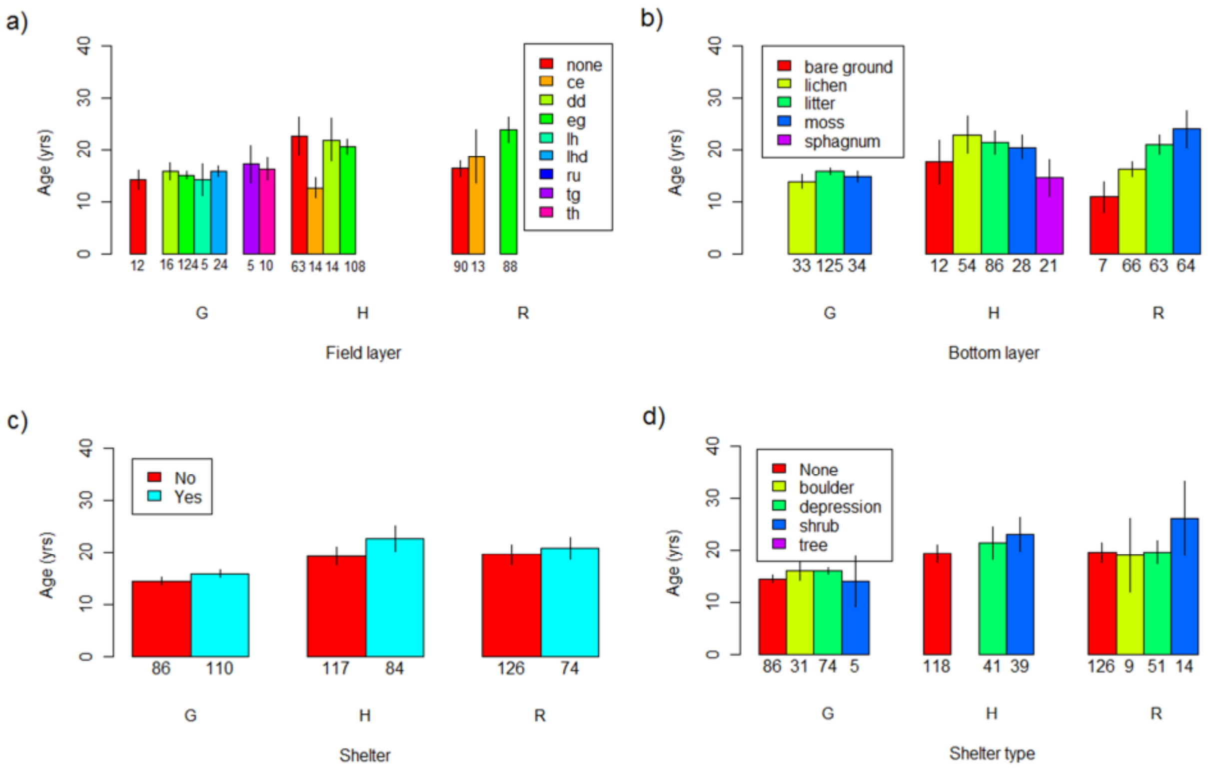

Figure 7: Histograms showing average specimen age (yrs), with 95 percent confidence intervals for each category for a) field layer, b) bottom layer, c) shelter and d) shelter type for Grødalen (G), Haltdalen (H) and Røros (R). Field layer vegetation consist of sedges (ce), deciduous dwarf shrubs (dd), evergreen dwarf shrubs (eg), low herbs (lh), low herb with dwarf shrubs (lhd), cloudberry (ru), thin leaved grass (tg) and tall herbs (th). Sample sizes (n) for each category are indicated below each bar.

Analysis across species:

General comparison among species

When determining differences between the three species (using control data), all but percent organic material in the soil were significant (Table 12, 13). Some of these differences resulted from control locations associated with spruce having less boulder/stone type growth substrate, less lichen and more depression type shelters. Also, control locations associated with birch were located more frequently on slopes.

