

# Growth of treeline trees

A spatial-temporal analysis of driving forces of tree growth at treeline

## Master Thesis of Simon Blatter

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## Summary

Recent treeline research has mainly focused on the contemporary issue of upwards shifting treelines in the view of climate change. Main drivers of treeline shifts at high altitudes on a global scale are assumed to be the increasing growing season temperatures. Although a part of the considered treelines shifted toward higher altitudes, a big share of them did not move. We assume that even if increasing season temperatures on a large scale drives tree growth at treeline; small-scale conditions could also play an important role. The fact that a considerable part of worldwide treelines didn't advance indicates for further limitations on a local scale. We had the unique opportunity in this thesis to quantify the importance of local factors on tree growth and explore how their relative importance changes over time by examining one of the best-documented treeline experimental sites at Stillberg near Davos (9°52'E, 46°46'N). At this site we studied spatial-temporal patterns of driving forces on height and diameter growth of *Pinus cembra*, *Pinus mugo* and *Larix decidua*. We analysed the effects of microsite conditions, climate and disturbance events on growth and quantified the relative importance. We took advantage of 40 years of observational data, tree-ring data from a subsample of 145 trees, and additional soil temperatures during the growing-season 2015.

On a general level we were able to illustrate that microsite characteristic, climate, and disturbance have layered effects. While factors of microsites and year-to-year climate variation influence growth on a broad spatial scale, local conditions are masking those effects by adding variance independent of the spatial scale. Considering the effect of microsite conditions on height growth of all species, there was evidence for higher diameter and height growth at lower altitudes and a height growth optimum at later snowmelt dates between the 140<sup>th</sup> and 150<sup>th</sup> day of the year for the first 30 years of observation. Further evidence for following species specific dependencies on microsite factors were found: *P. cembra* is susceptible to wind exposed sites while growth of *P. mugo* is closely related to warmer microclimates. The impact of year-to-year climate variation was assessed by calculating the species-specific common signal from tree-rings. The highest common signal was found for *L. decidua* ( $r=0.45$ ), while signals in *P. cembra* ( $r=0.24$ ) and *P. mugo* ( $r=0.17$ ) were significant lower. It is assumed, that lower common signals are mainly caused by 3.8 times higher disturbance frequencies for *P. mugo* and 2.4 times higher disturbance frequencies for *P. cembra* in relation to *L. decidua* for the last 20 years as well as due to carry-over of climate effects which are more likely for *Pinus* species with perennial needles. Although disturbance events are most frequent for *Pinus* species we could prove, that they are most important for growth variations in *L. decidua* (average growth losses of 53% due to severe freezing events and 61% due to stem damages). In contrast, *Pinus cembra* has only moderate height growth losses due to disturbance and *P. mugo* is affected so frequently by disturbance that damages do not longer lead to relative growth differences. Considering drivers of tree growth at treeline on a temporal scale, early life-stages seem to be most complex as numerous factors have decreasing importance on growth with time. At the time of stand and canopy closure, importance of elevation and microtopolgy decrease while forest-like climates are established. Disturbance and tree interactions (competition and facilitation) have two peaks in importance, one at early tree stages and one during tree stand closure. In contrast, climate impacts are not life-stage dependent but have increasing relative importance because other drivers lose their importance with time. On a spatial scale we could illustrate, that high-elevation levels and exposed ridge position are most critical for growth of treeline trees.

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# I. Introduction

## I.1. General Context

High-elevation treelines can be considered as the most obvious vegetation boundary separating treeless alpine vegetation from highest alpine forests (Körner & Paulsen, 2004). A treeline can be defined by a line connecting the highest patches of forest within a given slope or series of slopes with similar exposure (Körner, 1998). Treelines are rarely distinct lines; in fact, they are mostly formed as a transition zone between the end of closed forest and the upper limit of tree existence often called the treeline ecotone (I. Barbeito, Dawes, Rixen, Senn, & Bebi, 2012; Berdanier, 2010; Körner, 1998).

Treeline research is almost exclusively linked to studies of treeline position and formation under challenging climate conditions. There are global approaches which show evidence for advance in treeline position towards higher altitudes for many areas, and particular in places with higher winter warming or in areas with more diffuse treelines (Harsch, Hulme, McGlone, & Duncan, 2009). Climate warming is not only closely linked to treeline shifts but also affects the growth rates at the current treeline ecotone. There is evidence for increasing growth rates during the last two centuries at high-elevation treeline sites by various dendroecological studies (Innes, 1991; Motta & Nola, 2001; Rolland, Petitcolas, & Michalet, 1998). There is also indication that young life stages of *Pinus* species and *Larix decidua* might be affected differently in growth rates at early life stages (<100 years) than at old life stages (Motta & Nola, 2001; Rolland et al., 1998). Changing treeline patterns are likely to have also important impacts on services and functions which are provided by mountain forests and which are closely linked to the spatial extent and the condition of those ecosystems. Mountain forests in high altitudes are often crucial for providing protective functions to various kind of infrastructure against natural hazards such as avalanches, rock fall and landslides. For predictions of changes in spatial treeline patterns, it is necessary to understand and disentangle the driving forces of tree growth, tree establishment and tree survival at treeline.

One of the best-documented experimental sites for high-elevation treeline research is located in the Dischma-Valley near Davos at the 5-ha long-term afforestation Stillberg in Switzerland. Long-time observations (40 years) covering elevation levels at and above current treeline combined with updated data collected in summer 2015 offers a great opportunity as a study site for this thesis.

## 1.2. State of knowledge

Growth at treeline is generally considered to be mainly limited by short growing-season or low temperatures (Körner, 2003; Körner & Paulsen, 2004). Hoch, Popp, and Körner (2002) showed evidence for limited sink activity, where sufficient accumulated carbon assimilates couldn't be invested in growth due to thermal restrictions in shoot meristems. Beside temperature growth restriction, precipitation seems to have only small effects on growth rates at alpine treelines because drought rarely occurs (Jens Paulsen & Körner, 2014). While findings on temperature growth limitation may be a good explanation for high elevation treelines at a large scale, factors acting at small scales might mask the interaction between temperatures and growth (Harsch et al., 2009). Small-scale factors are microclimatic conditions such as aspect, wind velocities, radiation, soil types, and time of snowmelt (I. Barbeito et al., 2012; Häsler, Streule, & Turner, 1999; Schönenberger et al., 1988). Additionally, disturbance (e.g. frost and stem injuries) can mask temperature growth relations on a local level especially in high elevations (Kulakowski, Rixen, & Bebi, 2006). Disturbance is mainly linked to damages caused by avalanches and snow pressure (Bebi, Casteller, Mayer, & Stöckli, 2004; Häsler et al., 1999) or freezing damages affecting mainly *L. decidua* (Rixen, Dawes, Wipf, & Hagedorn, 2012), while stress is mainly linked to pathogenic snow fungi affecting evergreen Pinus species (Ignacio Barbeito, Brückner, Rixen, & Bebi, 2013). Beside those driving forces of growth also plant-plant interactions are likely to alter growth rates of treeline trees. Ignacio Barbeito (2013) showed with an experimental setup that *L. decidua* trees were mostly limited by competition at lower elevation where at higher elevations growth was more influenced by abiotic limitations and therefore the effect of competition decreased. Also increasing abiotic limitations due to a later snowmelt date led to a shift from competition to facilitation for all three species. In the context of Stillberg neighbour interacting effects were found to be closely linked to microsite effects (i.e. more neighbours in more favourable microsites for growth) (I. Barbeito et al., 2012).

Commonly there are two measurements used to quantify tree growth: Height growth and radial growth mostly derived from tree-ring width measures. While tree height growth decreases gradually with elevation towards the treeline, radial growth changes abrupt with elevation and temperature is assumed to act as a threshold effect (J Paulsen, Weber, & Körner, 2000). J Paulsen et al. (2000) also states, that radial growth is more dependent on correlation with year-to-year climate than height growth.

Treelines in the Alps are often defined by anthropogenic influences such as seasonal livestock grazing of alpine pastures which has lowered today's treelines significantly (Körner, 1998; Wallentin, Tappeiner, Strobl, & Tasser, 2008). The afforestation at Stillberg offers the great opportunity of a study site above the treeline defined by land use history, which is not related to former traits of land use. Further annual and decadal data offers the possibility to assess driving forces of tree growth for specific life stages as already done for the first three decades of the Stillberg afforestation by I. Barbeito et al. (2012).

As there is no shortage of data for the Stillberg afforestation, we are in a favourable position to be able to focus only on effects on tree growth from various factors and neglect their effects on mortality. This decision is supported by the decreasing rate of mortality during the last decades and therefore the finding that mortality is most important for the first two decades of the afforestation (I. Barbeito et al., 2012) and decreases to a much lower mortality level especially for the latest decade.

### 1.3. Aim of this study

The aim of this thesis is to analyse and disentangle the effect of different driving forces on growth of treeline tree species *Pinus cembra*, *Pinus mugo* and *Larix decidua*. Accordingly, the main focus of this thesis is a better understanding of temporal and spatial tree growth variations in the timespan between 1975 and 2015. The primary objective is to assess the effect of annual climate condition, microsite conditions, disturbance events and stress on growth rates of treeline trees. In particular we completed analyses previously performed by (Barbeito et al. 2012) by extending the period of observational data from 30 to 40 years, and by taking advantage of additional and more detailed data from treerings (140 years) and their soil temperatures during the growing season 2015. While previous studies (I. Barbeito et al., 2012; Josef Senn & Schönenberger, 2001) focused on continuous factors over time with impact on growth and survival of Stillberg trees, this approach only includes effects of drivers on growth but investigates a broad spectrum of continuous and discontinuous drivers with influence on tree growth. As a unique feature we are able to relate a multiple of driving forces on tree growth to specific periods of 40 years of measures. Specific research questions are:

#### (A) Site variability

- (1) How does the growth of treeline trees respond to elevation (increasing limitation by cold temperatures), neighbourhood (increasing competition) and microsite conditions?

#### (B) Year-to-year variability and temporal trends

- (2) What is the relative importance of mean seasonal temperatures, seasonal precipitation amounts and episodic events (frosts, pathogenic organisms and stem damages) for tree growth and how do they vary according to tree species, elevation, exposition and microsites?
- (3) How does the relative importance of different drivers change during the first 40 years of treeline trees at Stillberg?

## 2. Material and methods

### 2.1. Site description

#### 2.1.1. Study area

The study area is located at the 5-ha Stillberg long-term afforestation placed in the Dischma-Valley near Davos (eastern Switzerland; 47°28' N, 78°30' E). The afforestation is located on a north-east-facing slope between 2000 and 2230 m.a.s.l. This covers the elevation levels of the upper part of the current treeline (~2100 m.a.s.l.) and the part up to 130m above measured current treelines in this region (Josef Senn & Schönenberger, 2001). In 1975 approximately 92'000 seedlings of three treeline species *Pinus cembra*, *Pinus mugo* and *Larix decidua* were planted. High elevation provenances of these species were planted in square plots of 3.5 x 3.5 m alternating arranged in a quadratic grid with 25 trees per plot. Today there's only a low number of surviving trees of *Pinus cembra* (3%) and *Pinus mugo* (7%) which is linked to high mortality closely linked to pathogenic snow fungi (J Senn, 1999) in early life stages of the trees. Contrasting to the survival rates of the *Pinus* species, *Larix decidua* had highest mortality rates during the first years after planting but is with a survival rate of 58% by far the most abundant species today.

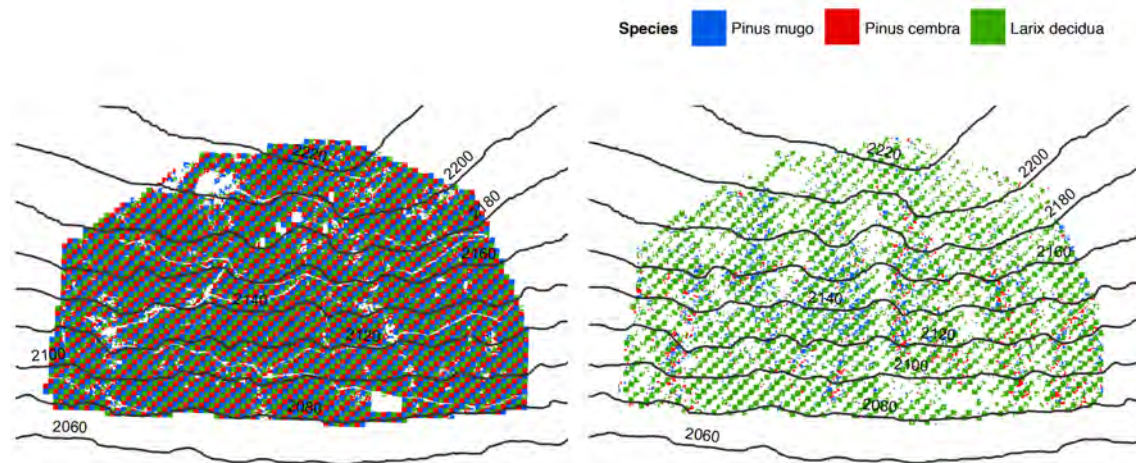


Figure 1: Tree species distribution and survival at Stillberg in a) 1975 and b) 2015

#### 2.1.3. Climate

The Stillberg study site is located in the temperate continental climate of the inner-alpine valleys in between the more humid northern “Randalpen” and the drier “Zentralalpen”. According to this, relative warm summers (mean July-temperature of 9.4°C) and relative cold winters (mean January-temperatures of -5.8°C) are common. Mean annual precipitation rate is 1050mm and maximum annual snow heights are in average about 146 cm, but can differ among sites from 420 cm at lee position to 60 cm in ridge positions (Josef Senn & Schönenberger, 2001).

Higher radiation of the evening sun leads to significant higher soil temperatures of 0.8°C ( $p < 0.01$ ) at the south-exposed slope better aligned to evening sun. Although this effect is partly compensated by warmer soil temperatures at the north exposition caused by earlier morning sun. Daily soil temperature trends (Figure 2) show significant differences of 0.4°C between microsites with early snowmelt and microsites

with late snowmelt ( $p < 0.01$ ). Higher soil temperatures are found for microsites with early snowmelts during the day but nearly the same temperatures were found during the night. Differences between exposures and microsites are closely linked to day length, the shorter the days get at the end of the growing season, the smaller are the soil temperature differences.

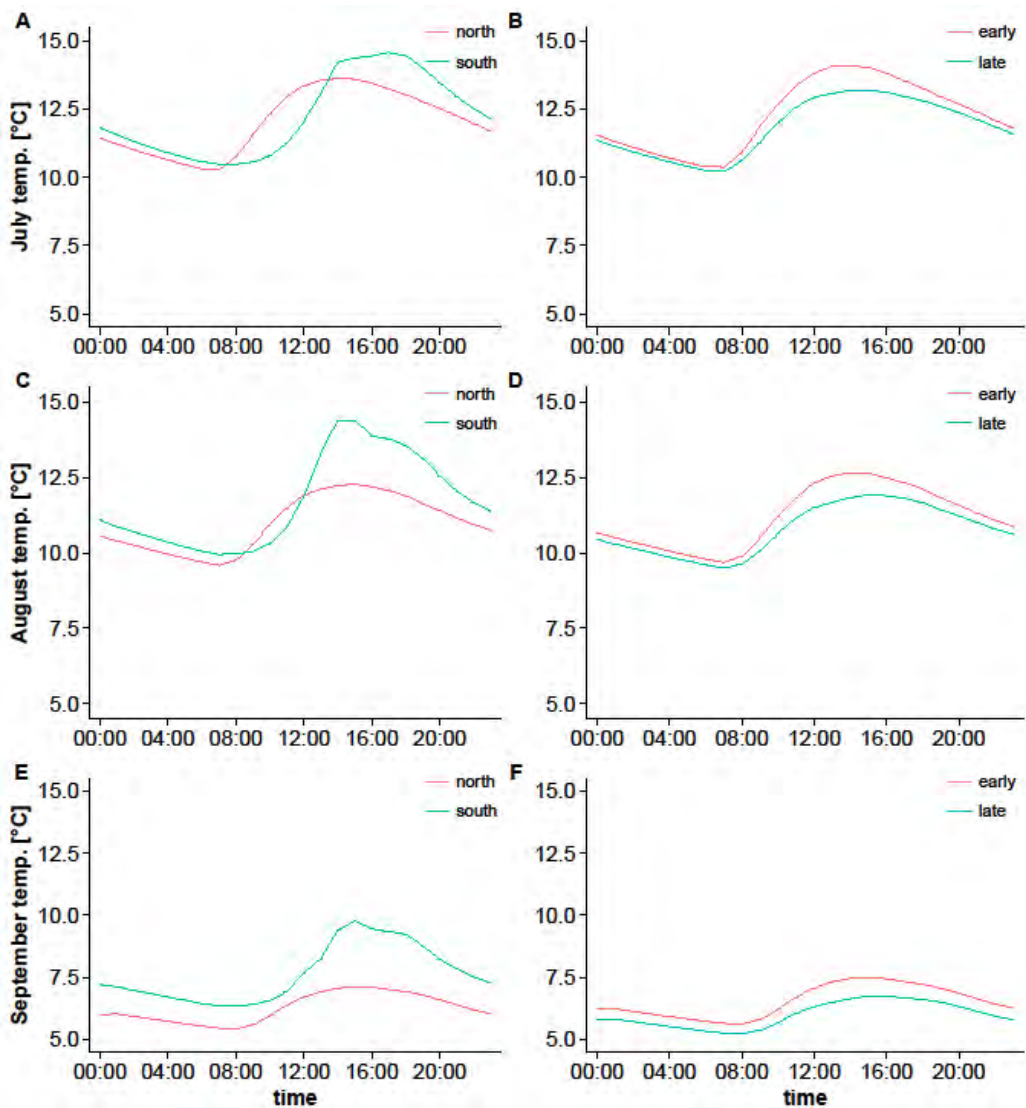


Figure 2: Daily trends of soil temperatures measured 5cm below ground for the months of July, August and September compared between the northern slope of Stillberg and the southern slope of Luckschalp and between microsites with early and late snowmelt dates.

During the last 40 years of the Stillberg survey climatic conditions gradually changed. Seasonal air temperature means measured from June till August increased significant ( $p < 0.0001$ ) over the last 40 years by total  $2.1^{\circ}\text{C}$  or  $0.05^{\circ}\text{C}$  per year (Figure 3). Dates of snowmelt (Figure 4) showed a slight but nonsignificant trend ( $p = 0.05$ ) towards earlier dates of snowmelts. Average snowmelt dates were shifted by 10 days towards earlier snowmelt in the last 40 years. This can be linked on one side to the trend of higher air temperatures but is most likely also strongly influenced by growth of the surrounding trees and therefore by the establishment of a forest microclimate.

