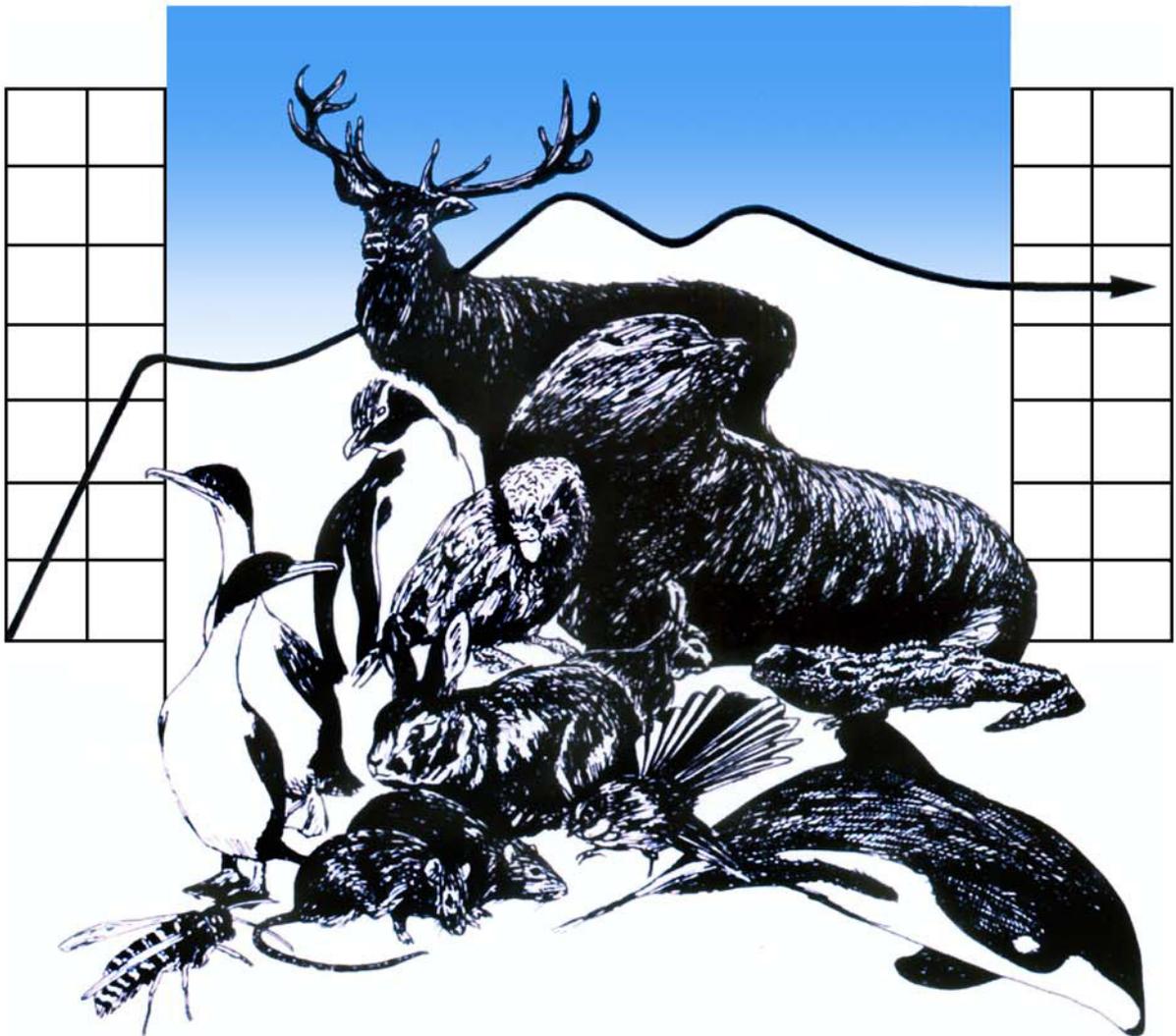


## DEPARTMENT OF ZOOLOGY



## WILDLIFE MANAGEMENT

**Climate sensitivity of *Libocedrus  
bidwillii* along an altitudinal  
gradient in Westland, New  
Zealand: Is the native conifer  
treeline limited by climate?**

**Benjamin Leutner**

A report submitted in partial fulfilment of the  
Post-graduate Diploma in Wildlife Management

**University of Otago**

**2010**

University of Otago  
Department of Zoology  
P.O. Box 56, Dunedin  
New Zealand

Climate sensitivity of *Libocedrus bidwillii* along an altitudinal gradient in Westland, New Zealand: Is the native conifer treeline limited by climate?

Benjamin Leutner\*

Dunedin, April 2010.

Research report for WILM403, University of Otago, Dunedin, New Zealand.

Internship at Landcare Research Ltd. Manaaki Whenua, Lincoln, New Zealand.

P.O. Box 40, Lincoln 7640

08.01.2010 – 19.03.2010

Supervisor: Ellen Gieraad, Landcare Research.