In Haltdalen, the age distribution for birch was narrow with the highest frequency in age classes around 20 years and with maximum ages of 30 years. Pine specimens were also narrow but with a more even distribution, with highest frequency of around 25 years and with maximum ages of 55 years. Spruce specimens had a wide age distribution peaking at

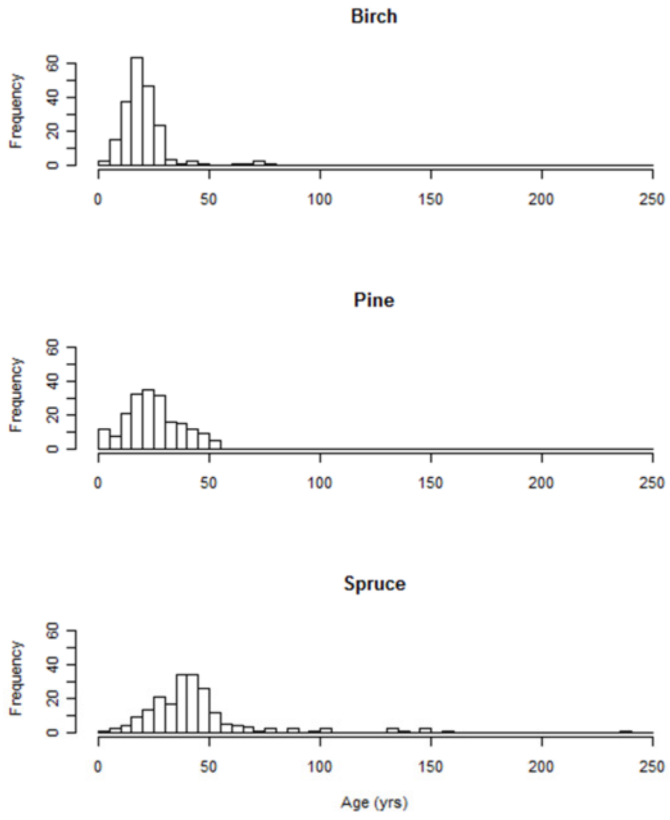

Figure 8: Frequency of birch, pine and spruce across age categories of 5 year intervals.

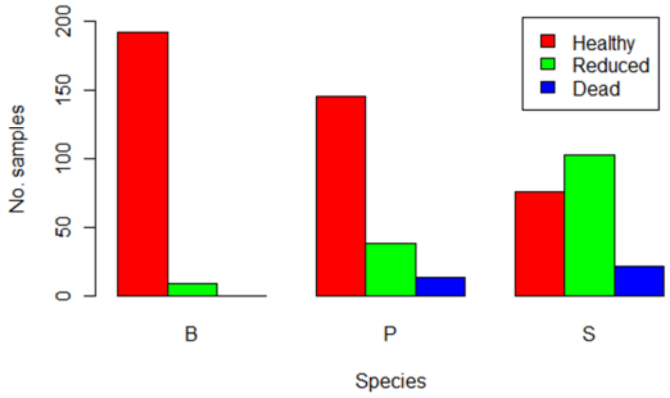

Figure 9: Number of birch (B), pine (P) and spruce (S) within the vitality class healthy, reduced or dead, at the intermedaite region, Haltdalen.

40-45 years with sampled ages measuring up to 240 years (Figure 8).

Birch and pine showed a dominance of healthy specimen whereas, spruces had more frequent reduced vitality (Figure 9). For birch, a large portion (c. 95%) of the specimens were healthy and reduced vitality was related climate damage (22%) and fungi (67%) as well as to unknown causes (11%). Pine had 74% healthy specimens with 19% of specimens with reduced vitality largely due to climate damages (71%). For this species, there were 6.6% dead specimens recorded. Spruce had less proportion of healthy specimens (38%) and in the portion of reduced specimens (51.5%) 69% were due to climate damages. There were also some dead spruce recorded in this region (10.5%) (Figure 9).

Comparing control locations with specimen locations for birch, pine and spruce, showed that bottom layer ($p=0.004$, $df=5$, $X^2=17.0$; $p=0.003$, $df=5$, $X^2=18.0$; $p<0.001$, $df=5$, $X^2=25.5$; respectively), shelter ($p<0.001$, $df=1$, $X^2=27.5$; $p=0.034$, $df=1$, $X^2=4.5$; $p<0.001$, $df=1$, $X^2=98.2$; respectively) and shelter type ($p<0.001$, $df=4$, $X^2=29.1$; $p=0.015$, $df=4$, $X^2=12.4$; $p<0.001$, $df=4$, $X^2=106.4$; respectively) significantly differed for all three species (Table 14). Locations dominated by litter, shelter, shrub shelters (except for pine) and depression shelters were significantly more abundant in the specimen locations then in the control locations for all three species. Bare ground was also less evident in specimen locations. Percent organic material was not significant for any of the species within this study. For

Table 14: P-values resulting from chi-squared tests of the explanatory variables, comparing control locations with plant locations for each species, birch, pine and spruce.