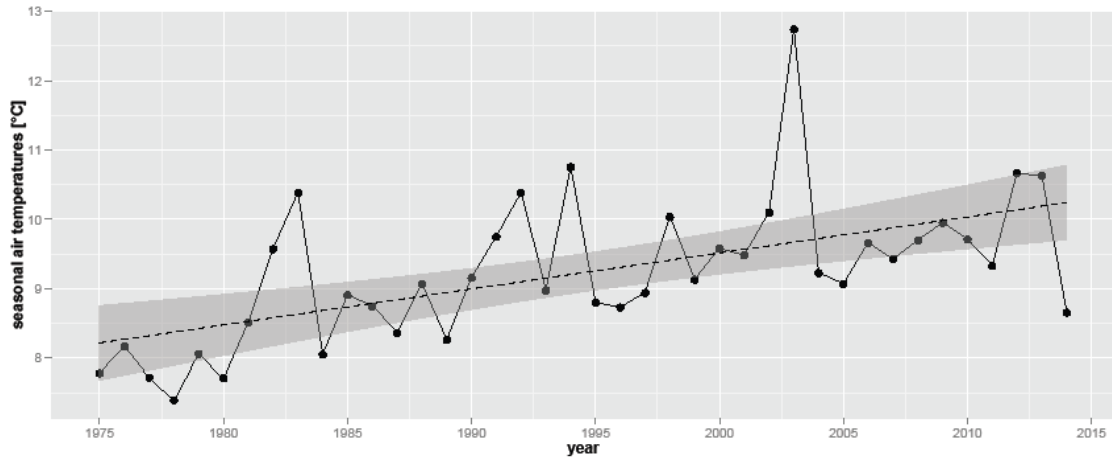


Figure 3: Annual mean seasonal air temperatures in °C for the months of June, July and August measured at the bottom of Stillberg including linear regression and 95% confidence intervals.

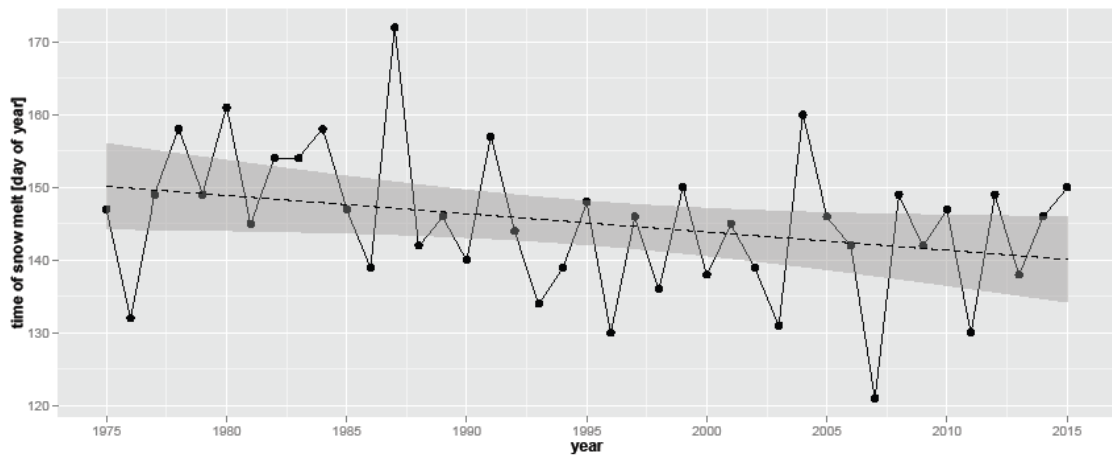


Figure 4: Annual snowmelt dates measured at the bottom of Stillberg including linear regression and 95% confidence intervals.

### 2.1.2. Microsite factors

North-east-facing steep slopes structured by avalanche gullies are characteristic for the Stillberg site. Due to this strongly structured, steep slope there's a resulting distinct small-scale heterogeneity. Microsites are divided in the categories gullies, ridges and north- or north-east-facing slopes. These sites differ fundamental with respect to the incoming solar radiation. Measurements from the beginning of the afforestation prove that north-eastern slopes have, due to higher radiation influx, in average 3 – 4°C higher soil temperatures, 5 weeks earlier snowmelt dates and a five to ten days longer vegetation-period (Schönenberger et al., 1988). Ridge positions are characterized by increased wind exposure and can therefore be colder due to cooling effects. In winter wind is likely to cause snowdrift and therefore increasing the risk of snow free periods during winter. The date of snow disappearance is also significant earlier on ridge positions than average snowmelt dates. In contrast, snow movement mainly influences gully positions. Avalanches lead to snow dislocation and are linked with a shift in snowmelt either to earlier or to later dates depending on the location of snow deposition. Beside direct effects of breakage, avalanches can also be linked to increased risks of snow fungi infestations due to high snow deposits. One important field of interest in the beginning of the Stillberg afforestation dealt with various microsite conditions, which were recorded per square plot of 25 trees at the time of tree establishment. The following variables were recorded: a) wind b) solar radiation and c) snowmelt.

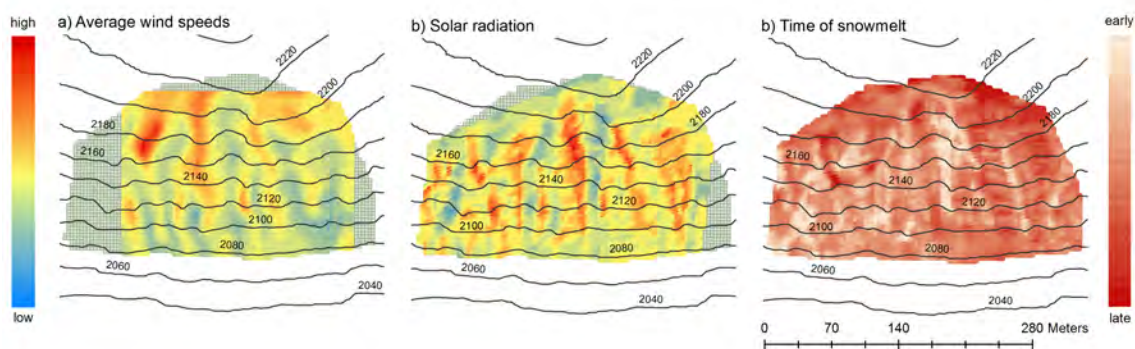


Figure 5: Maps of microsite measurements at the beginning of the Stillberg afforestation

In addition digital elevation models for the calculation of exposition, curvature, slope and altitude were used. Gullies, ridges and plane slopes were classified by curvature calculations.

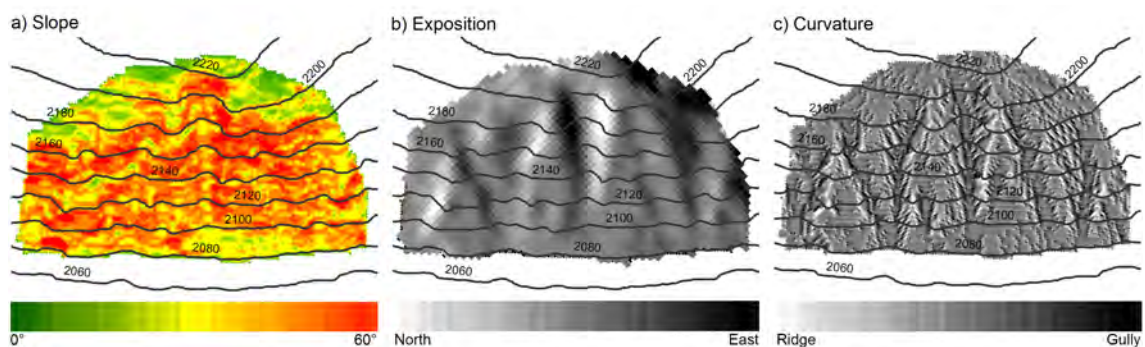


Figure 6: Maps of Slope, Exposition and Curvature at Stillberg derived from digital elevation models (© Swisstopo)

## 2.2. Key concepts and terminology

To avoid different or misleading interpretations of important terms we define the use of important terminology and try to clarify in which context they are used.

**Factors acting on growth:** All variables influencing spatial or temporal variability of lateral or height growth including site conditions, climate, and disturbance events.

**Driving forces (drivers) on growth:** All factors which are suitable to describe spatial variation in lateral or height growth. These are mainly site conditions and disturbance events (e.g. frost, stem injuries, and snow fungi). Climatic factors are not included, because they are not causing spatial variation

**Spatial growth variation:** Differences in yearly or decadal growth rates between microsites or elevation levels.

**Microsite conditions:** Unique characteristics, which classify different microsites on a small spatial scale. Microsite conditions are characterised by the time of snowmelt, microtopography, and exposition.

**Microsite climates:** Are characterized by growing-season temperatures, radiation, and wind. They are defined by their microsite conditions.

**Continuous and discontinuous drivers:** Continuous factors are influencing growth over the whole observation period while discontinuous drivers are linked to episodic events caused by disturbance.

**Disturbance events:** Those events are affecting only a certain number of trees and are often linked with increased mortality. Disturbance consists of frost events, snow fungi, and stem injuries.

**Neighbour interactions:** Biotic interactions between single trees either increasing their growth rates (facilitation) or decreasing their growth rates (competition).

**Climate sensitivity:** Year-to-year growth variation caused by growing-season temperatures and precipitation measured as a common signal per species.

**Biological year:** To quantify the effect of monthly climate factors on yearly growth rates the definition of the “biological year” for climate factors was used, which is frequently used for studies of alpine species (Carrer & Urbinati, 2004; Ettl & Peterson, 1995). The biological year is defined as the time period ranging from October of the year before to September of the same year as the growth.

## 2.3. Available time series data

For this thesis time series of growth, climate and disturbance events were used. This time series have been assessed either for every plot or a subsample of plots and assessed for every year or only in a 10-year time interval. For easier understanding all different types of time series are described in Figure 7.

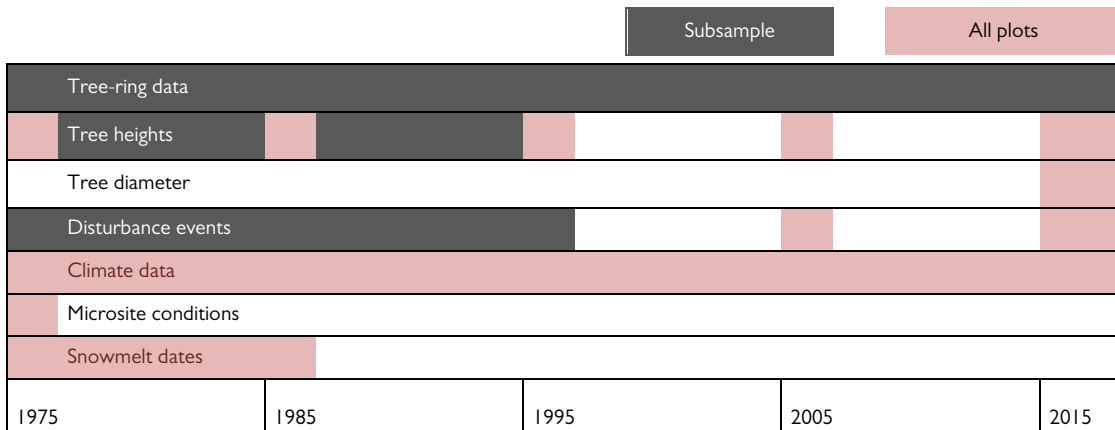


Figure 7: Descriptions of time series

### 2.3.1. Growth rates

There are two measurements for tree growth at Stillberg: Height growth and diameter growth. Height growth is measured along the stem axis from bottom to the top. Every ten years height measures were recorded for every single plot, till 1995 for every single tree and from then on only for a subsample of three trees per plot. For a subset of 5700 trees per species, yearly tree height measurement for the period between 1975 and 1995 are available. Diameter growth in this study was mainly derived from tree-ring cores from a subset of 145 trees. This provides data for annual diameter growth for the whole period with some restrictions due to a lack of tree-rings in the first 5 years.

### 2.3.2. Disturbance events

We focused on the most frequent disturbance events damaging either tree tissues or tree stems. For damages on tissues of *Larix decidua*, mostly freezing events were responsible. Opposing to findings on *Larix decidua*, tissues of *Pinus* species were not sensitive to freezing events but were in exchange prone to damage of tissues due to pathogenic snow fungi *Gremmeniella abietina* and *Phacidium infestans*. For damages affecting tree stems the difference between disturbances leading to stem breakage or splitting and disturbances leading to a crooked growth form ("hanger-trees") is used. The difference between several disturbances causing stem damage is not being considered, because it is often hard to proof the causing disturbance events.

The annual subsample time series of tree growth between 1975 and 1995 is used in combination with data from the 2005 and 2015 survey to identify damaged trees. Disturbance interactions are calculated by comparing the growth rate of the year after between affected and unaffected trees.

### 2.3.3. Climate data

A meteorological station is located at the bottom of the afforestation at 2090 m.a.s.l. measuring air temperatures in 2m height, radiation, wind, relative humidity, precipitation and snow heights with daily measurements. These measurements were conducted for the whole period of 40 years. From this data monthly or seasonal sums for precipitation and means for temperature and snow height for every single year were calculated.

## 2.3. Collection of new data

### 2.3.1. Collecting of tree-ring cores

Dendrochronological methods use tree-ring cores or tree disks for getting year specific diameter growth rates. Tree-rings defined through denser late-wood at the end of every ring and less dense early wood at the beginning can be assigned to a specific year by counting backwards from the last known tree-ring next to the bark. In this case we used increment-borers to get tree-ring cores from the subsample of 145 trees covering all elevation levels and microsites. Tree-ring cores were obtained from each selected tree at heights ranging from 30 to 40cm and if possible parallel to the slope to get samples outside the influence of extreme pressure wood. By drilling through the whole stem two tree-ring cores and therefore an additional cross-reference to guarantee complete cores from pith to the bark is gained. The tree-ring cores were mounted on channelled wood boards and were sanded for further lab use.

### 2.3.2. Soil temperatures

In addition to air temperature measurements from the meteorological station 120 temperature loggers were buried 5cm deep into the soil and collected hourly temperature data between 2015 and September from various altitudes and microsites. Additional to the Stillberg also measurements from the opposing south-exposed Luckschalp slope collected.

### 2.3.3. Tree sampling

For every drilled tree with additional soil temperature logger additional data including tree height, stem diameter and damages was collected. The biggest challenge was the identification of the trees, which were measured in earlier surveys.

## 2.4. Statistical analysis

### 2.4.1. Tree-ring processing

Ring widths were measured at a resolution of 0.01 mm by using a LINTAP measuring device and the tree-ring chronology measurement program TSAP-Win. Missing tree-rings at the beginning were identified by comparing the number of rings left of the pith with the number of rings on the right side. To detect errors in tree-ring dating including missing or false rings, single measurements were crossdated using the Program COFECHA (Holmes, 1983). COFECHA prepares tree-ring data by subsetting the series in shorter fragments, applying a cubic spline to remove low-frequency variance and reduce variability among small rings by applying a log transformation. Now a master chronology is calculated by the mean of all transformed and filtered fragments. Single fragments are then compared with their master chronologies and correlation indices are computed by shifting the fragments for- and backwards against their master chronologies. Best

correlated positions of fragments and outlying measurements are highlighted and should be double-checked.

In order to make yearly growth variation comparable independent of life stage dependent growth variation, detrending methods from the dplR package for R (A. G. Bunn, 2008) were used. By detrending the tree-ring chronologies the low frequency variability due to biological or stand effects (A. Bunn & Korpela, 2015) got removed and created dimensionless ring-width indices. The used method divided the ring-widths by a growth model, in this case a stiff spline.

Simultaneous to the ring measuring frost-rings occurring in tree-ring cores were recorded. Such frost-rings occur when xylem vessels collapse due to freezing events and enlarged cells are built to compensate the collapsed cells (Schweingruber, Börner, & Schulze, 2007). As frost-rings do not occur uniformly on all parts of the stem (V. B. Stöckli, 1996) and as frost rings are more common in young and small individuals due to thinner bark (V. Stöckli & Schweingruber, 1996), frost-rings are only a secure measure for the presence of freezing damages but not for their absence (Rixen et al., 2012). Therefore the frost-rings were only used as a measurement to compare frost damages in between different tree species and to determine if there are years with higher frost-ring frequency.

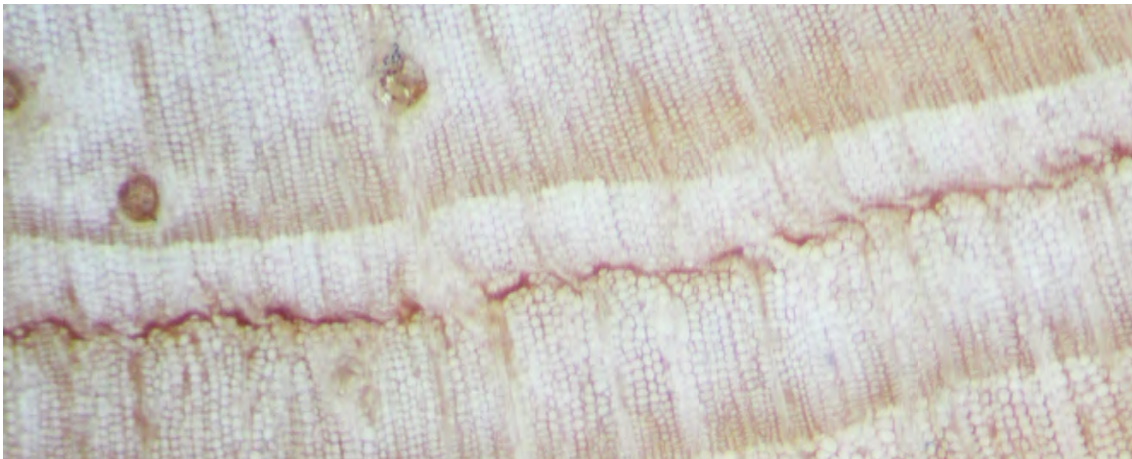


Figure 8: Example for observed freezing damage in *Pinus cembra* observed in form of a frost-ring in the early wood of an annual growth ring.

Additional the common signal of climate sensitivity was determined by calculating in between tree correlations and estimating the standard errors over time using a random subsample of 20 ring-widths per species and year.

#### 2.4.2. Analysis of variance

In order to compare differences between mean growth rates between different treatments of treeline trees two kind of variance analysis were used: T-tests for the comparison of two samples and one-way ANOVAs for more than two samples. Both tests have in common, that they assume independence of observations and normal distribution of the residuals. A chi-squared test was used to check the independence of observations and quantile-quantile plots to test for normal distribution of the residuals.

#### 2.4.3. Generalized additive Models

Generalized additive models (GAMs) (Hastie & Tibshirani, 1986) are used to analyse nonlinear relationships between height growth and other continuous factors. The advantage in using GAMs is that they are perfectly suitable for highly non-linear and non-monotonic relationships between the response and the set

of explanatory variables (Guisan, Edwards, & Hastie, 2002). As additional advantage, GAMs are perfectly suitable to detect threshold in interactions between response and explanatory variables (Ignacio Barbeito et al., 2013). GAMs are a nonparametric extension of multiple linear regressions. They make use of a link function to establish a relationship between the mean of the response variable and a 'smoothed' function of the explanatory variable (Guisan et al., 2002). Height growth rates as response variable and tested several predictor variables against it.