\*Contact: [b.leutner@gmx.de](mailto:b.leutner@gmx.de)

## **Abstract**

New Zealand's treelines are unusually low in global context and globally valid temperature thresholds don't seem to apply here. Understanding the limiting factors is crucial in order to predict possible shifts of the treeline in response to global climate change. In this dendroclimatological study we examined increment cores of *Libocedrus bidwillii* trees on three sites along an altitudinal gradient towards the treeline in Westland, New Zealand. In order to establish the importance of various climatic factors, annual ring width chronologies were related to a local 90 year climate data set by means of correlation function analysis and generalized least square linear model fitting (GLS). No increase in climate sensitivity was found towards the treeline. We found several significant yet weak explanatory factors for the lower two sites, however only very few for the highest, the treeline site. Furthermore we examined the specific leaf area (SLA) of juveniles and adults and found a significant decrease for juveniles but not for adults, which indicates juvenile recruitment as a possibly limiting factor. We conclude that slow-growing and stress tolerant *Libocedrus bidwillii* trees, which define the local treeline, are unable to profit from warmer temperatures unless juvenile recruitment is the limiting factor and is enhanced. Adult trees appear not to be limited by climate variables included in this study, and therefore we can not predict a shift of the native treeline due to climate change.

**Keywords:** *Libocedrus bidwillii*, New Zealand, treeline, dendroclimatology, climate sensitivity, climate change, altitudinal gradient, specific leaf area.

## Contents

Abstract.....	2
Contents.....	3
List of figures.....	4
List of tables.....	4
Introduction .....	5
Methods.....	6
Study site and species.....	6
Field sampling.....	7
Chronology development.....	7
Climate relationships.....	8
Results.....	11
Site and tree characteristics.....	11
Tree ring chronologies.....	12
Growth - climate relationships.....	17
Discussion.....	19
Acknowledgements.....	21
References.....	22

---

## List of figures

Figure 1. Study area with sample sites: Mt. Fox, Westland, New Zealand. ....	6
Figure 2. Climograph of Hokitika.....	9
Figure 3. SLA of juvenile and adult foliage. ....	11
Figure 4. Frequency distribution of annual ring widths.....	13
Figure 5. Summary statistics for mean ring width of all three sites.....	14
Figure 6. Mean sensitivity per site.....	14
Figure 7. Cross-dated ring series of the individual cores.....	15
Figure 8. Standardized and residual master series.....	16
Figure 9. Correlation function results.....	18

## List of tables

Table 1. Summary statistics of sampled trees per site.....	12
Table 2. Ring width statistics of the three sites. ....	12
Table 3. Results of the LME models.....	13
Table 4. Results of the GLS models.....	19

## Introduction

New Zealand's alpine treelines are unusually low compared to others around the world (Körner & Paulsen, 2004). They also coincide with warmer growing season temperatures than expected from globally derived rule-sets (Körner & Paulsen, 2004, Wardle, 2008). Most of the New Zealand treelines are formed by broadleaved *Nothofagus* species. However, in some places, most notably on the West Coast, *Nothofagus* is substituted by slow-growing conifer species, which reach equal altitudes and form the local treeline (Reif & Allen, 1988). Considering that introduced conifer species, such as *Pinus contorta* can establish well beyond the native treeline, the question at hand is: what is limiting the native conifers? While the *Nothofagus* treeline has received some attention (Norton, 1984, Norton & Schönenberger, 1984, Norton, 1985, Cullen et al., 2001), only little is known on New Zealand's native treeline conifers.

Globally, treeline elevation is thought to be limited mainly by climatic conditions, particularly by temperature (Körner & Paulsen, 2004). Dendrochronology is one way to assess the importance of climatic influences on tree performance (Fritts, 1976). It assumes that environmental conditions are reflected in the annual increment growth of tree stems. Thus, by measuring tree ring width throughout the past and relating it to climate records, the sensitivity of trees to climate can be revealed. In order to know whether the treeline is actually determined by climate we can look at the change of climate sensitivity with altitude. If trees are more sensitive to climate towards the treeline, which has been observed in numerous places around the world (Kullman, 1993, Cullen et al., 2001, Savva et al., 2006), it can be concluded that their upper range is limited by climatic factors.

Consequently, if the treeline is determined by climate, trees should be able to take advantage of more favourable growth conditions as expected by climate change and shift or extend their range (Grace et al., 2002). New Zealand has over 600 alpine species, many of which are endemic. It is estimated that a 3°C rise in temperature could result in treelines shifting to higher altitudes, leading to a reduction in the extent of areas above treeline, and an estimated 200 - 300 species becoming extinct in the next 100 years (Halloy & Mark, 2003). This is considered to be one of the most significant climate change impacts to the New Zealand biota.