	BIRCH	**PINE**	**SPRUCE**
Chi-sq.			
Field	0.673	0.743	<<0.001
Bottom	0.005	0.003	<0.001
Land cover	0.001	0.312	0.414
Shelter	<0.001	0.034	<<0.001
Shelter type	<0.001	0.015	<<0.001
Slope	0.279	0.041	<0.001
Mann-Whitney test			
Organic material (%)	0.571	0.421	0.298

Table 15: P-values resulting from correlation tests of percent organic material against height (m) and age (yrs) for each species.

		Birch	**Pine**	**Spruce**
Organic material vs.	Height	0.001	0.006	0.636
	Age	0.674	0.060	0.296

birch, there were also significant differences between land cover types (p=0.001, df=2, X^2=13.4) (Table 14) where lee side was more frequent in specimen locations. Specimen locations for pine were found more often at the bottom of slopes then in control locations. In addition, locations associated with spruce specimens had significantly less field layer vegetation (p<0.001, df=6, X^2=40.0) related to sedges as well as being more associated with bottom positions of slopes.

Height responses among species

For birch there were significant differences in height among the field layer vegetation (p<0.001, df=4, F=6.5) (Figure 10a), bottom layer vegetation (p<0.001, df=4, F=10.6) (Figure 10b), land cover type (p<0.001, df=2, F=14.3), shelter(p<0.001, df=1, F =27.2) (Figure 10c), shelter type(p<0.001, df=4, F=10.1) (Figure 10d), and slope position (p=0.004, df=2, F=5.7). Within the field layer vegetation, locations dominated by sedges had significantly shorter specimens than locations associated with deciduous dwarf shrubs (p<0.001), evergreen dwarf shrubs (p<0.001) as well as locations without field layer vegetation (p=0.002). Within bottom layer vegetation, locations associated with bare ground or *Sphagnum* had significantly shorter specimens than locations with lichens (p=0.008, p<0.001, respectively), litter (p=0.001, p<0.001, respectively) and bryophytes (p<0.001, p<0.001, respectively). Specimens were significantly taller when located on lee sides than when located in heath environments (p<0.001). They were also significantly taller when associated with shelter (p<0.001) which was related to shelters categorized as shrubs (p<0.001). Birch specimens were also significantly taller when growing on a slopes than when located on flat terrain (p=0.003).

For pine there were only significant differences within the bottom layer vegetation (p<0.001, df=4, F=9.6) (Figure 10b). Pine specimens had the same result as birch specimens for the bottom layer where taller specimens were associated with litter (p<0.001), lichens (p<0.001) and bryophytes (p<0.001). Locations dominated by *Sphagnum* (p=0.026) also had significantly taller specimens than with bare ground.

For spruce there were significant differences in height among the bottom layer vegetation (p<0.001, df=3, F=7.2) (Figure 10b), land cover (p=0.01, df=1, F=6.7), shelter (p <0.001, df=1, F=41.3) (Figure 10c) and shelter type (p<0.001, df=4, F=13.0) (Figure 10d). There were significantly taller specimens in locations with bryophytes than in locations dominated by lichens (p<0.001) as well as locations having shelter present (p<0.001). Shelter types with significantly taller specimens were depressions (p<0.001) and shrubs (p<0.001). Lee sides were also associated with significantly taller specimens than when growing in heath environments (p=0.010).

Amount of organic material in the soil at specimen locations showed correlation with specimens height (increasing height with increasing amount of organic material) for birch (p=0.001, df=48, t=3.5) and pine (p=0.005, df=48, t=2.9) but not for spruce (p=0.636, df=43, t=0.5) (Table 15) (Figure 11).