#### **2.4.4. Decision tree based analysis**

Decision trees and decision forests are used to identify relationships among predictor variables and their relative importance over time in chapter 3.4. The used approach is similar to I. Barbeito et al. (2012) but with additional data for the period 2005 to 2015.

Decision trees are constructed by repeatedly splitting a set of categorical or numerical predictor variables, defined by a simple rule based on a single explanatory variable, into increasingly homogeneous subsets. Results of decision trees are commonly displayed on a dendrogram (De'ath & Fabricius, 2000). Those single decision trees act as a basis for further random forest models. Random forests combine many independent decision trees in one single model, making benefit of smaller generalization errors and higher robustness to noise (Breiman, 2001). Using predictor variables with low correlations between each other can reduce additional generalization errors. Using those random forest models a permutation importance rank by permuting predictor variables and the difference in the prediction accuracy before and after permuting can be calculated (Strobl, Boulesteix, Kneib, Augustin, & Zeileis, 2008).

For this analysis, the approach of Breiman (2001) was used, which is implemented via the `randomForest` package in R to grow random forests containing 200 decision trees for each decade. By calculating permuting importance scores for every decade and predictor variable and by comparing them between each other, relative importance ranks were created. Predictor variables were checked for redundancy in order to minimize generalization errors. Highest correlation between predictor variables was  $-0.35$  for exposition and snowmelt or wind and radiation.

### 3. Results

#### 3.1. Measurements of growth and its drivers

##### 3.1.1. Site factors

Soil temperatures are often used to describe microtopographical differences (mainly represented by radiation, exposition and time of snowmelt) between different sites (Balisky & Burton, 1995; I. Barbeito et al., 2012). Therefore soil temperature measurements are presented (Figure 9) as a measure of the importance of microtopography. The observations from 105 temperature loggers buried at 5 cm depth for the growing season in 2015 indicates that temperature differences in soil temperatures between different microsites are smaller than 0.5°C. The main factor for differing soil temperatures is the number of surviving trees per plot ( $p < 0.001$ ) and species ( $p < 0.01$ ). Both are appropriate measures for the degree of shading through tree canopies. Driven by the effect of shading, soil temperatures in high elevations are even a little bit higher than in low elevations.

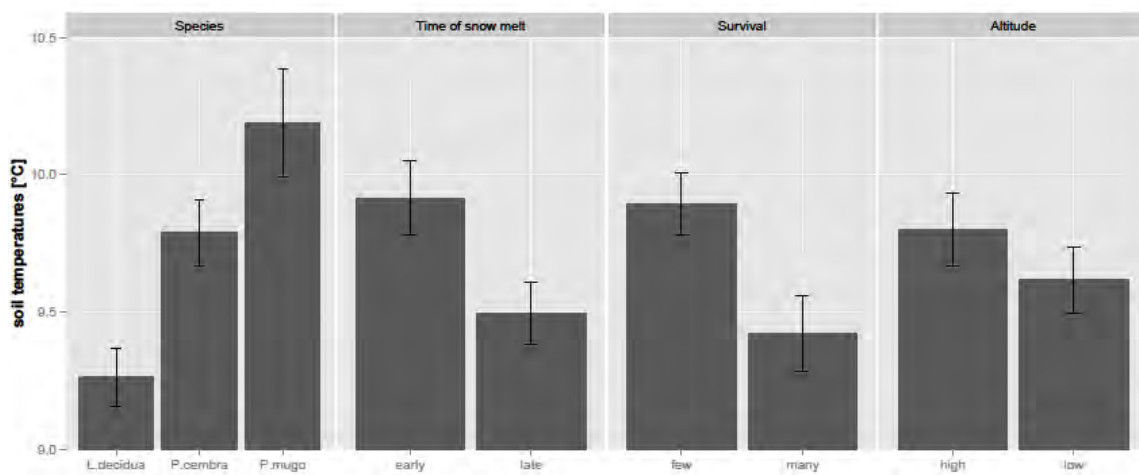


Figure 9: Mean soil temperatures measured 5cm below ground from July to September 2015 with standard-error-bars compared between species and different sites.

Site-specific height growth relationships also include additional microclimatic measurements as wind and exposure. These are described for all four decades separately in chapter 3.4.

### 3.1.2. Tree growth rates

Secondary annual diameter growth rates were derived from tree-ring measurements over the whole time span and were supplemented and compared to absolute height growth rates measured from a subsample between 1975 and 1995.

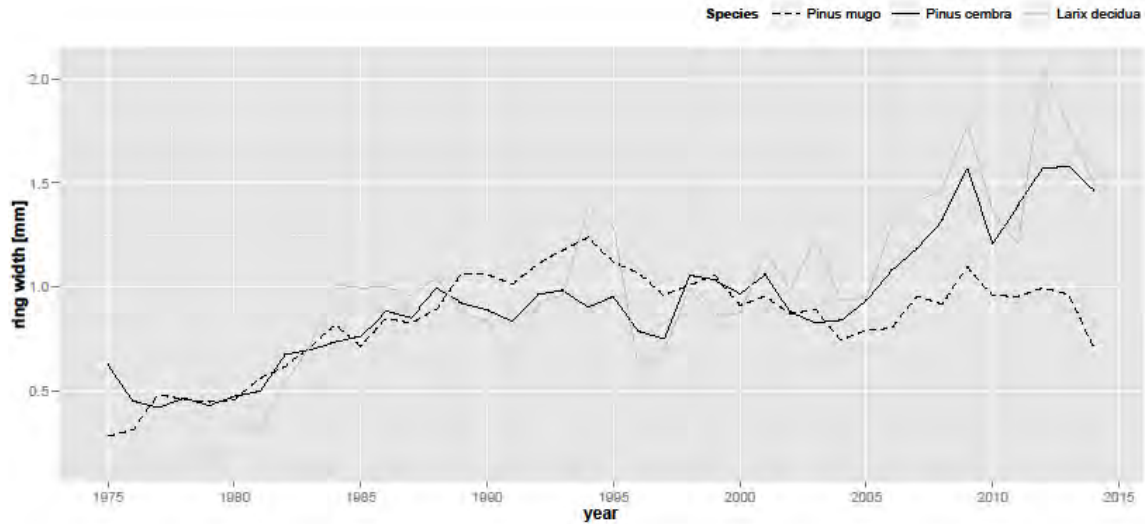


Figure 10: Mean annual tree-ring growth rates from 30 year splines for each tree species

Table 1: Pearson correlations between mean tree-ring chronologies of each species. Values in brackets for correlation coefficients between mean detrended chronologies.

Species 1	N	Correlation coefficient	Species 2	N
<i>Pinus mugo</i>	44	0.62 (0.62)	<i>Pinus cembra</i>	55
<i>Pinus mugo</i>			<i>Larix decidua</i>	
<i>Pinus cembra</i>	43	0.91 (0.60)	<i>Larix decidua</i>	

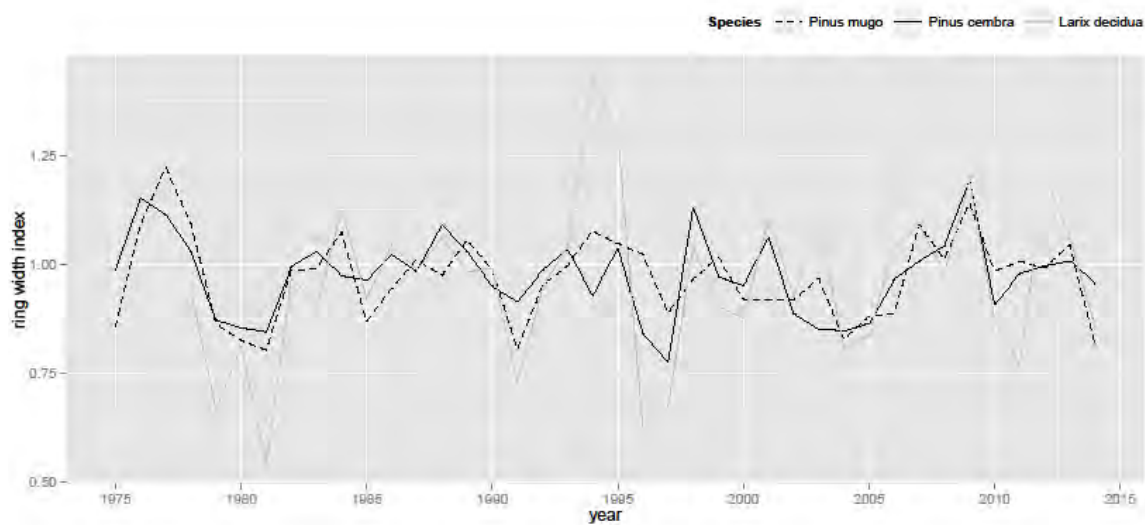


Figure 11: Mean detrended annual year ring growth rates from 30 year splines for each tree species

Tree-ring growth rates are increasing with age for *Pinus cembra* and *Larix decidua*. For *Pinus mugo* the highest tree-ring growth rates occur after 20 years and slightly decreasing or stagnating growth rates can be found for the last 20 years (Figure 10). Therefore a higher correlation between *Pinus cembra* and *Larix decidua* than between *Pinus mugo* and the other two species is observed (Table 2).

Considering the detrended ring width data for all tree species we cannot detect a uniform pattern (Figure 11). However there are some years with similar trends such as 1981, 1991, 2004 and 2009. Comparing the growth patterns between different microsities (early or late snowmelt) and elevation levels no consistent differences in detrended growth indices during the whole period could be found. Comparing south and north exposition, different yearly growth trends for the *Pinus* species and especially for *Pinus mugo* but only moderate different yearly growth trends for *Larix decidua* were observed.

Table 2: Intercorrelation between tree-ring chronologies of single trees as measurement for their common signal

Site Factor	<i>Larix decidua</i>		<i>Pinus cembra</i>		<i>Pinus mugo</i>	
	N	Common signal	N	Common signal	N	Common signal
North	94	0.454	83	0.244	71	0.167
South	17	0.446	4	0.257	15	0.16
North: Early	34	0.437	54	0.227	45	0.143
North: Late	60	0.489	29	0.267	26	0.161
North: High	42	0.503	37	0.252	35	0.202
North: Low	52	0.445	46	0.23	36	0.18

The Series intercorrelation (Table 2) in dendroecology is a measure for the strength of a signal (typically the climate signal) common to all sampled trees of a site (Grissino-Mayer, 2008). Typical ranges of interseries correlations are in between 0.55 and 0.75. 0.4 is the threshold for reliably crossdating according to Grissino-Meyer (2008).

The conducted analysis show that intercorrelation between trees of the same species are not significantly different from each other when comparing different site factors, but differences in intercorrelations are considerable when comparing them between species. *Larix decidua* has intercorrelation values which are nearly twice as high as the values of the *Pinus* species.

Although those detected low common signals lead to uncertainties in crossdating, these intercorrelation values are still useful to assess the climate sensitivities of single tree species or for trees of specific site conditions.

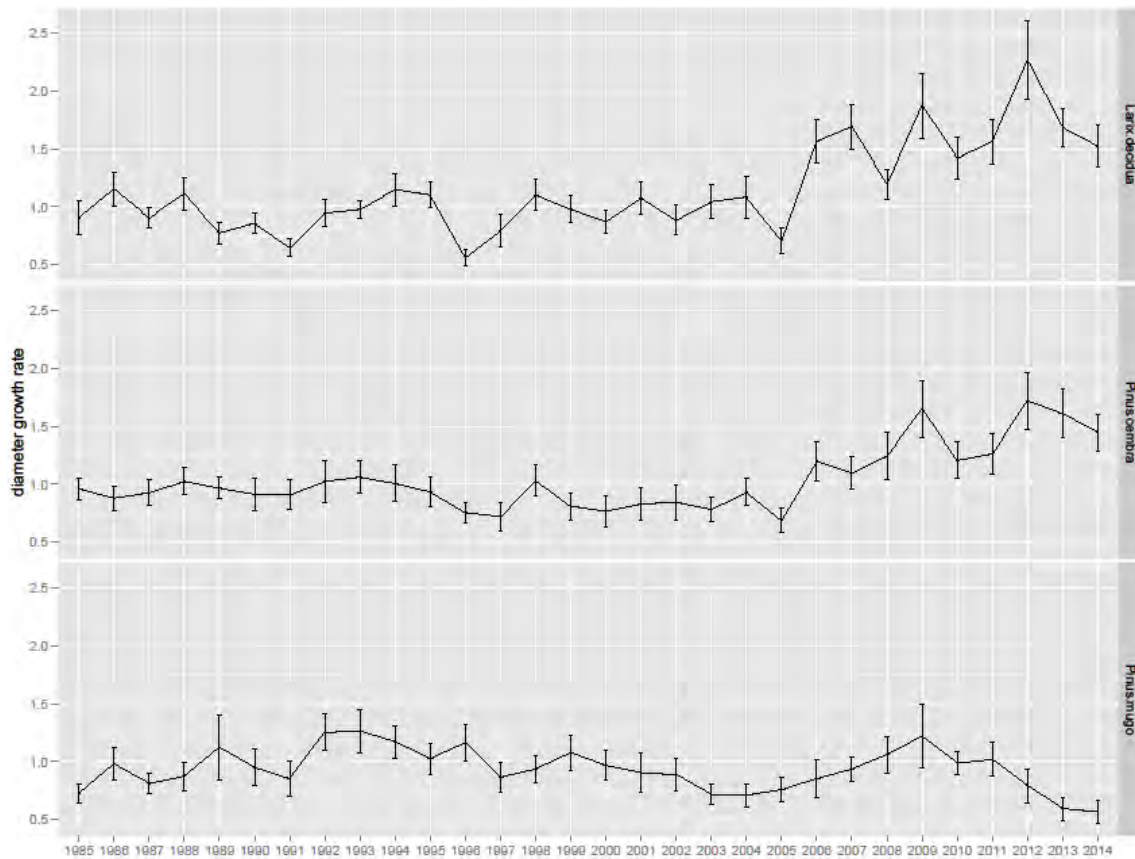


Figure 12: Mean tree-ring growth rate series with standard error derived from a sample of 20 measurements per year and species to make standard errors comparable.

Using the standard errors of the growth rate series (Figure 12) as measure for dispersion a slight trend towards higher dispersion of tree-ring growth rates with time for *Larix decidua* ( $r = 0.64$ ) and *Pinus cembra* ( $r = 0.64$ ) can be deduced, but there is no evidence for a linear trend against time for the standard errors of *Pinus mugo* ( $r = -0.09$ ).

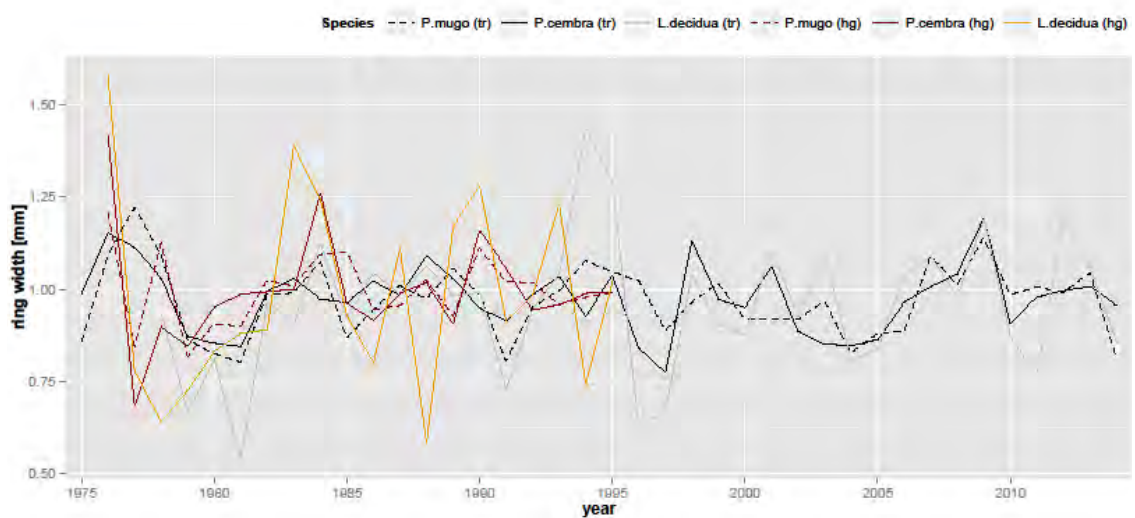


Figure 13: 20 years of detrended annual height growth rates (hr) compared with 30 years of annual year ring growth rates (tr).

Comparing detrended diameter growth rates from tree-rings and annual measured height growth rates (Figure 13) only low correlation between both measures are visible (Table 3). Yearly rates in height and in diameter growth seem not to be clearly dependent on each other.

Table 3: Pearson correlations between diameter growth rates from tree-ring data and annual height growth rates from 20 years and number of trees measured in 1995.