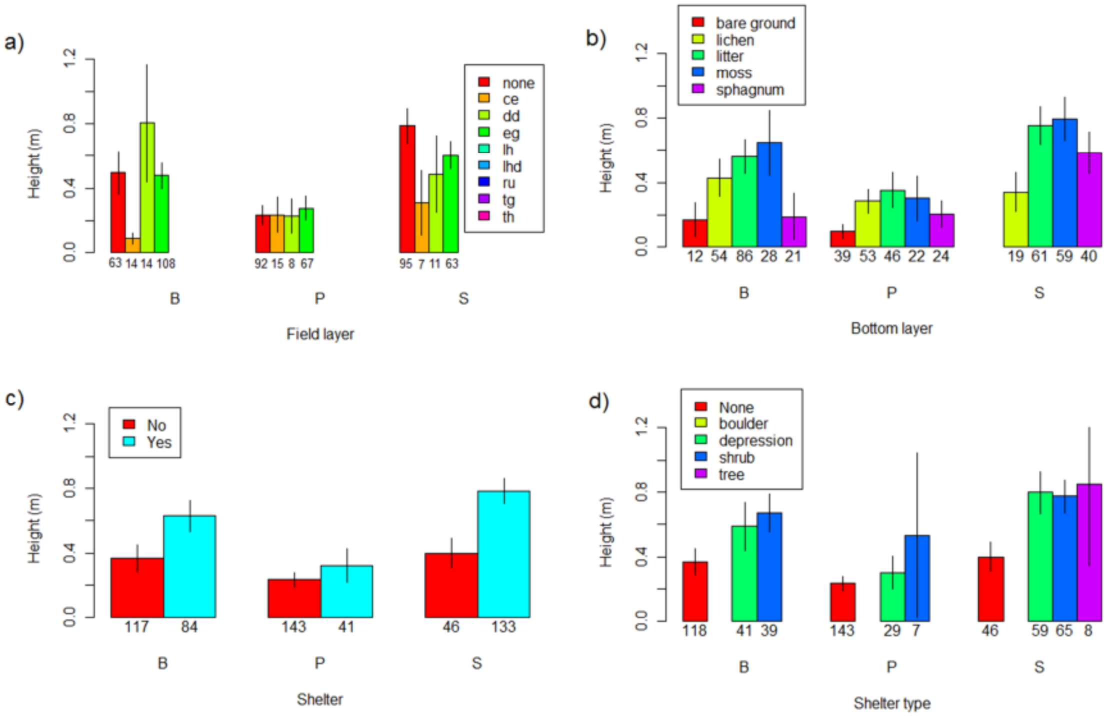

Figure 10: Histograms showing average specimen height (m), with 95 percent confidence intervals, for each category of a) field layer, b) bottom layer, c) shelter and d) shelter type for birch (B), pine (P) and spruce (S). Field layer vegetation consist of sedges (ce), deciduous dwarf shrubs (dd), evergreen dwarf shrubs (eg), low herbs (lh), low herb with dwarf shrubs (lhd), cloudberry (ru), thin leaved grass (tg) and tall herbs (th). Sample sizes for each category are indicated below each bar.

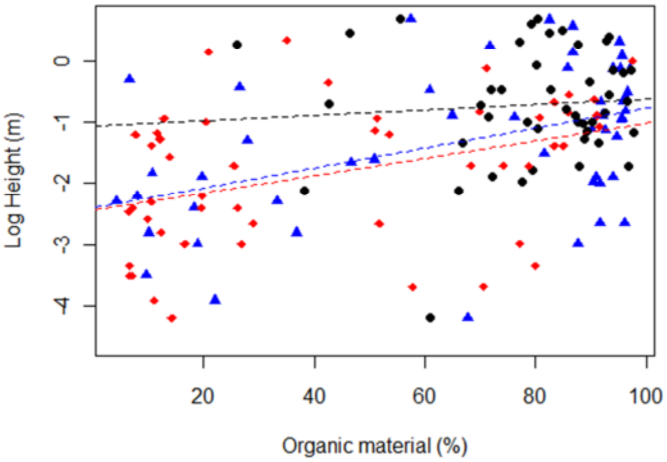

Figure 11: Percent organic material versus height (m) of the plant samples from Haltdalen for birch (blue, rectangles), pine (red, squares) and spruce (black, circles)

Age responses among species

Age of birch specimen were significantly different among field layer vegetation (p<0.001, df=4, F=5.1) (Figure 11a), bottom layer (p<0.001, df=4, F=6.6) (Figure 11b), shelter (p =0.007, df=1, F=7.4) (Figure 11c), and slope position (p=0.01, df=2, F=4.8). Similar to the results found for height measurements, field layer vegetation consisting of mostly sedges had significantly younger specimens than when associated with deciduous dwarf shrubs (p=0.003), evergreen dwarf shrubs (p<0.001) or no field layer vegetation (p<0.001). Locations dominated by lichens (p<0.001), litter (p<0.001) and bryophytes (p=0.003) were also associated with significantly older specimens than locations associated with *Sphagnum*. Locations associated with shelter also had significantly older specimens than locations without shelter (p=0.007). Locations on a slopes were also associated with significantly older specimens than flat locations (p=0.007).

Pine locations showed less significant difference in age with only bottom layer vegetation (p=0.009, df=4, F=3.5) and only locations dominated by lichens had significantly older specimens than localities on bare ground (p=0.001) (Figure 11b).

For spruce, significant age differences between specimen locations were found for bottom layer (p =0.006, df=3, F=4.2) (Figure 11b) and shelter type (p<0.001, df=4, F=5.931) (Figure 11d). Specimens were significantly older in locations dominated by litter than in locations dominated by *Sphagnum* (p=0.013). Specimens in locations associated with shrub vegetation were also significantly older than when no shelter was present (p<0.001).

Amount of organic material in the soil at specimen locations showed no correlation with specimen age for any of the species (Table 15).

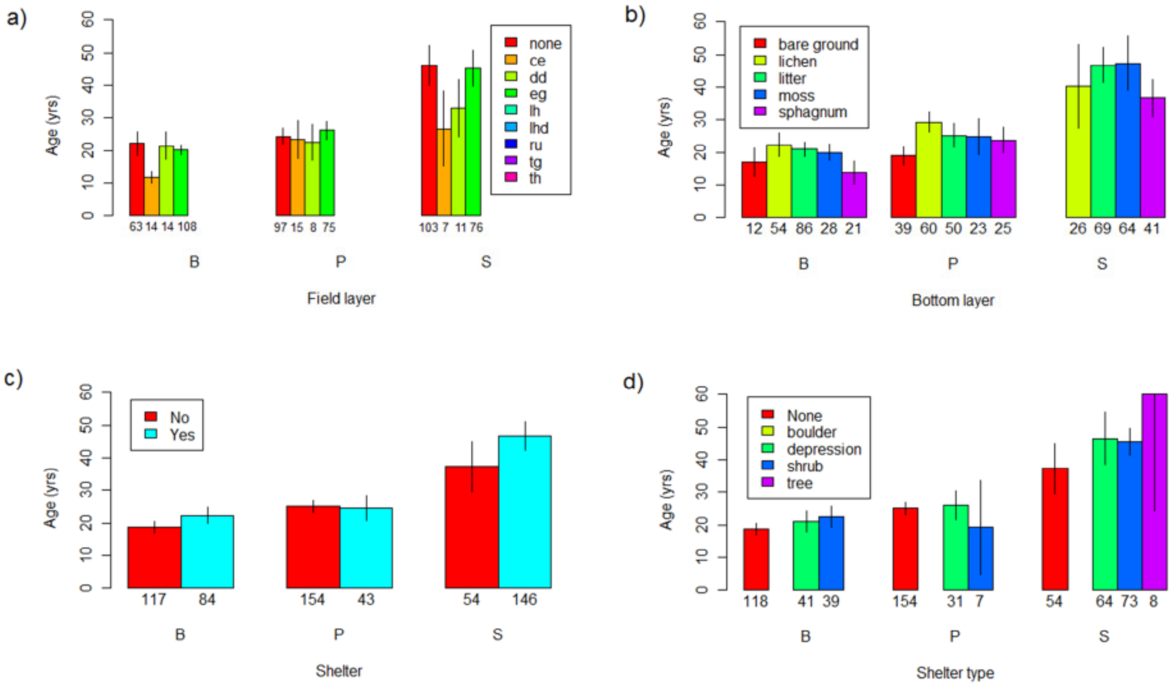

Figure 12: Histograms showing average specimen age (yrs), with 95 percent confidence intervals, for each category of a) field layer, b) bottom layer, c) shelter and d) shelter type for birch (B), pine (P) and spruce (S). Field layer vegetation consist of sedges (ce), deciduous dwarf shrubs (dd), evergreen dwarf shrubs (eg), low herbs (lh), low herb with dwarf shrubs (lhd), cloudberry (ru), thin leaved grass (tg) and tall herbs (th). Sample sizes for each category are indicated below each bar.