Species	Correlation coefficient	N height growth measurements
<i>Pinus mugo</i>	0.19	1346
<i>Pinus cembra</i>	0.14	600
<i>Larix decidua</i>	0.08	3098

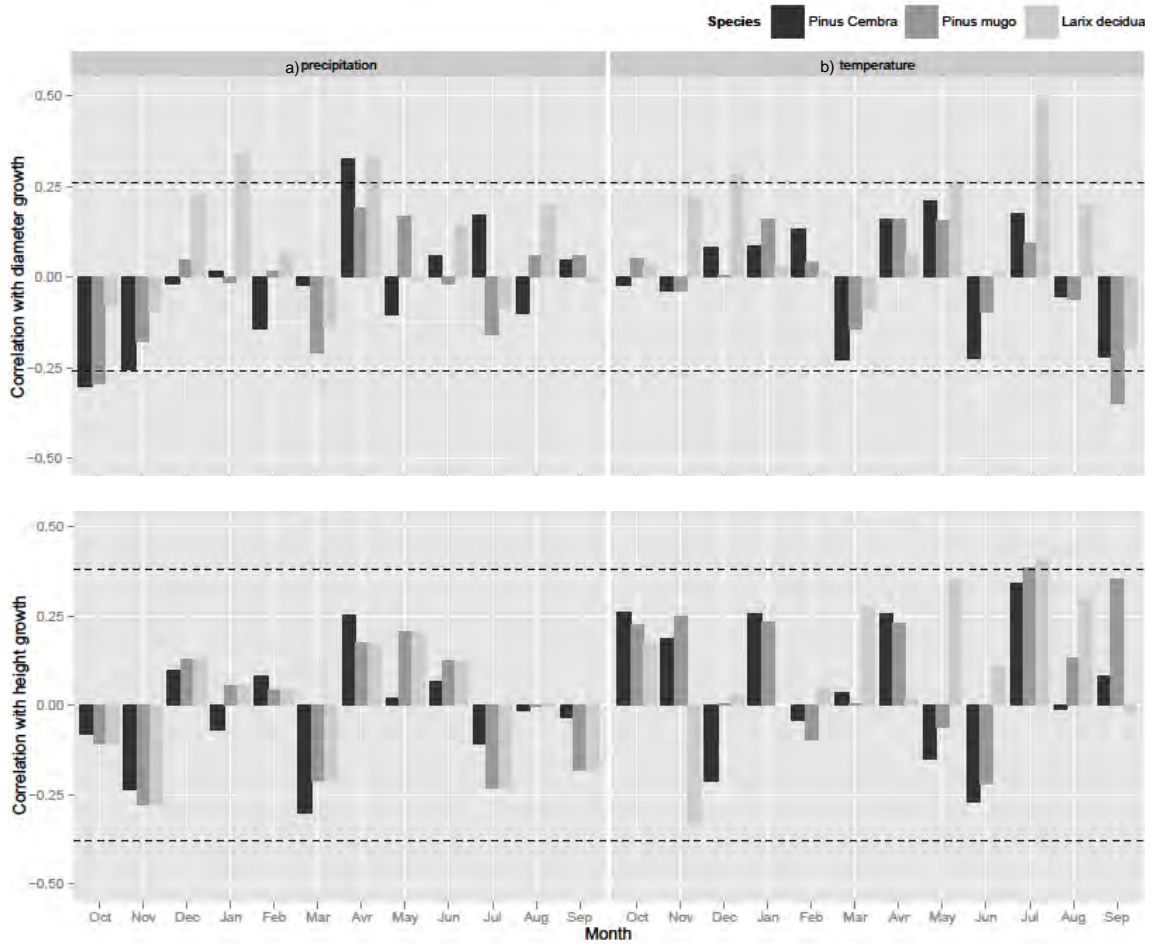


Figure 14: Correlation functions between annual height and detrended tree-ring growth rates and a) monthly precipitation sums or b) monthly mean temperatures. Yearly growth rates are correlated with climate data of the same biological year, ranging from October of the year before to September of the same year as the growth.

Analysing the relation between climate and growth we found low correlation coefficients for height and diameter growth rates (Figure 14). Highest correlation values were found for *Larix decidua*. Although there are overall low correlation values, it can be assumed that a correlation between July mean temperatures and growth rates as shown by Esper et al. (2008) and Paulsen et al. (2000) is very likely.

Through the availability of detailed long-term tree height data from four decades we are able to track height difference trends over the whole period. Significant differences in height growth rates between high and low elevations for the first three decades and for all tree species according to I. Barbeito et al. (2012) can be identified. New additional data for the period from 2005 to 2015 shows similar results as the prior decade for the Pinus species but clear differences in height growth rates for *Larix decidua* between 2005 and 2015. *Larix decidua* in high elevations have height growth rates which are about twice as high as in the period from 1995 to 2005 and for the first time the high elevation height growth rates of *Larix decidua* are slightly higher than those at low elevations.

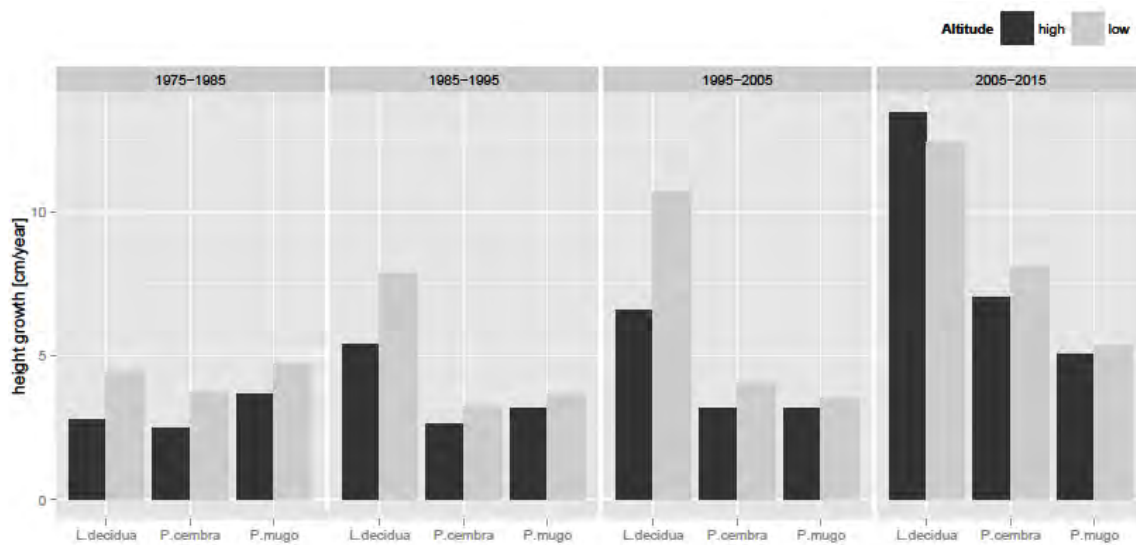


Figure 15: Annual mean growth rates per decade for different elevation levels and all species. The high elevation level corresponds to altitudes above 2150 m.a.s.l. and the low elevation levels correspond to altitudes lower than 2150 m.a.s.l.

### 3.1.3. Disturbance events

Disturbance events at high altitudes seem to be an integral part of the forces driving growth and mortality of treeline trees. One well-known disturbance factor is frost. Freezing events take place several times per year, but only cause damage once a year or once every second year for Pinus species and normally at the beginning of the growing-season (Rixen et al., 2012). Dendroecological investigations from 2015 show frost event damage in form of collapsing xylem vessels for all species but only damages in needles due to freezing for *Larix decidua*. The spatial distribution of frost-damaged shoots of *Larix decidua* surveyed from 1975 to 1995 for a subsample indicates higher susceptibility to freezing damage for *Larix decidua* at high altitudes and in ridge positions with higher wind speeds and radiation (Figure 16).

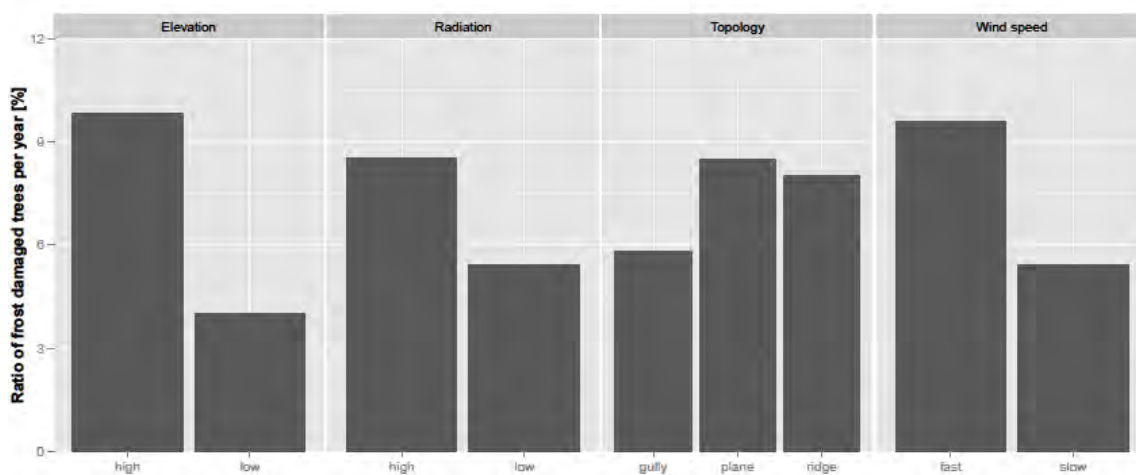


Figure 16: Annual ratio of damaged trees of *Larix decidua* due to frost events per site for a subsample with an average sample size of 2760 trees in the period between 1975 and 1995.

Frost ring findings in tree-rings further suggest that there are years with severe damage that occur about every second year and that frost ring occurrence is decreasing with age.

In contrary to findings of freezing damages specific to *L. decidua*, pathogenic snow-fungi are found to be specific on *Pinus* species with perennial needles. There are mainly two important pathogenic snow fungi, which affect *Pinus mugo* and *cembra* at Stillberg. *Phacidium infestans* infest only needles of *Pinus cembra*, while *Gremmeniella abietina* infest *Pinus cembra* and *mugo*. *P. infestans* is most abundant at sites with early snow melt mainly in east expositions and there is no correlation with microtopography, radiation or wind. A spatial association with mature *Pinus cembra* trees as stated by Ignacio Barbeito et al. (2013) is most likely

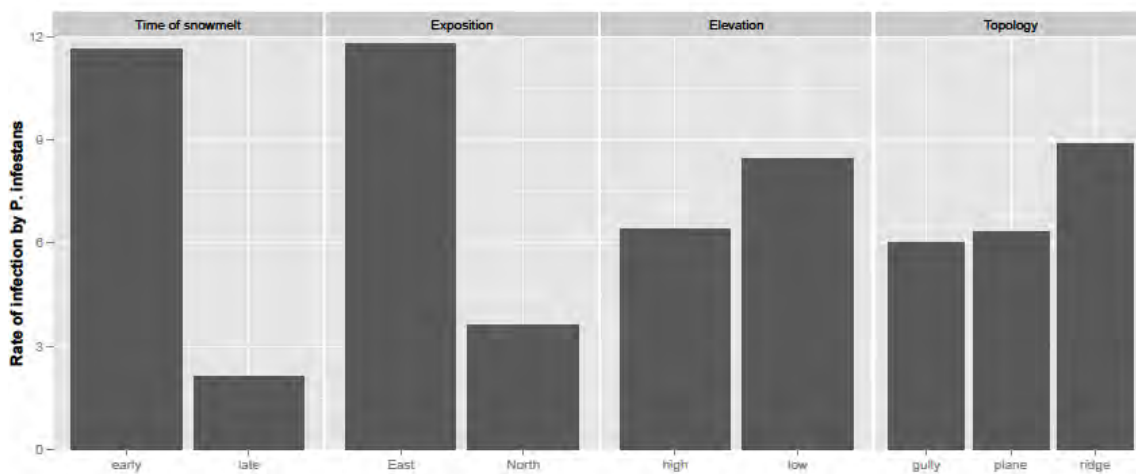


Figure 17: Annual ratio between affected and unaffected *Pinus cembra* trees by *Phacidium infestans* per site for a subsample with an average sample size of 3175 trees in the period between 1975 and 1995.

*Gremmeniella abietina* seems to be more abundant than *P. infestans*. In 2015 54% of all individuals of *P. mugo* were affected by *G. abietina* while 33% of *P. cembra* were affected by *P. infestans*. There seems to be no clear spatial pattern of distribution of *G. abietina* in 2015 and there is only a slight trend to higher elevations and north exposition and against ridge sides. Surprisingly the time of snowmelt does not have a significant effect on the spatial distribution of *G. abietina*.

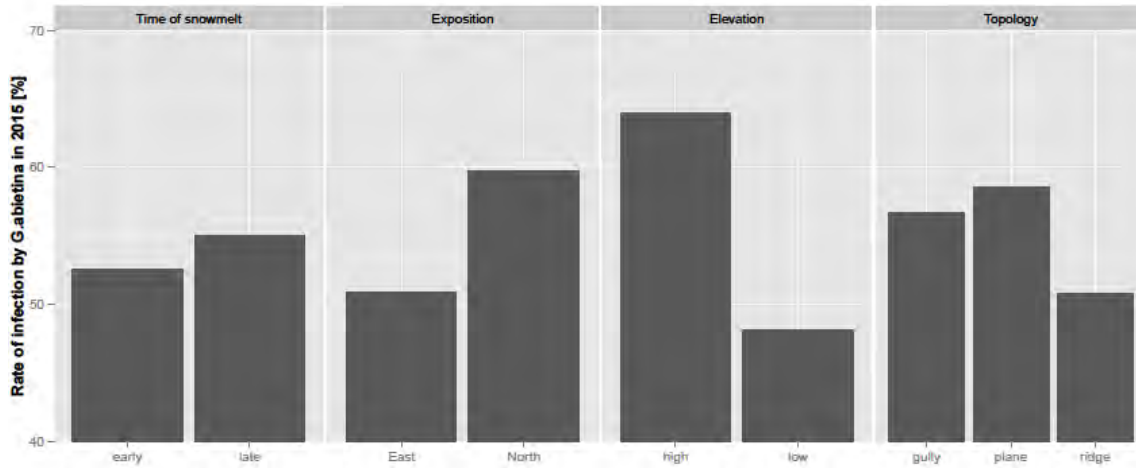


Figure 18: Ratio between *Gremmeniella* affected and unaffected *Pinus mugo* trees in 2015 compared between different sites.

Also damages affecting the stem of trees occur regularly caused mainly by disturbance events. It can be distinguished mainly between a) breakage of the whole stem, b) splitting parallel to the stem axis and so called “hanger” which are growing crooked (>30° from perpendicular).

Looking at occurring stem damages in 2015 (Figure 19) especially *P. mugo* is conspicuous. About every fourth tree of *P. mugo* has no upright growth form and is therefore called “hanger”. Also for *L. decidua* hangers are most frequent. Overall breakage and splitting are less frequent but for *P. cembra*, where breakage is the most frequent form for stem damage. There is no clear spatial correlation between occurrence of stem damages and sites.

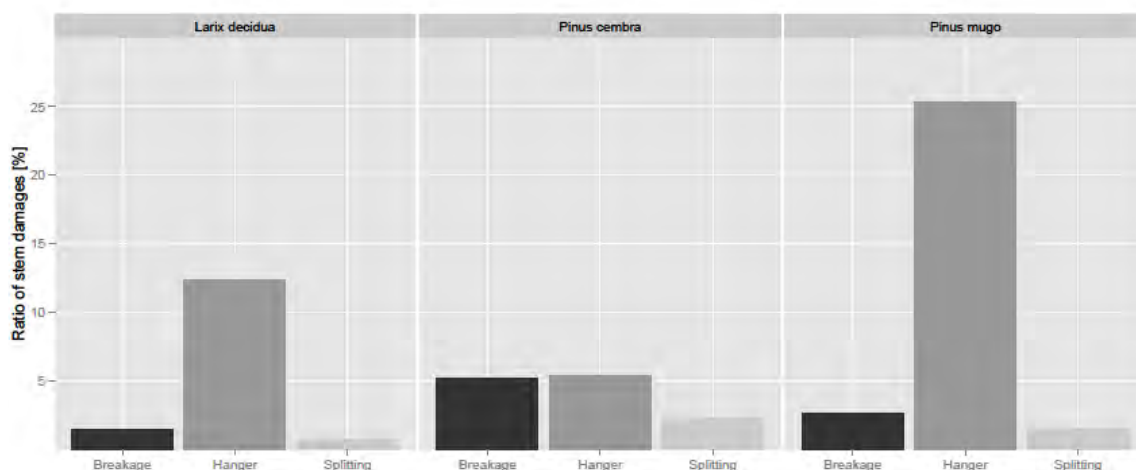


Figure 19: Ratio of different stem damages per tree species calculated from observations in 2005 and 2015. Splitting refers to trees growing in an angle more than 30° from vertical.

Breakage was most frequent at high elevations and northeast exposed gullies with late snow melt dates. Splitting was also strongly associated with high elevations and northeast exposed gullies but in contrary to breakage at sites with early snow melt dates. In contrast to those findings, “hangers” were most frequent at lower elevations with northeast exposition, independent of microtopography and snowmelt date.

Further there would be disturbance events like avalanches or intermittent hailstorms, which we will not consider in this thesis due to a lack of, recorded events of hailstorms and due to no consistent time series of avalanche records with its spatial distribution.

## 3.2. Assessing the effects of site variability on ten-yearly growth rates

### 3.2.1. Altitude

Altitude is a good predictor for height growth for all species during the first three decades but with decreasing accuracy for both *Pinus* species. For *Larix decidua* the negative effect of altitude was even increasing in the third decade. For the fourth decade the negative effect of altitude was suddenly decreasing and the quality of altitude as a predictor get significant lower. For *Larix decidua* the correlation even changed from negative to slightly positive.

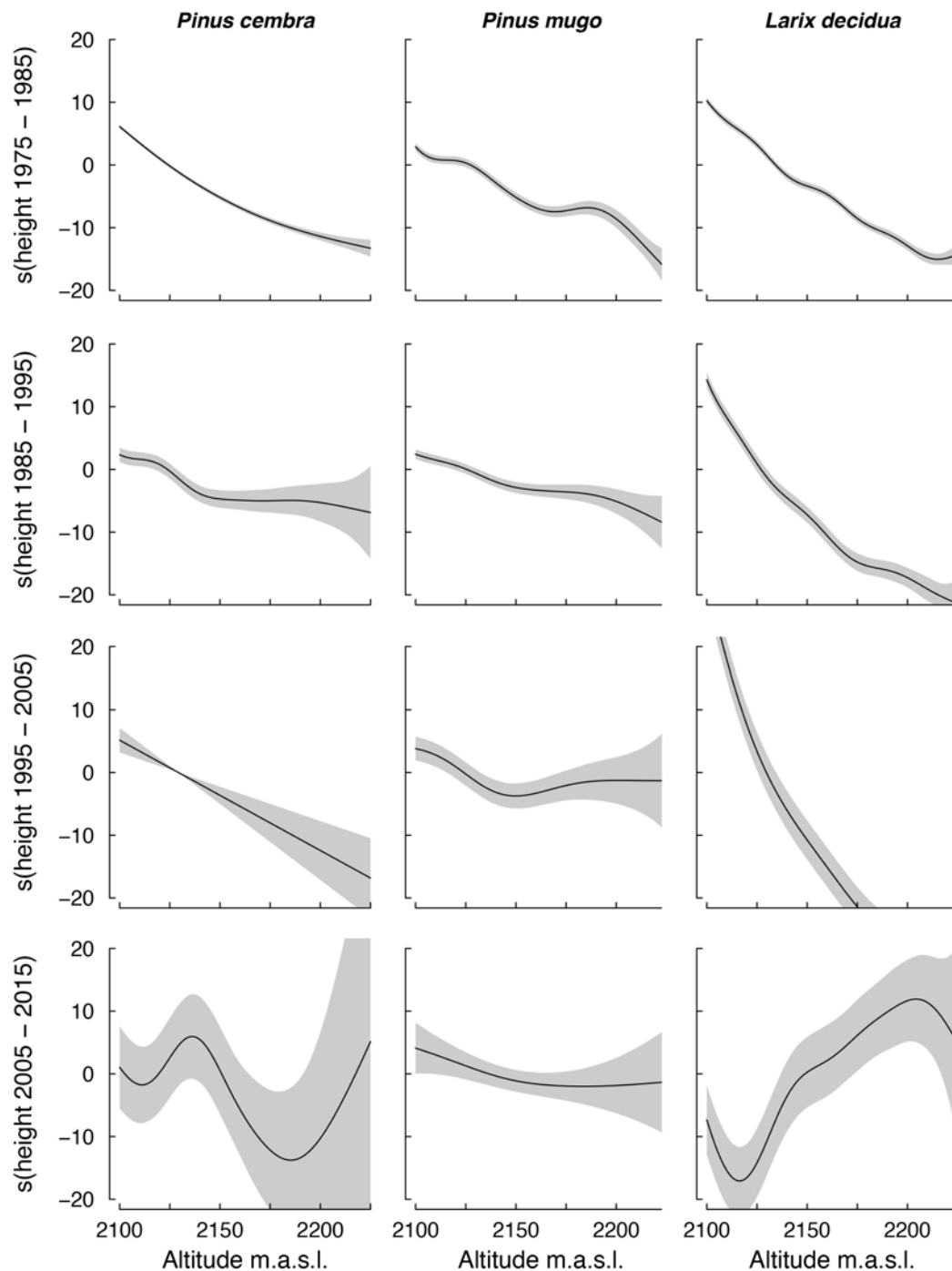


Figure 20: GAM functions for the relationship between the fitted height growth values scaled to zero and the elevation. The plots include 95% confidence intervals in light grey.