DISCUSSION:

Favourable location characteristics were found to vary across both regions and species. The amount of organic material within the soil facilitated height growth in dry regions but not in the coastal region. This influence on height growth was only evident for birch and pine. The occurrence of shelter (depressions, shrubs or boulders) facilitated seedling recruitment equally across all regions and species. For birch, shrub shelter types as well as dwarf shrub vegetation facilitated growth and survival of specimens at the inland regions. However, dwarf shrub vegetation did not show any influence on height growth and survival for pine and spruce. Pine growth and survival was less affected by shelter presence than both birch and spruce. Determining these facilitation agents supplies the necessary building blocks for modelling future recruitment and growth of seedlings and saplings in the tundra. Since these facilitation agents depended on regional climatic conditions and location characteristics, it becomes more difficult to produce broad predictions that accurately predict recruitment response to climate change.

Recruitment across climatic regions

Importance of moisture on growth and survival

The amount of organic matter in the soil is a good indicator of moisture. For most soil types in the Scandinavian mountains, an increasing amount of organic material means that more moisture is stored and available over a longer time than without organic material in the ground (Bliss 1963). Therefore, one would expect to see an increasing positive effect of organic material on growth and survival as conditions become drier. This positive relationship is found for birch over the coastal-inland moisture gradient, where amount of organic material did not influence growth and survival in the most oceanic region while it had a clear positive effect in the two drier regions. The amount of organic material in the soil also had positive effects on survival but this was visible only in the least oceanic region. This indicates that birch is more tolerant to survive drier conditions but that height growth more easily reduced under drier conditions.

Low height growth and low recruitment was associated with locations dominated by bare ground whereas locations dominated by dwarf shrub vegetation positively influenced height growth and survival. It is clearly beneficial for birch to grow in association with dwarf shrub vegetation in this alpine environment. This vegetation type has been shown to work as shelter for small seedlings by providing protection against wind scouring and can increase snow cover, it also allows for greater moisture availability in the soil (Bliss 1963; Carlsson and Callaghan 1991). Studies indicate that competition is not a limiting factor in the forest-tundra ecotone and therefore association with surrounding vegetation can facilitate growth rather than suppresses it (Maher *et al*. 2005; Maher and Germino 2006). Survival was only effected by this relationship in more inland regions (Haltdalen and Røros). Therefore, the effects of growing separate from surrounding vegetation are not detrimental to seedling survival when located in regions with greater moisture availability (Holmgren *et al*. 1997; Germino *et al*. 2002).

Influence of shelter on growth and survival

Occurrence of shelter was an important facilitation agent for birch recruitment within all three regions. High wind velocities have strong deleterious effects on seedling recruitment within the forest-tundra ecotone, making sheltered locations more favourable. This dependence on shelter for recruitment was supported by the greater height growth and survival of seedlings and saplings when associated with shelter. These locations facilitate recruitment by accumulating drifting snow and thus building up thick insulating snow packs (Holtmeier and Broll 2010b). Therefore, sheltered locations provide protection from the harsh winter conditions and allow for increased soil moisture during the early growing season from the melting snow pack (Dalen and Hofgaard 2005; Hofgaard *et al*. 2009; Holtmeier and Broll 2010b).

Shrub type shelters facilitated height growth in the intermediate- and inland region. This facilitation agent has been associated with earlier snow melt allowing for longer growing seasons (Callaway 1995) and increased available moisture in the soil (Bliss 1963) protecting against summer drought. Height growth was more sensitive to types of shelter present then the general survival of the seedlings/saplings. This indicates that survival to older ages is less dependent on the benefits supplied specifically by shrub type shelters but more on the general benefits such as protection from wind desiccation (Holtmeier and Broll 2010a).

Species-specific recruitment strategies

Importance of moisture for various species

Locations with high amounts of organic material facilitated height growth of pine and birch but not spruce. Considering that sheltered locations provide a variety of benefits in terms of greater moisture availability by mediating snow accumulation (Carlsson and Callaghan 1991; Holtmeier and Broll 2010a) one would expect that spruce seedlings, which are tightly associated with these locations would not greatly depend on soils ability to maintain moisture. In addition, since vitality of spruce specimens were more reduced by climatic stressors (e.g. ice abrasions) in the tundra, the height growth is more dependent on shelter protection than on soils ability to maintain moisture. Regardless of the positive effects of organic material on height growth, the amount of organic material in the specimen locations did not differ significantly from the control locations. The lack of significant difference suggests that the amount organic material in the soil is not the main limiting factor for seedling recruitment in the tundra.