### 3.2.2. Wind

There is a similar trend for all tree species to decreasing height growth with increasing average wind speeds. This negative effect is highest for *Larix decidua* during the third decades and is associated with high uncertainties and low predictive power for all species during the last decade.

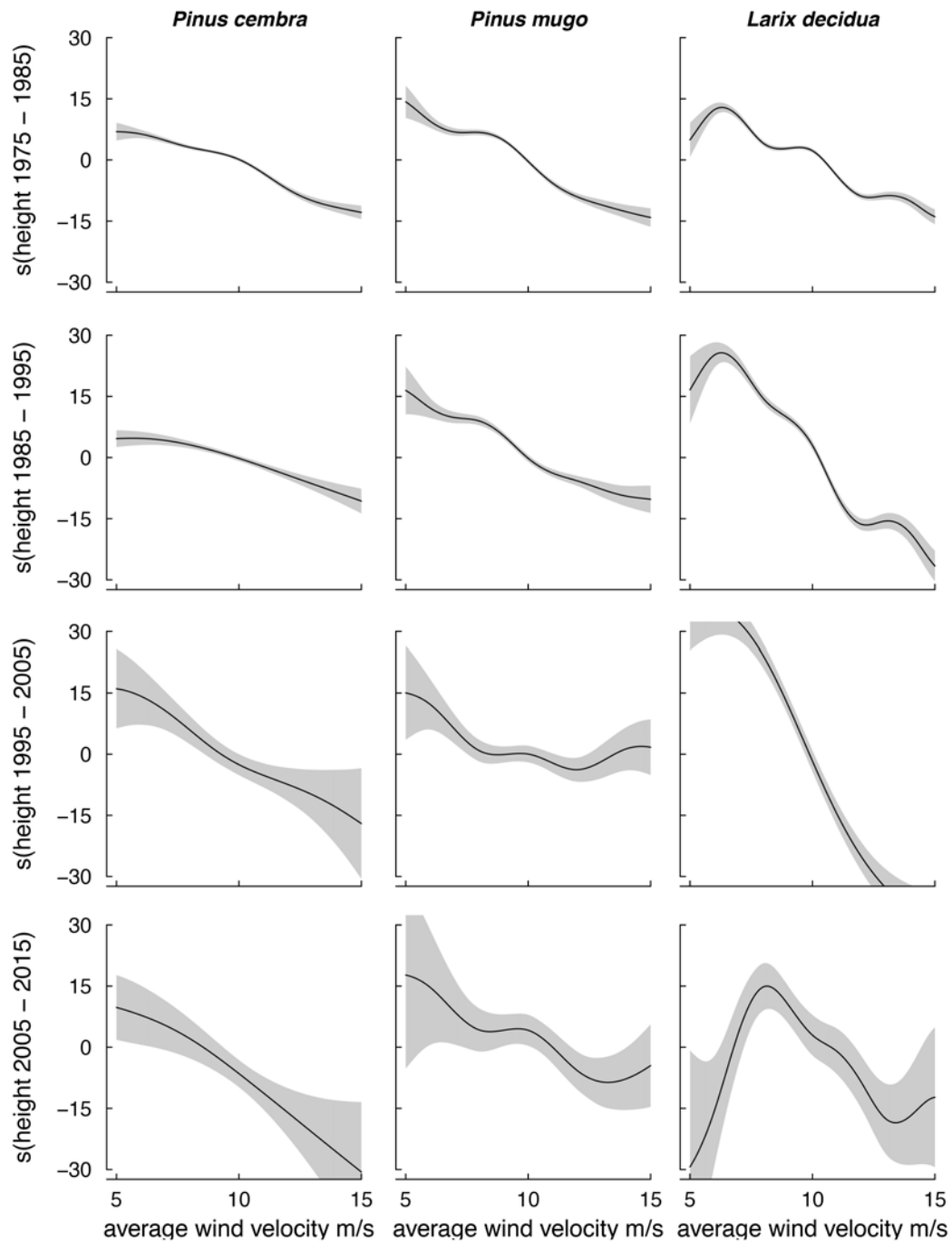


Figure 21: GAM functions for the relationship between the fitted height growth values scaled to zero and average wind. The plots include 95% confidence intervals in light grey.

### 3.2.3. Radiation

The importance of the effect of radiation on growth rates is decreasing with time. In the first two decades higher radiation seems to be favourable for height growth rates if not above a certain threshold where the growth rates reach maximum and decrease for higher radiation than the threshold. In the last two decades the effect of radiation on tree growth decreased.

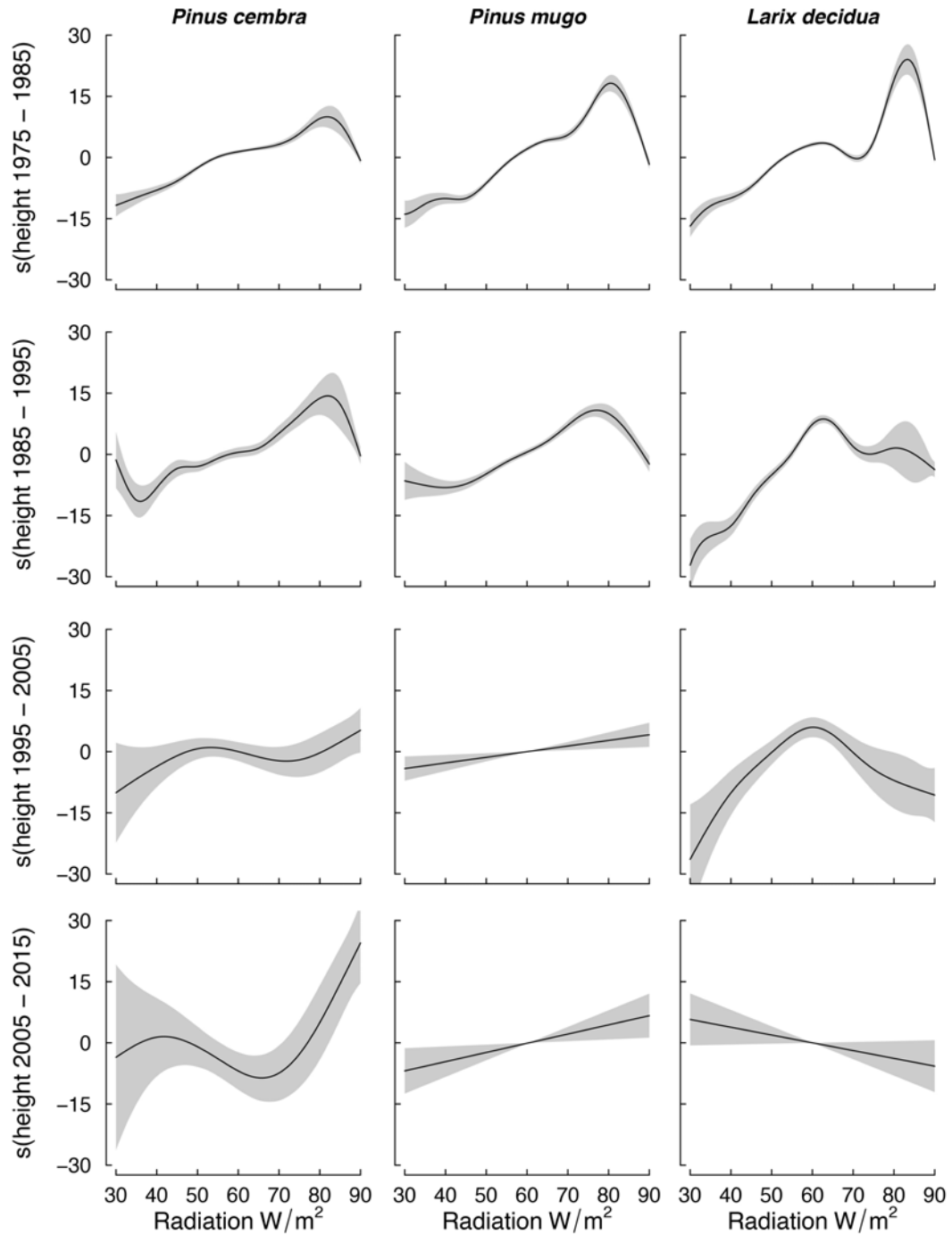


Figure 22: GAM functions for the relationship between the fitted height growth values scaled to zero and average solar radiation during the growth-season. The plots include 95% confidence intervals in light grey.

### 3.2.4. Time of snowmelt

All three species show a height growth optimum on snow melt dates between the 140<sup>th</sup> and 150<sup>th</sup> day of the year in the beginning with a shift to an optimum at later snowmelt dates and a trend to a linear correlation without optimum for the last decade and even for the last two decades for *Pinus mugo*.

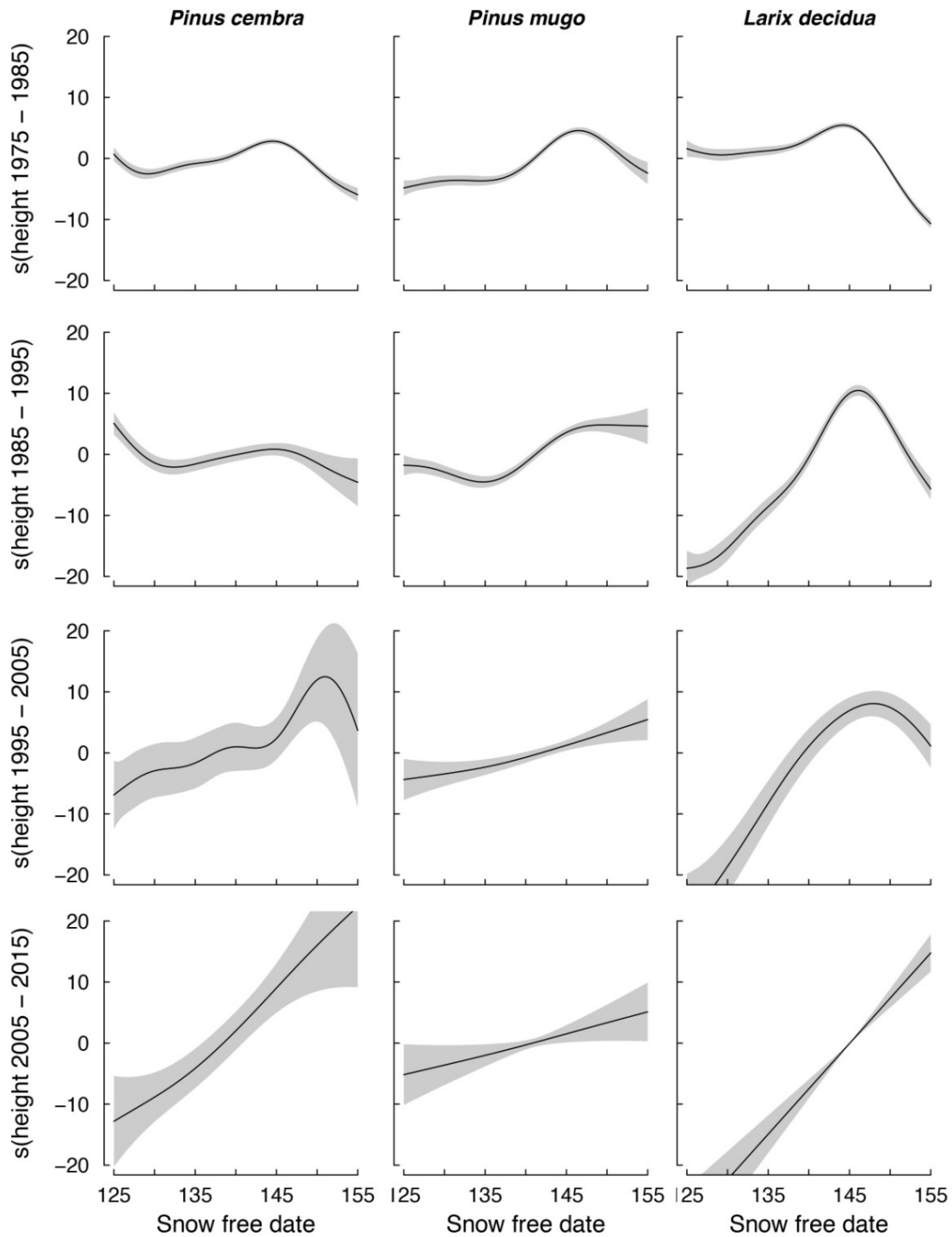


Figure 23: GAM functions for the relationship between the fitted height growth values scaled to zero and snow free dates (average from 1975-1982). The plots include 95% confidence intervals in light grey.

### 3.3. Assessing the effect of factors on year-to-year growth variation

Year-to-year growth variation is assumed to be a product of yearly climate variation and the degree of damages due to disturbance events. We assume that climate and disturbance effects on growth are likely to interfere with each other. We take account of effects from disturbance events on same year and next year growth rates while using the biological year to compare climate with growth rates.

#### 3.3.1. Frost events

Intensities of frost events are closely linked to loss in height growth in the next growing-season. Individuals of *Larix decidua* with high frost damage intensities show average height growth rates nearly half as high as they would be without frost damage. In contrast to those findings tree-ring growth shows no significant response ( $p < 0.1$ ) to frost rings in the year before.

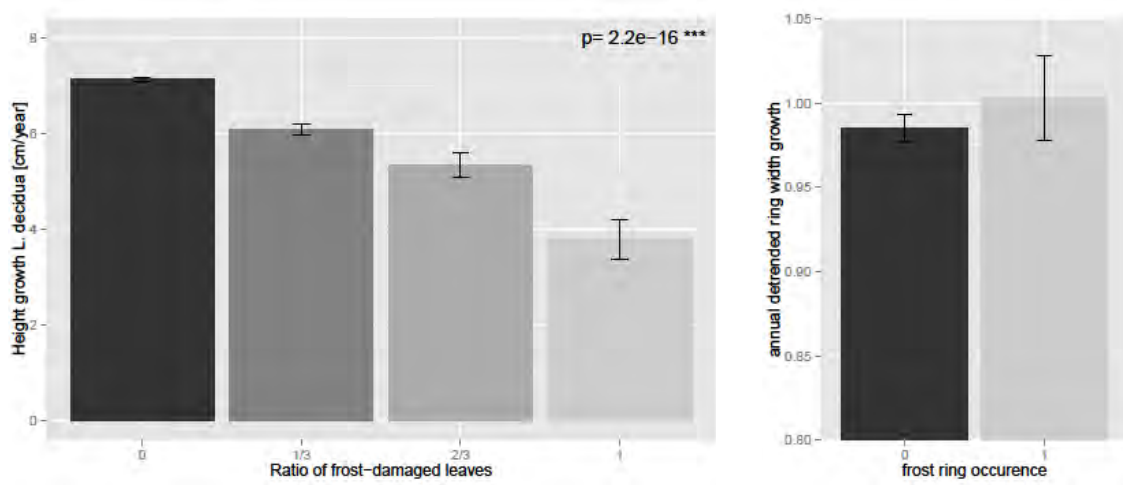


Figure 24: Ratio of frost damaged leaves compared with next year mean height growth rate of *L. decidua* for a subsample of 2760 trees and occurrence of frost rings compared with next year detrended ring width growth for a subsample of 145 trees.

### 3.3.2. Snow fungi

For the effect of *Gremmeniella abietina* on *Pinus mugo* there was a lack of data, therefore only the effect on growth for the last decade could be assessed. Negative effects on height growth could only be asserted for high intensities of infestation, which affects all tissues and not only a part of them. For low and intermediate intensities no significant effect was found. Contrasting to strong effects of *Phacidium infestans* on mortality of *Pinus cembra* (I. Barbeito et al., 2012), there is a negative effect on next year growth rates of *Pinus cembra* in the period between 1975 and 1995. There is even a trend to higher growth rates for affected *Pinus cembras*.

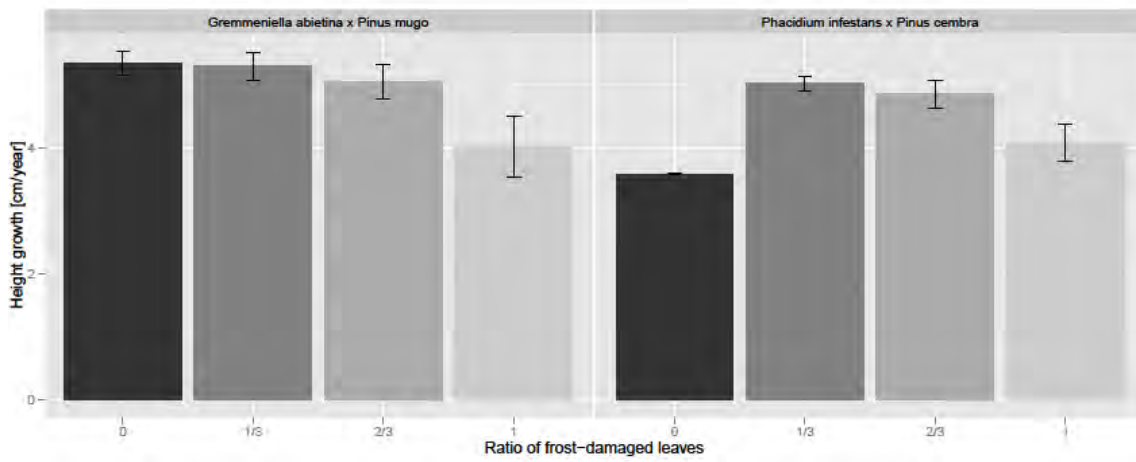


Figure 25: Effect of infestations by snow fungi *Gremmeniella abietina* and *Phacidium infestans* on annual height growth of *P. mugo* and *P. cembra* for a subsample of 2760 trees regorded between 1975 and 1995.

### 3.3.3. Stem damages

Stem damages have a significant effect on height growth rates of *P. cembra* and *L. decidua* ( $p < 0.01$ ) but no significant effect on height growth of *P. mugo*. For both species with significant effect of stem damages on height growth rates there is no clear effect of stem splitting on growth but significant lower height growth rates for hangers and trees with broken stems.