Bare ground was unfavourable for all three species; either they were not found in association with bare ground locations, as seen with spruce, or they were significantly shorter. High light exposure can enhance the negative effects of extreme high temperatures during the growing season and water stress due to the greater evaporative demand in full sunlight, which causes vegetation covered locations to be more beneficial in this exposed environment (Van Miegroet *et al*. 2000; Germino *et al*. 2002). Thus, the harsh conditions in the forest-tundra ecotone make it more favourable to grow in association with other vegetation rather than be exposed to the environmental stressors of the alpine zone (Callaway *et al*. 2002; Maher *et al*. 2005). Nevertheless, organic layers under deciduous dwarf shrub vegetation have been found to exhibit high amounts of phenolic acids and tannins, which have negative effects on root elongation in spruce (Gallet 1994). My study shows that for spruce and pine, deciduous dwarf shrub vegetation did not facilitate height growth and survival as seen with birch. These findings suggest the possibility that deciduous dwarf shrub vegetation can be more beneficial for some species and not others. Nevertheless, determination on whether specific dwarf shrubs are actually acting as a limitation agent requires more detailed analyses than applied in this study.

Importance of shelter for various species

Occurrence of shelter was an important facilitation agent for recruitment of all three species, yet shelter showed no effect on height growth and survival for pine. Pine species grow well in dry, snow-poor sites (Kullman 2007) and have fast growth, which allow it to survive and grow well in exposed locations within the forest-tundra ecotone. This tolerance is where this species separates itself from the other two focal species. In contrast to pine, the occurrence of shelter proved to be very beneficial to spruce in terms of both increased height growth and greater survival. Shelter provides protection against unfavourable climatic variables such as low ground temperatures and ice abrasions during winter months, which is linked to spruces associated in tight clonal groups, tree islands or krummholz groups (Marr 1977; Holtmeier 1981; Van Miegroet *et al*. 2000). An apparent reduction in spruce specimen vitality due to climate variables indicates that recruitment in exposed locations can be detrimental to this species. Therefore, spruce recruitment is more limited to locations with sheltering properties than pine recruitment.

Conclusions:

Based on the species-specific requirements for recruitment at the alpine zone, this study looked at what location characteristics were favouring recruitment and whether this varied across regions and species. There are multiple variables effecting tree recruitment in the forest-tundra ecotone such as wind (Holtmeier and Broll 2010a), herbivory (Hofgaard 1997; Cairns and Moen 2004; Hofgaard *et al.* 2010), ground temperatures (Holtmeier 2009), parasites (Stöcklin and Körner 1999; Holtmeier and Broll 2010b) and snow cover (Sturm *et al.* 2001a; Holtmeier 2009). In this study, favourable location characteristics were clearly linked to the occurrence and types of shelter, and moisture regimes depending on species and regional climate conditions. Organic material as well as shrub vegetation acted as facilitation agents for greater growth and survival in the drier regions. Facilitation of growth and survival of spruce seedlings/saplings was highly linked to sheltered locations whereas pine was more dependent on the amount of organic material for height growth. This study emphasises the need for understanding more specifically what relationship the focal species has with its surrounding environment before attempting to determine more broad scale responses of tree populations within the forest-tundra ecotone. The response of the forest-tundra ecotone to changes in regional climate depends on the successful recruitment of seedlings in the tundra. By investigating what variables are affecting species-specific recruitment at the regional scale in terms of broad climatic differences as well as local variation within the region, predictions on the ecotone response to climate change can become more accurate.

This study was only able to determine that there were positive effects associated with certain vegetation types within relatively broad categories. Continued research on the facilitation and limitation of deciduous dwarf shrubs on various species recruitment could prove to be interesting. The increasing temperature trends have been shown to increase vegetation cover and abundance of shrub vegetation in arctic regions (Fraser *et al.* 2011; Sturm *et a*l. 2001b). Considering the contrasting effects of shrub vegetation on different species, any shifts in shrub abundance could have a facilitative or limiting effect on tree species recruitment. Therefore, knowledge of inter-specific interactions can allow for greater understanding of tree species responses to changes in its environment.

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