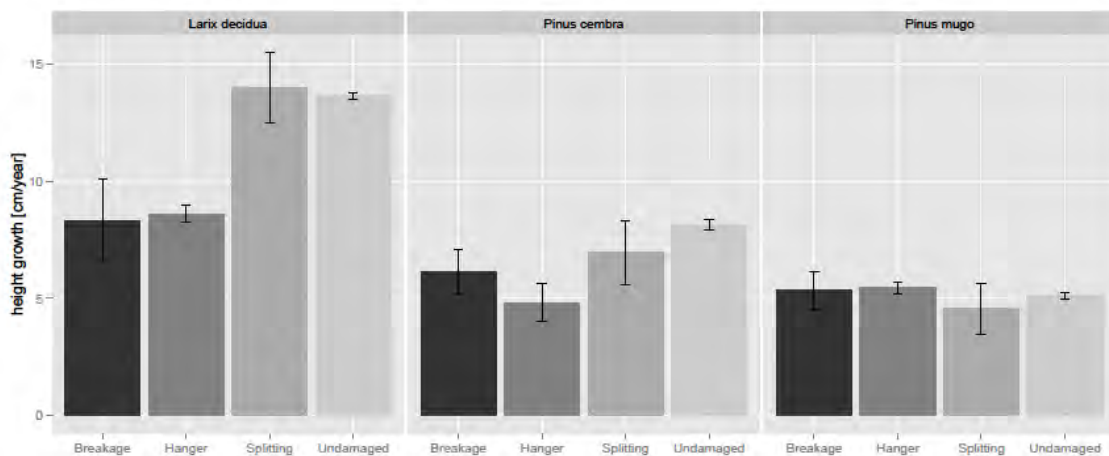


Figure 26: Effect of stem damages measured in 2015 and 2005 on average annual growth rates for the same time period for all species.

### 3.3.4. Precipitation and summer temperatures

As showed in chapter 3.1.2 annual tree-ring growth rates are most sensitive to mean July temperatures and April precipitation sum. We used a combination of these two measurements to assess the effect of combinations between mean temperatures and precipitation amount.

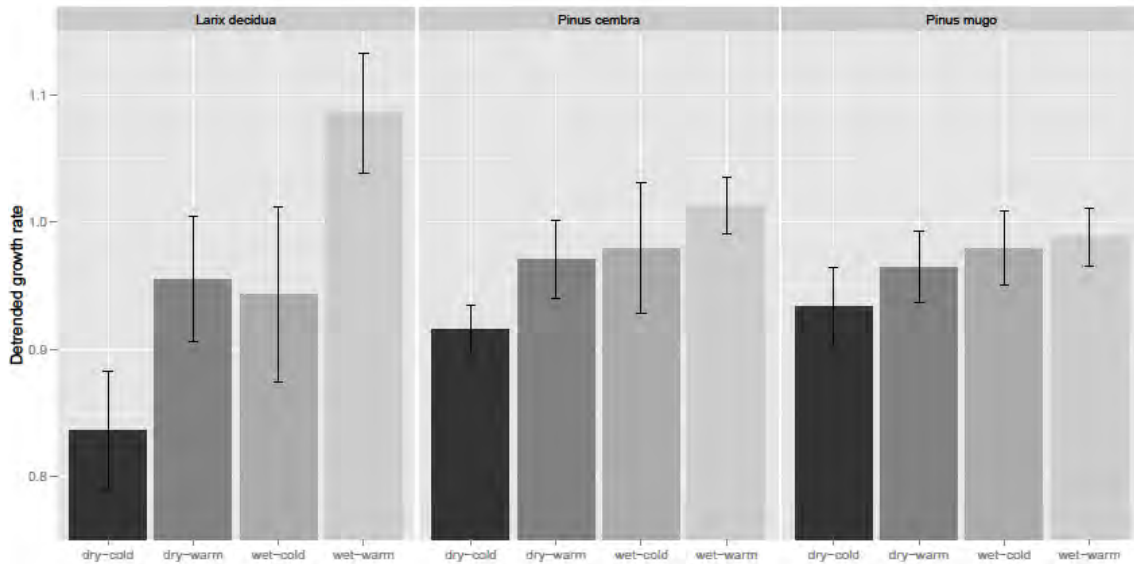


Figure 27: Mean detrended yearly growth indices from tree-rings with standard-error-bars for summer climate combinations of April precipitation sum and July mean temperatures per species. Numbers of samples are: Dry cold (13), dry-warm (7), wet-cold (5), wet-warm (12).

Tree-ring growth of *L. decidua* and *P. cembra* (Figure 27) was significant higher in wet-warm summers than in dry-cold summers ( $p < 0.01$ ). Contrasting to findings for *L. decidua* and *P. cembra* only a nonsignificant trend for *P. mugo* ( $p > 0.1$ ) towards higher tree-ring growth rates during wet-warm summers and lower tree-ring growth rates for dry-cold summers could be detected. Combinations of dry-warm and wet-cold summers seem to lie in between the tree-ring growth rates of dry-cold and warm-wet summers but with high uncertainties due to a lack of years with dry-warm or wet-cold summer climate.

### 3.3.5. Snow

There are no significant correlations between seasonal measurements of average snow height, snow free days or time of snowmelt and yearly diameter or height growth rates from tree-rings ( $p < 0.1$ ).

### 3.4. Importance of drivers on growth over time

#### 3.4.1. Microsites and elevation

For the importance ranking, based on a random forest model, we used all drivers but the competition factor and supplemented our drivers by the sum of all damages asserted to specific trees in 2015 were used. Adequate damage data for the previous decades was not available therefore this factor is only taken into account for the last decade. Damages were most frequent for *P. mugo* (83% damaged), less frequent for *P. cembra* (52% damaged) and least frequent for *L. decidua* (22% damaged).

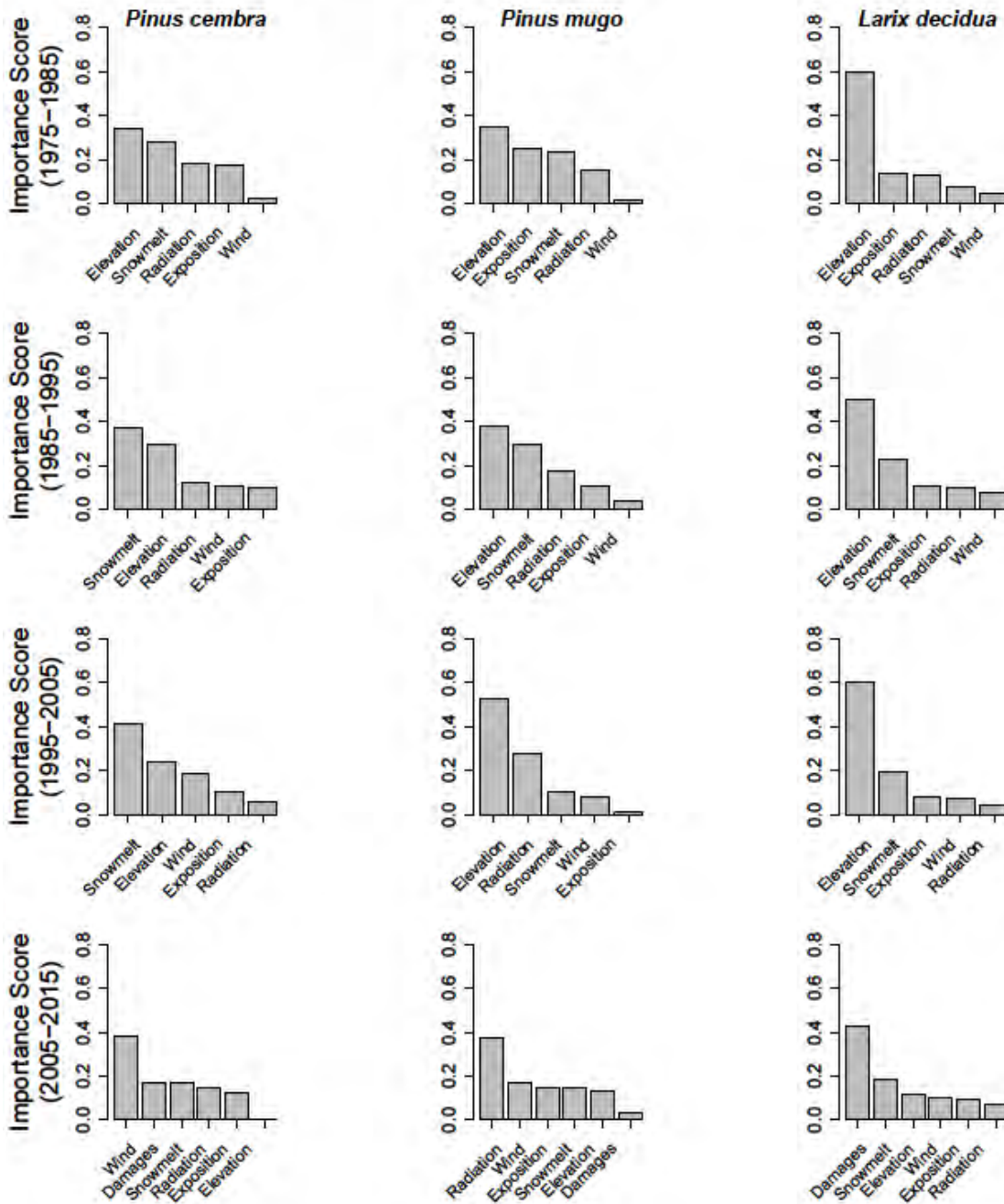


Figure 28: Permutation variable importance, in rank order, of environmental predictors of height growth, where importance was measured by the drop in classification accuracy after predictor removal in a random forest of 200 decision trees. Methods are taken from I. Barbeito et al. (2012).

For *P. cembra* snowmelt date is the most important driver for height growth considering the whole period of the last 40 years. For the first decade only elevation was more important and between 1985 and 2005 time of snowmelt remained the most important factor. Nonetheless a change in importance seems to take place in the last decade when wind gets the most important driver and the snow melt date remains together with the damage sum only second most important driver. Elevation can be assessed as very important for height growth of *P. cembra* in the beginning but with a drastically decreasing importance for the last two decades while wind shows a contrary trend as driving force of height growth and gains drastically importance in the last two decades. Radiation and exposition have nearly the same low effect on height growth of *P. cembra*. Damages seem to be about similar important as time of snow melt at least in the last decade.

In contrast to *P. cembra*, *P. mugo*'s height growth rates seem to be closely linked to elevation during the whole period of 40 years. Second most important driver for *P. mugo* is radiation, whose importance is constantly increasing over the last 40 years and which is the most important factor for the last decade. Snowmelt is important during the first two decades and loses importance afterwards. Exposition, wind and damage sum have no significant effect on height growth differences between single trees of *P. mugo*.

The height growth rates of *L. decidua* are in relation to the other species disproportionate high dependent on elevation. For the first three decades elevation is responsible for more than 50% of the importance score but loses importance in the last decade. Exposition and snowmelt date are the second most important drivers for height growth over the whole time span of 40 years. While exposition matters mainly in the first decade snow melt date is for the last three decades always the second best explanatory variable for height growth. The damage sum is the most important driving factor for the last decade. Wind and radiation have a rather low influence on height growth of *L. decidua*.

Over all tree species elevation and snowmelt dates are the most important drivers for height growth, although elevation loses clearly his disproportionate importance from the decades before. There are factors, which affect mainly one species. Damage sums are obviously important for *L. decidua* and *P. cembra* in the last decade but not for *P. mugo*. In contrary to the other two species, wind becomes highly important for *P. cembra*. It's also conspicuous that differences in importance ratio between height growth drivers are getting smaller with time.

### 3.4.2. Importance of disturbance compared with microsities

After comparing elevation with different microsite characteristics and showing that disturbance effects are highly important, at least for *L. decidua* in the last decade we want to analyse the cumulative effect of disturbance on growth over 40 years compared with the effect of different microsities (reduced to snow melt dates). Disturbance was grouped into the three categories low disturbance with no registered damages, medium disturbance with low intensity damages and high disturbance with multiple damages or damages with high intensities. Only for *L. decidua* the disturbance has severe impacts on growth, which is significant higher than impacts of different microsities on growth. While intermediate intensities of disturbance have only moderate impact on growth of *L. decidua*, high disturbance intensities lowers average tree heights by about 1m or diameter by 2.5 cm. Response of tree height corresponds well to responses in stem diameter only differences in absolute height between species are not translated to diameter measures, where differences between species are marginal.

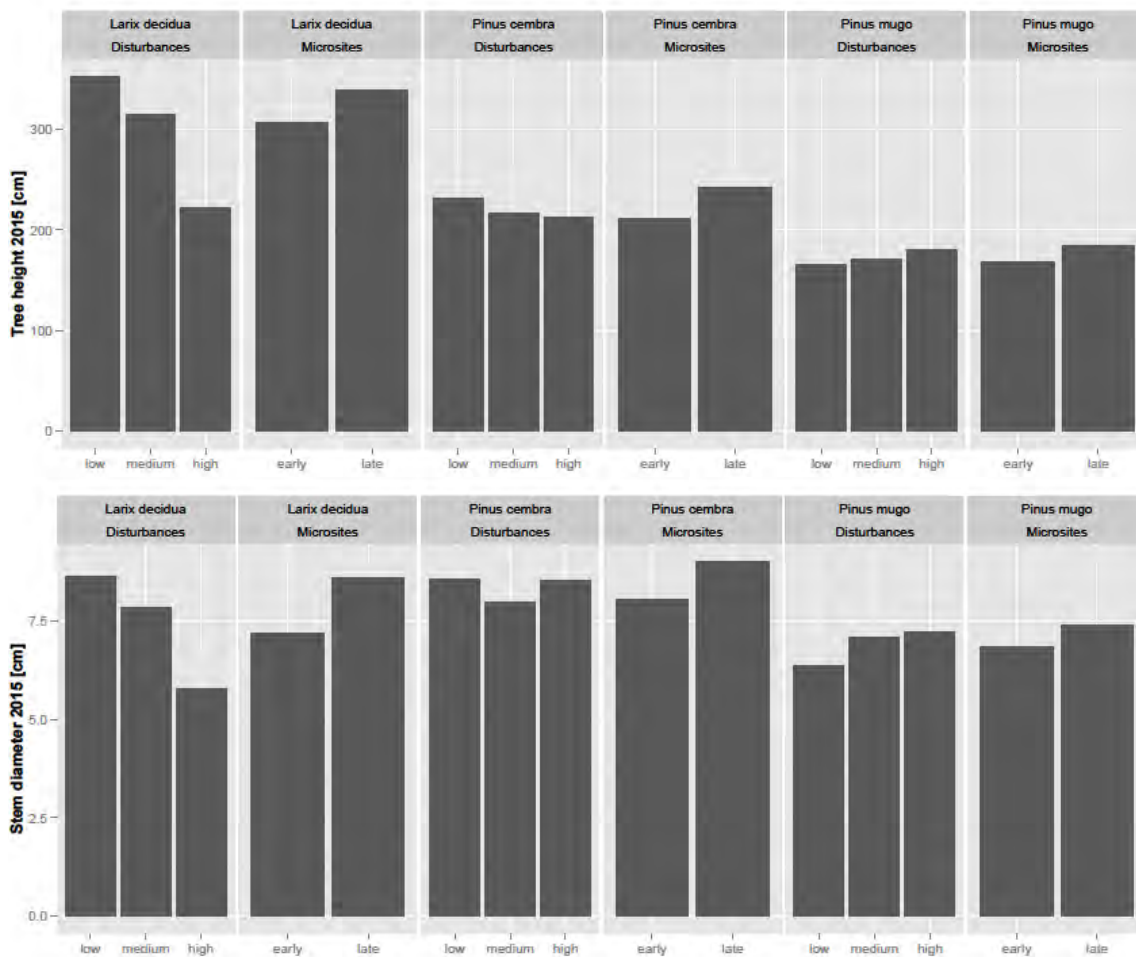


Figure 29: Comparison between the effect of disturbances and microsities on diameter and height growth.

## 4. Discussion

### 4.1. Effect of heterogeneous small-scale site conditions on growth variation

#### 4.1.1. Elevation, microsite characteristics and their effect on tree growth

The prevailing view for limitations at high altitude treelines states that seasonal summer temperatures are the main controlling factor of upper tree limits (Gehrig-Fasel, Guisan, & Zimmermann, 2008; Holtmeier & Broll, 2007; Körner, 2007). As changes in elevation are physically tied to changes in air temperatures and atmospheric pressure they contribute significantly to variation in growth over elevation gradients and limit possible growth at the upper treeline. Mean air temperature during the growing season decreases by 0.6°C per 100m elevation and is assumed to contribute for the most part of decreasing growth rates with elevation. This relation between elevation and growth is consistent with findings of the first 30 years of Stillberg where elevation is the most important driver of height growth. Although elevation is closely linked with temperature it should be considered that elevation may be associated with other environmental factors in addition to temperature. Freezing events for *L. decidua* are significantly more frequent at high elevations of Stillberg. Positive correlation between elevation and winter desiccation was found in the Rocky Mountains by Cairns (2001). In addition also less favourable microsites (e.g. due to higher vegetation competition) at high elevations might increase the effect of elevation on height growth. Although elevation gradients seems to have large impacts on height growth they can easily be masked by microtopographical effects which are able to mimic temperature differences of relatively large elevation gradients over very short horizontal distances (Scherrer & Koerner, 2010).

Exposition is closely linked with values for mean wind speeds and radiation. Schönenberger et al. (1988) showed that east exposed slopes receive about two times more incoming radiation than north-exposed slopes and have a period of positive radiation balance which is 8 month long instead of 6 months for north-faced slopes. Also shallow northeast expositions at top of Stillberg received higher positive radiation balances. The ridges ranging along the slope line mainly influence wind exposure. Due to those ridges east-exposed sides of ridges have significant lower wind exposure than north-exposed sides and ridges. Schönenberger et al. (1988) showed evidence for average wind speeds twice as high on the top of ridges than on the east-exposed sides of them. Wind exposures and radiation counteract each other. High wind exposures lower temperatures and high radiation increases temperature. Therefore microclimates with high wind speeds and low radiation are coldest and microclimates with high radiation and low wind speeds are warmest. Those two effects are clearly shown in GAM-plots of chapter 3.4., where clear correlations between height growth, average wind speeds and radiation are shown for the first two decades. Additional to the impact on microsite temperatures high wind speeds are also strongly associated with further side effects. High wind speeds increase the risk of mechanical damage due to stem breakage or by ice crystal abrasion due to blowing snow (I. Barbeito et al., 2012; Hadley & Smith, 1986) and height growth can also be reduced due to wind chill of growth meristems (Grace, Allen, & Wilson, 1989). Higher wind speeds also lead to snow shift and therefore to a higher probability of snow free days during winter. Regarding the relationship between radiation and height growth a thresholds at high radiation for all species after which height growth is decreasing rapidly can be detected. This could be explained by cold-induced photoinhibition, which refers to depression in photosynthesis as a result of a combination between cold stress and an excess of sunlight absorption which cannot be used and leads to either the inactivation or oxidation of photosynthetic protein (Ball, Hodges, & Laughlin, 1991; Germino & Smith, 2000).

The date of snowmelt is considered to have high impact on mortality of treeline trees and a moderate impact on height growth (I. Barbeito et al., 2012; Josef Senn & Schönenberger, 2001). Snowmelt dates show a spatial heterogeneous pattern caused by microtopography, heterogeneous radiation intensities and

snow movements due to wind and avalanches. Snowmelt dates are linked to various different effects with either positive or negative consequences on height growth. Positive consequences due to late snowmelt are considered to be either related to protective functions of snow cover like insulation from cold temperatures, protection against freezing events (Rixen et al., 2012) and protection from browsing by the black grouse (*Tetrao tetrix*) (Streule, für das forstliche Versuchswesen, & Birmensdorf, 1973) or linked to provision of nutrition (I. Barbeito et al., 2012) and higher water availability (Hättenschwiler & Smith, 1999). Negative consequences of late snowmelt could be higher exposure to snow creep and its sheering effect on stems (Hättenschwiler & Smith, 1999), a shorter growing season and higher risks of snow fungi infections (Ignacio Barbeito et al., 2013; J Senn, 1999). Considering the analysed data it can be stated that all three species show a height growth optimum on snow melt dates between the 140<sup>th</sup> and 150<sup>th</sup> day of year in the beginning with only moderate consequences for tree growth. In the three last decades for *L. decidua* and the two last decades for *P. cembra* the day of snowmelt gained importance and height growth optimum shifted to later snowmelt dates. Although results from the last two decades should be treated with caution due to a bias because snowmelt dates are reflecting snowmelt between 1975 and 1983 while being compared to actual data. Therefore plots with late snowmelt dates at the beginning are likely to have earlier snowmelt dates today due to a shift in snowmelt dates of about 10 days and due to snowmelt dates defined by closer tree stands. This could lead to the conclusion that the optimum snowmelt date was rarely exceeded in the last ten to twenty years.

#### 4.1.2. Changing importance of microsites

Importances of continuous drivers on height growth of treeline trees is life-stage dependent and changes in importance are characteristic for each species. The only driver with similar trend for all species was elevation, which had overall decreased impact on height growth. I. Barbeito et al. (2012) explained those observations with a decoupling from microsite soil temperatures to an increased coupling of tree tissue temperatures to air temperatures, as trees grow taller. In addition also increased growing-season temperatures about 2.1°C (Figure 3) are likely to be linked to a decreased limiting effect of elevation on height growth.

For *P. mugo* most important drivers on height growth are factors closely linked to warmer microclimates. During the first three decades, the most important driver was elevation, which was replaced by radiation for the last decade. Also radical change in tree heights on the opposing south-exposed slope of Lukschal indicates thermophile preferences of *P. mugo* at high altitudes. *P. mugo* is highly affected by stem damages and snow fungi leading to highly irregular growth forms of often multiple and crooked stems. Therefore height growth is not a very good measurement for tree vitality because over ground biomass and the effect of drivers might be estimated wrong. Also damages affect growth of *P. mugo* fundamental but have a low importance rank, because they do not explain growth differences due to an affection of nearly every single tree.

Height growth of *P. cembra* is highly dependent on the date of snowmelt. Later snowmelt dates are favourable for higher height growth rates and indicates that snow fungi have a subordinate role for growth and positive effects of late snowmelt outcompete negative effects. As proposed before, elevation loses importance in the last three decades due to a decoupling from microsite temperatures. Surprising is the high increase of wind in the last decade. According to Kronfuss and Havranek (1999), it can be assumed that wind reduces height growth of *P. cembra* by a significant cooling of air and further also damaged needles due to winter wind cuticle abrasion (Hadley & Smith, 1986) are likely to contribute to lower growth rates. Streule and Häsler (2006) showed similar effects in an experimental setup with wind shelters.

Height growth of *L. decidua* is disproportionate high dependent on elevation related to other factors for the first 30 years but with a radical change in the last decade, where importance of elevation decreases significantly. Those findings can be associated with increasing importance of forest-like climates after canopy closure of tree stands. As trees grow taller and canopies get closer we assume a change in local climates from microsite driven local climates to so-called forest-like climates. Therefore a change from heterogeneous small-scale climates to more homogeneous local climates can be assumed. Decreasing variance in growing-season soil temperatures during the last 40 years confirm this assumption. While differences in soil temperatures at 3 cm depth represent 3°C between different microsities in 1975 (Turner, Rochat, & Streule, 1975), I. Barbeito et al. (2012) could only detect differences in soil temperatures smaller than 1°C between different microsities for the growing season in 2007. Observations from 105 temperature loggers in 2015 indicate even that temperature differences in soil temperatures between different microsities decreased under 0.5°C. In 2015 the main factor for differing soil temperatures is the number of surviving trees per plot ( $p < 0.001$ ) and species ( $p < 0.01$ ). Both are appropriate measures for the degree of shading by tree canopies. Driven by the effect of shading soil temperatures in high elevations are even a little bit higher than in low elevations. Those knowledge and findings in GAM-analysis showing increasing uncertainties in the last decades for all species and all drivers of height growth support assumption, that microclimates loses importance while effects of closed canopies lead to forest-like climates especially for *L. decidua* but also for *P. cembra* and for *P. mugo* at sites with shadowing effects of neighbouring plots.

#### 4.1.3. Interactions at treeline as a function of elevation and microsities

A main difficulty in assessing interactions between treeline trees is to disentangle the network of interactions between trees from artefacts due to correlations between number of competitors and site conditions. Artefacts are caused by the context that plots with higher survival and lower mortality are more likely to have better side conditions in respect to growth than plots with high mortality. In a natural setup it is not possible to clearly separate interaction effects from site-specific artefacts without very detailed knowledge of side conditions. Therefore it is not worthwhile to compare interaction in form of survival directly to other predictor variables of growth.

Ignacio Barbeito (2013) dealt with this problem by using an observational competition index approach for height growth rates and an additional experimental thinning setup for diameter growth rates. In the thinning setup several plots with *L. decidua* in the upper and lower part of Stillberg where thinned by removing 20% of the trees and neighbouring plots without thinning were selected as control-plots. After six years micro-cores were taken from each plot and compared between thinned and unthinned plots. Barbeito found evidence from his observational approach that (1) increasing abiotic stress due to a later snowmelt led to a shift from competition to facilitation for all tree species and (2) the importance of competition decreased with elevation. Results from the thinning experiment additional suggests for *L. decidua*, that (3) competition is masked at higher elevations by the influences caused by abiotic stress, while at lower parts competition is more important and limits their diameter growth significantly. It can therefore be concluded, that competition matters most for diameter and height growth in the lower part of the afforestation at sites with low abiotic stress and that facilitation could only be measured for height growth at sites with high abiotic stress independent of elevation.

Interactions between treeline trees are life-stage and species dependent (Dullinger et al., 2005; Maher & Germino, 2006). Facilitation for example is crucial for seedling establishment but is assumed to have a decreasing effect on growth during later life-stages. Importance of competition can be estimated for *L. decidua* by comparing height growth differences between thinned and unthinned plots described by Ignacio

Barbeito (2013). Those height growth differences indicate highest competition of *L. decidua* during canopy closure, which is after about 20 years. It's also very likely, that low survival of *Pinus mugo* and *Pinus cembra* leads to lower competition effects due to low canopy densities. Considering those findings effects of competition seems to have largest impact on *L. decidua* while affecting *P. mugo* and *P. cembra* at a negligible level.

In relation to other drivers on tree height and diameter growth, interactions seem to have a buffer effect. While competition reduces higher diameter and height growth rates at better side conditions (lower elevation and less abiotic stress), facilitation increases low height growth rates at poor side conditions (high abiotic stress). Facilitation effects on diameter growth rates can hardly be estimated due to a site selection of the thinning experiment with low abiotic stress.

#### 4.1.4. Site specific approach on disentangle driving forces on tree growth

Spatial growth patterns at Stillberg are highly driven by environmental gradients and microsites. By spatially separating effects of various drivers on growth, it was possible to assess their importance dependent on microsite condition and elevation level. The assessment shows qualitatively, that high elevation sites and microsites with late snowmelt suffer from stronger negative impacts on growth.

Table 4: Relative Importance of driving forces on growth compared between elevation levels and microsites. Effects are ranging between negative impact (- -), slight negative impact (-), slight positive impact (+) and positive impact (++)

Driving Forces	Low Elevation		High Elevation	
	Early snowmelt and ridges	Late snowmelt And gullies	Early snowmelt and ridges	Late snowmelt and gullies
Competition	--	-	-	
Facilitation	+	+	+	++
Freezing events	-		--	-
Stem Breakage	--	--	-	--
<i>G. abietina</i>	-	-	--	--
<i>P. infestans</i>	Spatially linked to mature <i>P. cembra</i>			
Cooling	-		--	

## 4.2. Disturbance, climate and year-to-year growth variation

### 4.2.1. Effect, relative importance and temporal trends of different disturbance events

*P. infestans* infections seem to have nearly no negative impact on height growth of *P. cembra*. There is even a trend to higher height growth rates for affected *P. cembras*. These results are not surprising as mainly neighbouring trees of mature *P. cembra* with favourable growth conditions are affected. *G. abietina* caused significant height growth losses for *P. mugo* but only if all needles were affected. Affected *P. mugo* were more often found at sites with late snow melt dates, at higher elevations and at north-exposed gullies. This is according to findings from J Senn (1999) that *G. abietina* profits from later snowmelt due to favourable moist condition under the snow cover. Colder summer temperatures at north-exposed gullies at high elevations could additionally lower the resistance of *P. mugo* against *G. abietina* due to limited accumulation of assimilates. Overall snow fungi seem to have no crucial effect on height growth rates in contrast to the effect on mortality found by Ignacio Barbeito et al. (2013). Infections by snow fungi occur most often when trees are smaller than maximum heights of the snow cover. After a certain tree height, the number of infected trees decreases.

Freezing events affecting *L. decidua* have more severe consequences than similar amounts of damaged needles by snow fungi. The most obvious explanation for those differences in severity of the damage is the difference in affected parts of the trees: while snow fungi particularly infect the lower branches of trees that are not crucial for height growth, freezing events damage mainly newly developing long shoots of *L. decidua* (Rixen et al., 2012) which are more important for height growth. Importance of freezing events decreases with increasing stand closure, as small-scale forest-like climates get less harsh. Effects of frost damage on diameter growth could not be proofed.

Stem damages are most frequent in the last decade for *P. mugo* (29.6%) and only half as frequent for *P. cembra* (13.1%) and *L. decidua* (14.6%). Those relatively high frequencies of stem damage for *P. mugo* – in particular damages in form of “hanger” – seems to be closely linked to their crooked growth form and their exposure to microsites (mainly gullies) prone to disturbance by snow movements. Also hangers often affect *L. decidua* but in contrast to *P. mugo* this is not related to their growth form. In fact those trees are mostly bending down nearly to the ground. Cause is most likely snow pressure acting on tree canopies and bending trees till reaching a certain threshold at which the maximum elasticity of the stem is reached. Breaking is most frequent for *P. cembra*; we suggest that lower elasticity and more brittle wood of *P. cembra* is accountable for a higher probability of stem breakage due to snow movement. Splitting is the least frequent stem damage for all species most likely due to the fact, that splitting occurs mostly instead of breakage for stems with intermediate diameters (15-20cm), as such stems have reduced flexibility, but are still flexible enough to resist breaking (Schönenberger, 1978). As most diameters are below 15cm, splitting is rather rare. Regarding the effects of stem damages it has to be distinguished between *P. mugo* and the other two tree species. Stem damage of *P. mugo* has no impact on height growth rates which can be explained by the fact, that most likely every single tree of *P. mugo* has suffered under stem damage at least once during their life-history and therefore there are no trees without reduced growth rates due to stem damages. For *P. cembra* and *L. decidua* breakage and “hanger” lowered their height growth rate significantly. Uncertainties are higher for breakage, because the effect of breakage on height growth is dependent on the position of the breakage. If large parts are lost by breakage and no adventitious sprouts are left, height growth reduction cannot be recovered (Kajimoto et al., 2002). Stem damage is highly life-stage dependent, Frey (1977) refers to a “second critical age period” after establishment for the trees. While the elasticity of the stem has already declined, the stability against bending of the stem does not yet withstand all impacts. This happens after reaching critical tree diameter from 6 to 14cm (Bebi, Kulakowski, & Rixen, 2009) or in a range of tree heights between 1 and 5 m (Mayer, Ott, & Eiberle, 1991). These findings and average measured stem diameters of 8.3 cm for *P. cembra*, 7.1 cm for *P. mugo* and 8.4 cm for *L. decidua* in 2015 are

consistent with conclusions from Horak (2004) that the critical period for stem damages has begun for the trees at Stillberg and is still going on today as average stem diameter are still beyond 14cm.

#### 4.2.3. Climate signals in tree-rings

It is widely known that ring width from trees growing in high-altitude treeline environments are increasingly sensitive to temperatures with elevation as growth limitation increases (Frank & Esper, 2005; Kulakowski et al., 2006). Diameter growth at high elevations generally reflects temperature variation, whereas at lower elevation annual precipitation variation has higher influence on diameter growth (Briffa, Jones, Schweingruber, Karlén, & Shiyatov, 1996). Compared with the climate sensitivity of height growth rates, diameter is a better measure due to higher error-proneness. Yearly height measurements are on one side hard to measure on the same accuracy level as diameter measures and on the other side they are highly affected by disturbance events like breakage or irregular growth. Loss of climate signal strength can be caused by low frequency noise due to disturbance and growth heterogeneity or by carry-over effects from previous growing season (Babst et al., 2013). Carry-over effects can be found most likely in tree-rings of *Pinus* species with perennial needles. This is also consistent with findings that *P. cembra* has significant lower climate correlation in tree-rings than *L. decidua*, while being exposed to similar rates of disturbance and having both evenly height growth forms.

#### 4.2.3. Effects of year to year climate variation on growth

Year to year climate variation acts independent of microsites on all trees and results in increased or decreased yearly diameter growth rates and most likely also in yearly height growth variation. Climate effects influence continuous effects of elevation and microsites by causing yearly variation without interfering continuous trends, which are more or less constant over time. Regarding interactions between yearly climate variation and disturbance, dendrochronological findings show that disturbance effects are able to suppress climate responses in diameter growth.

Suppression of climate responses is best shown in tree-rings of *P. mugo* where the common signal of climate response is lowest. High disturbance frequencies in *P. mugo* lead to a nonsignificant effect of annual climate factors on growth rates. In contrast to this there is a clear correlations between summer climates and *P. cembra* or *L. decidua*. Best correlations are found for both species with July temperatures and April precipitation sums. Climate effects on diameter growth were highest for *L. decidua* and *P. cembra* and most important for both species was temperature. While temperature was the main driving force of yearly variation due to summer climate, precipitation strengthened the effect of temperature on diameter growth. Diameter growth rates of years with high July temperatures were 19.8% higher than in years with low July temperatures for *L. decidua* and 6.8% higher for *P. cembra*. Comparing between years with high July temperature combined with high April precipitation and years with low July temperature combined with low April precipitation those diameter growth differences increased to 29.8% for *L. decidua* and 19.8% for *P. cembra*. Higher impact on diameter growth rates in *L. decidua* could be related to above mentioned carry-over effects. Climate signals could therefore affect multiple tree-ring widths for *P. cembra* with perennial needles in comparison to *L. decidua* with annual needles. Therefore growing trends are less “sharp” and the importance of noise in the growth series is getting more important for *P. cembra*. Contrary to findings of correlations between summer climates there are no significant correlations between seasonal measurements of average snow height, snow free days or time of snowmelt and yearly diameter or height growth rates from tree-rings ( $p < 0.1$ ). It can be assumed that spatial differences in snow melt and snow heights are more important than overall snow heights.

#### 4.2.4. Importance of disturbance and climate related to microsite conditions

Disturbance events act normally on a narrow spatial extent and damages are associated with a specific number of trees. Disturbance events cause therefore a spatial heterogeneity, which cannot be explained by climatic variation or microclimatic conditions. Kulakowski et al. (2006) highlighted that although strength of climate growth relationships are increasing with elevation, disturbance regimes at high elevations are often limiting and are likely to mask climatic influences on tree growth.

Putting disturbance events in relation to broad-scale effects of climate and effects of microsite conditions, we can think of disturbance as a layer masking parts of the sub layers. This sub layers consist of spatial variability due to heterogeneous microsite conditions and year-to-year climate variability. The importance of this disturbance layer is life stage dependent. While disturbance effects are crucial for the first 40 years, decreasing importance due to decreasing importance of stem damages, freezing events and snow fungi in older life-stages of the trees can be expected. This model of layered effects on tree growth is consistent with findings from the tree-ring approach where the common climate signal for the same tree species are very low (Table 2) especially for *P. mugo* which is most affected by disturbance events. Also the fact that the only years with similar trends in tree-ring growth among species are years with severe disturbance events (e.g. damage due to stem breakage in 1981 and hailstorm in the summer before 1991) supports the hypothesis where disturbance is overlaying climate growth relations. Additional to dendrochronological evidence the relative importance ranking for the last decades shows evidence for higher importance of disturbance than microsite conditions at least for *L. decidua*.

### 4.3. Temporal Approach on disentangle driving forces on tree growth

On a temporal scale, drivers on growth of treeline trees have increasing or decreasing importance linked to their life-stage. Interactions are important during two life-stages; at early stages (e.g. as saplings) facilitation is most important whereas competition is most important during canopy closure. Disturbance is most important during young life stages, biotic disturbance due to snow fungi or browsing is limited to life stages with tree heights near to snow heights. Susceptibility to abiotic disturbance damages like breakage or freezing is highest after canopy closure, when slenderness is highest but flexibility already declined. The meaning of microsities and elevation is decreasing with time while forest-like climates establish and microclimatic conditions mostly depend on densities of tree stands. The only factor which is not temporal dependent is climate sensitivity of the trees like proved by (Esper et al., 2008). Climate sensitivity is constant but gains relative importance after other factors influence declines. In early years, climate signals are often superposed by noise due to mechanical stress.

Overall it can be stated, that interactions of driving forces on growth are most complex during early life-stages and during life stages associated with canopy closure. At those two points disturbance and interactions are most important for tree growth. As the number of driving forces decreases with time, annual climate variation and small differences in growing-season length due to elevation and exposition are likely to become more formative for the next life-stages at Stillberg. Differences in growth rates for the next decade are likely to be linked to temporal shifted life stages: While *L. decidua* has already reached maximum growth rates at lower altitudes, in higher elevations those maximum growth rates are just about to arrive.

#### 4.4. Diameter and height growth

Height and diameter growth were used as main response variables in this analysis because those were the measurements available or at least easy to collect. What we wanted was a measure representative for the amount of invested carbon assimilates as a factor for productivity and vitality of the trees. But height and diameter neglect the fact that a part of biomass is invested in root growth; to be more precise, 11-14% of the biomass of 23 year old Stillberg trees was allocated as roots with no significant differences in altitude (Bernoulli & Körner, 1999). Those findings are consistent with recent findings, that specific root mass and root diameter do not change with altitude (Alvarez-Uria & Körner, 2011). As the root mass ratio is constant for different elevations, it should not lead to an overall misinterpretation of tree responses by only considering above ground measures. Differences between tree height, diameter and leaf ratio are especially conspicuous concerning their response to elevation. While height growth decreases gradually with elevation for all species, only diameter growth of *P. cembra* and *L. decidua* decreases gradually with elevation, while *P. mugo* has only a nonsignificant trend towards smaller diameter growth rates at higher altitudes (Figure 30). Height and diameter growth responses of *P. cembra* and *L. decidua* on elevation are very similar and are responsible for differences of about 1/3 lower growth rates at high altitudes compared with lower elevations. J Paulsen et al. (2000) proposed abrupt changes in diameter growth with elevation, implying threshold effects of temperature, what could not be confirmed in this study. A trend to higher leaf mass ratio with increasing elevation was found for *Pinus* species (Bernoulli & Körner, 1999) which suggests a more stunted morphology with shorter stems, but more branches. We can prove, that height growth is more sensitive to elevation than diameter growth. Based on our data we would also propose, that height growth is more sensitive to microsite conditions, while diameter growth has a slight increased climate sensitivity compared to the height growth.

Considering differences between investment in height and diameter growth and differences in leaf ratio between different elevations only using height growth brings the risk of an overestimation of elevation as main driver of growth especially for *Pinus mugo* and does not consider morphological changes with elevation leading to higher investment in more branches and leaf mass.

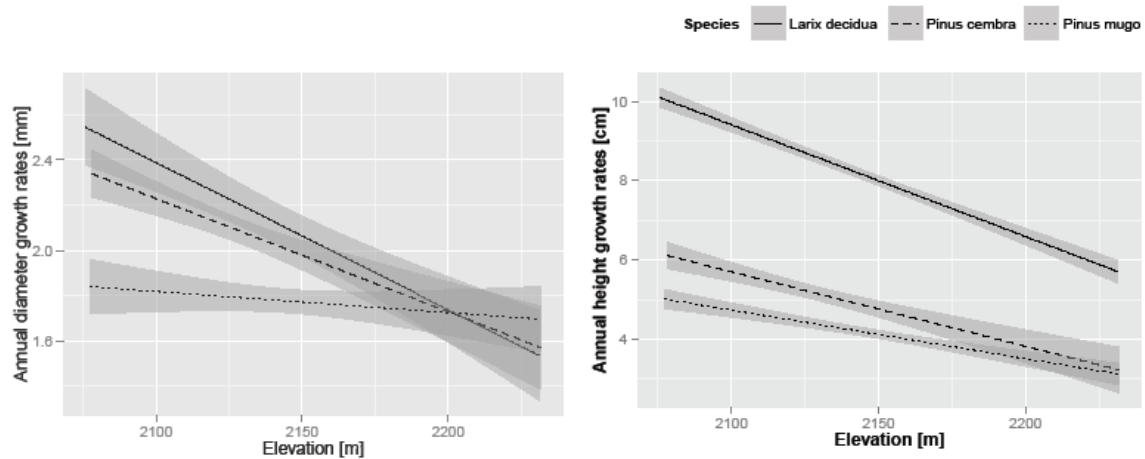


Figure 30: Relationship between elevation and mean annual tree-ring or height growth rates per species. Mean growth rates are from 4 decades of height measurements and 140 tree-ring cores.

## 5. Conclusion

We were able to identify crucial drivers of height and diameter growth at treeline regarding species-specific characteristics as well as spatial and temporal variability. For all species, drivers of height and diameter growth act as a collective with competing or cumulative effects. While altitude, microsites and life-stage dependent growth characteristics affect growth continuously and with long-term (>10years) trends, climate variation and disturbance creates year-to-year variation in growth rates. Disturbance is considered to have a higher impact on yearly growth variation than climate during the first 40 years and especially for the *Pinus* species. This is consistent with findings for *P. mugo* and *P. cembra* of higher noise occurrence and lower climate signals in tree-rings especially.

While the basics interplay between climate, disturbance and microsites is the same for all species, the scope of their effect is specific for each species. Differences in persistence of needles, susceptibility to specific damages and ecological requirements lead to different growth responses for every species. Higher height growth rates of *P. cembra* are linked to microsites with later snowmelt dates although *P. cembra* is already spatially linked to ridge sites with general earlier snowmelt dates. It seems that small differences towards later snowmelt dates are important to provide favourable start conditions for height growth during growing-season, meanwhile very late snowmelt dates are not favourable for height growth in early stages, when snow cover is hardly influenced by tree canopies. We conclude, that later snowmelt dates are on the one hand associated with positive effects like better water and nutrition availability during growing-season but are on the other hand also associated with less topographically exposed microsites. Exposed microsites are mostly associated with higher wind speeds, which seem to have a rather negative effect on height growth of *P. cembra*, especially in the last decade. Damage due to disturbance events is rather rare and has low impact on total height growth of *P. cembra*. In contrast to *P. cembra*'s low susceptibility to disturbances, *P. mugo* is prone to disturbance events (mainly stem damages) and to infections mainly by snow fungus *Gremmeniella abietina*. Disturbance events affecting *P. mugo* are very frequent, reduce height growth to a minimum and lead to creeping growth forms. Therefore disturbance is important for general growth forms of *P. mugo* but isn't appropriate to describe growth differences between single trees, because nearly every tree is affected by disturbance. Relative importance ranks of driving forces on growth of *P. mugo* show highest dependencies to microsite factors guaranteeing warmer microclimates such as radiation, elevation and wind. More upright growth forms with significant higher height and diameter growth rates of *P. mugo* at the opposite south-exposed Luckschalp slope also indicate preferences towards warmer microclimates for *P. mugo*. Disturbance events affecting *L. decidua* are to a considerable degree rarer than for *P. mugo* but have in contrast, a considerable higher effect on growth variation among different trees. About 20% are affected by damages mostly caused by freezing events or stem damages. Damages of *L. decidua* have severe impacts on height growth rates. Frost causes in average nearly 50% losses in the following annual height growth rate and stem breakage and hanger reduces annual height growth rates by 40%. Those severe impacts on height growth are assumed to be caused by the fact, that relative height growth losses can hardly be compensated for *L. decidua* due to shading effects and competition for light. In addition *L. decidua* is the species with highest negative correlations between height growth and elevation for the first 30 years. This can be explained on the one hand by less growth limitations compared to *P. mugo* and on the other hand by higher height growth rates as *P. cembra* resulting in higher possible height differences.

On a temporal scale we were able to quantify the importance of local factors on tree growth for every decade, which gave us the possibility to explore changes in relative importance with ontogeny and species-specific behaviour. Early life-stages seem to be most complex as numerous factors have decreasing importance on growth with time. Microsite conditions and elevation are prime examples for this. As tree stands get closer and canopies close, temperatures are less influenced by elevational gradients and radia-

tion or wind differences. Soil temperatures and tree stand temperatures get decoupled from microtopographical driven temperatures and air temperatures above tree canopies. Disturbance and interactions are found to have two peaks in importance. First during tree establishment, as trees are at the one hand lower than snow cover heights and therefore prone to snow fungi infections and on the other hand are in need of facilitation to compete with adverse impacts which are more severe at early life-stages. Second, disturbance and competition are important during life-stages when tree stands get more dense and the capability to absorb mechanical impacts on stems decreases. The only factors which are constant over time are yearly climate variations. While climate sensitivity is constant over all life-stages, its importance increases with time as other factors loses their impact. Comparing all treeline species, growth drivers of *L. decidua* were most dependent on life-stages because also changes in tree stands are most radical.

We could illustrate that spatial variability defines growth differences between sites. We could illustrate, that high and exposed ridge position are most critical for growth of treeline trees. Heterogeneous microtopography is therefore the main cause for spatial growth variation. This leads to a final conclusion, that even if growth at treeline is on a large spatial scale driven by decreasing temperatures with elevation, interactions between growth and many different drivers are far more complex on a smaller spatial scale.

## 6. References

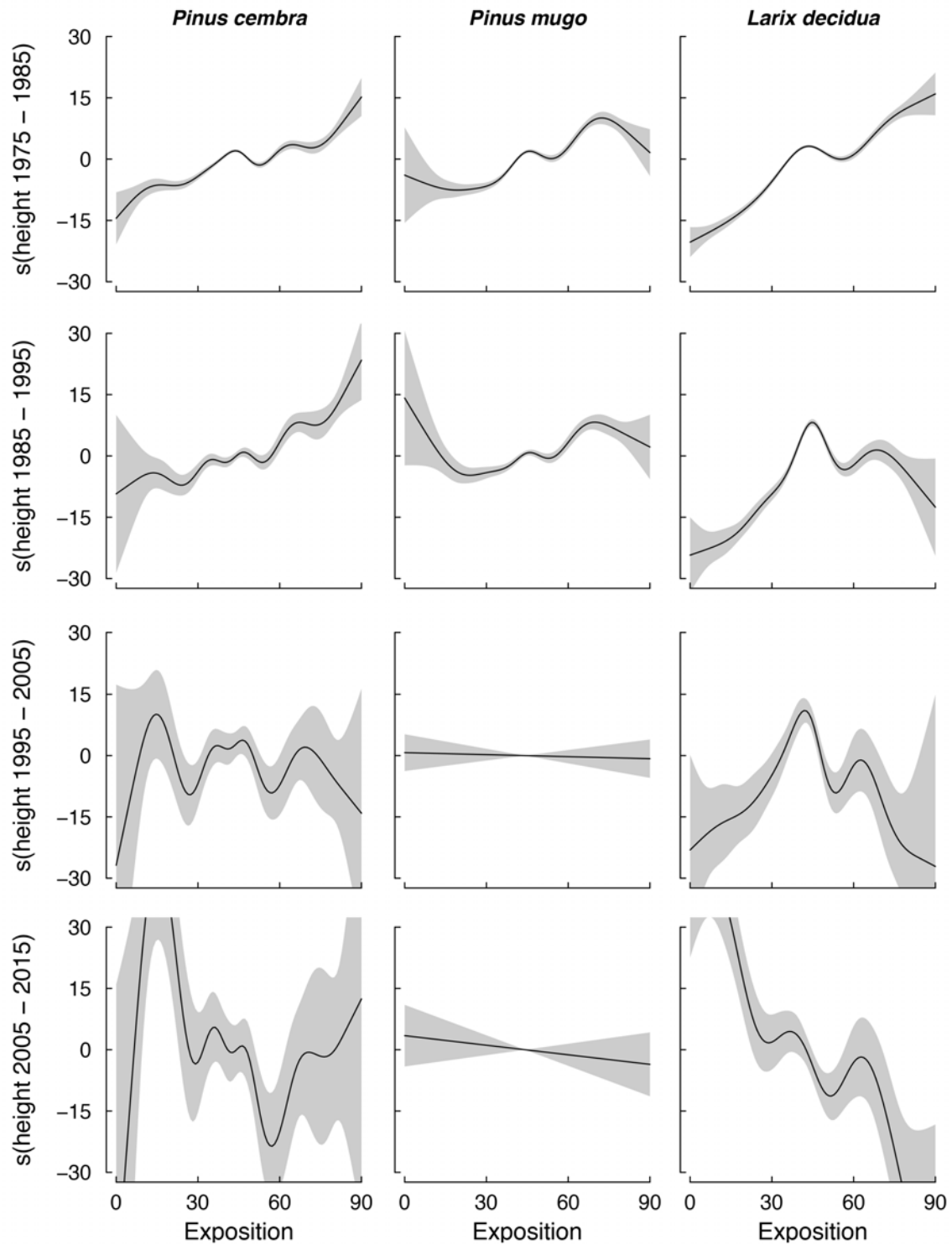
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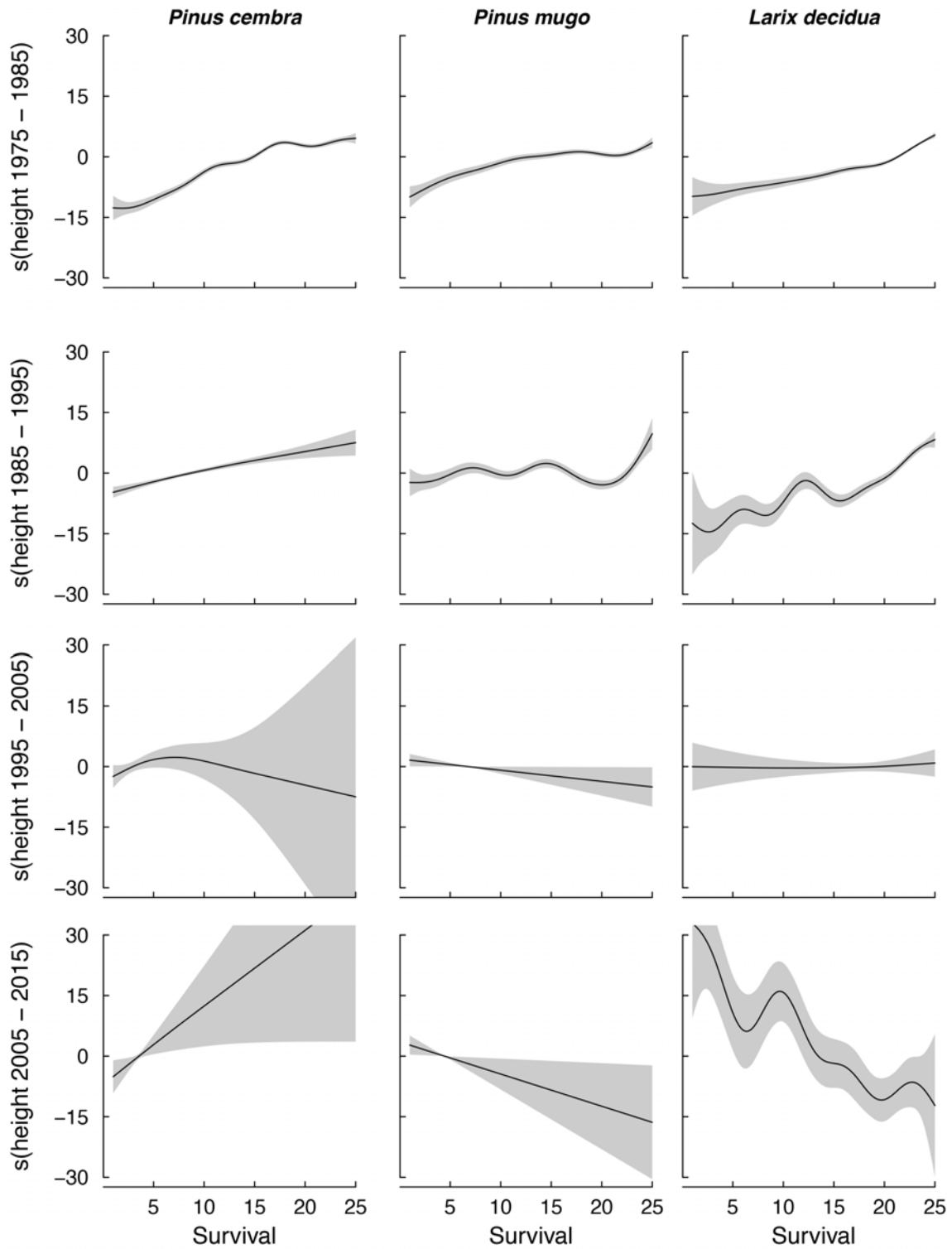
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## 7. Appendix

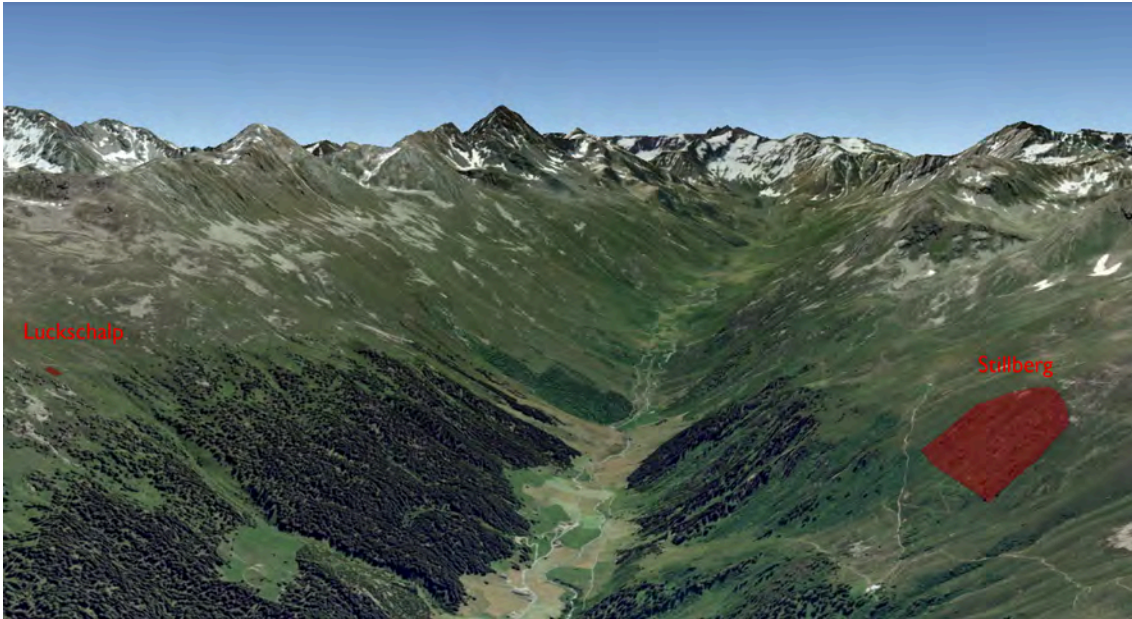
### 7.1. Supplementary figures



Appendix I: GAM functions for the relationship between the fitted height growth values scaled to zero and exposition. The plots include 95% confidence intervals in light grey.



Appendix 2: GAM functions for the relationship between the fitted height growth values scaled to zero and survival. The plots include 95% confidence intervals in light grey.



Appendix 3: Overview Dischmatal with afforestation of Stillberg and reference afforestation Luckschalp

## 7.2. Declaration of originality

I hereby confirm that I am the sole author of the written work here enclosed and that I have compiled it in my own words. Parts excepted are corrections of form and content by the supervisor.

Title of Work:

Growth of treeline trees

a spatial-temporal analysis of driving forces of tree growth at treeline

Authored by:

Simon Andreas Blatter

With my signature I confirm that I have committed none of the forms of plagiarism described in the 'Citation etiquette' information sheet. I have documented all methods, data and processes truthfully. I have not manipulated any data. I have mentioned all persons who were significant facilitators of the work. I am aware that the work may be screened electronically for plagiarism.

Place, date

Signature