In order to make reliable predictions of treeline responses to climate change, it is vital to understand the factors and mechanisms that determine treeline altitude in regions such as

New Zealand. Since globally derived climatic rule-sets fail to describe the anomalously low New Zealand treelines it is unsure whether they are actually limited by climate. This study aims to clarify this for the New Zealand conifer treeline in order to improve predictions in regard to climate change.

## Methods

### Study site and species

The study was conducted at and below the treeline at Mt Fox, Westland, New Zealand (Figure 1). The forest can be classified as conifer-broadleaved hardwood dominated forest with typical tree species being *Libocedrus bidwillii* (New Zealand cedar, Cupressaceae) and *Podocarpus hallii* (Hall's Totara, Podocarpaceae) and *Metrosideros umbellata* (Southern Rata, Myrtaceae) (Reif & Allen, 1988). *Nothofagus* is fully absent in these forests. The treeline is never abrupt, and a wide variety of shrub species sometimes form an ecotone of several hundred meters wide (Wardle, 2008). Emergent *Libocedrus bidwillii* are generally the trees that attain the highest altitude. At its upper altitudinal limit at treeline around 1000-1050m a.s.l. *L. bidwillii* is still an erect, 8-12 m tall tree (Haase, 1990). With increasing altitude, *L. bidwillii* dominated forests are replaced by various species of genetically fixed shrubs (Norton, 1983), including *Phyllocladus alpinus*, *Podocarpus nivalis*, *Dracophyllum* spp., *Hebe* spp., *Olearia* spp. (Norton & Schönnenberger, 1984).

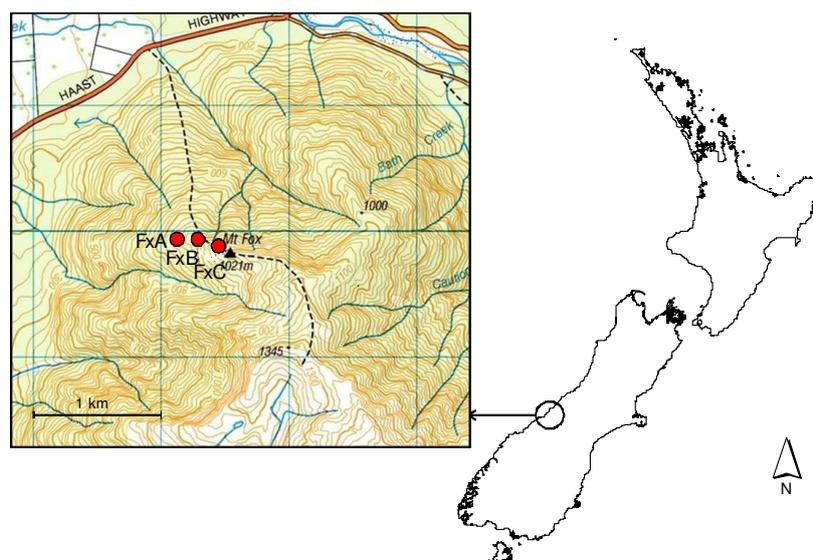


Figure 1. Study area with sample sites: Mt. Fox, Westland, New Zealand.

## Field sampling

We established a transect through treeline at Mt Fox (Figure 1), in January 2010. The transect had three “sites” or altitudinal bands at 850-875 m (FxA), 925-950m (FxB) and 1000-1025m (FxC) . Sampling was restricted to sites near the tree line (approximately 1050m), rather than over a larger elevational range, because *Libocedrus bidwillii*, the studied species, has a small altitudinal range, and rapid changes in climate sensitivity can occur over relatively small elevations (Norton, 1985). At each site, 8-10 of the largest, and presumably oldest, trees were selected for increment core sampling. To reduce the confounding effect of topography on microclimate, we sampled on slopes of a consistent SW-W facing aspect. From each tree, 1–2 cores were extracted at about breast height (1.3m). Diameter at breast height (DBH), tree height, and the height of the first branch were measured for each tree. Furthermore aspect and slope were recorded. In total, 61 cores were collected from 28 living *Libocedrus bidwillii* trees. Additionally leaf samples of juveniles and adults were collected on all sites, scanned, dried and weighed in order to estimate the specific leaf area, i.e. leaf area per unit weight.

## Chronology development

Cores were mounted, sanded, polished, and dated following the standard methods described by Stokes and Smiley (1968). Rings were measured to the nearest 0.01 mm using a binocular microscope, Henson measuring bench, and the MEASURE2X program (VoorTech Consulting, 1999). The program COFECHA v.6.0.6 (Holmes, 2007) was used to cross-date individual tree ring series and identify possible dating or measurement problems. The CrossdateR (Bigler, 1996) package in R v.2.10.1 (R Development Core Team, 2009) was then used to visually examine the quality of the crossdated tree-ring series, and periods flagged in COFECHA as poor cross-dating areas were examined and adjusted as necessary.

Series were standardised by fitting a negative exponential curve through the mean ring-width value using the R package dplR v.1.2.9 (Bunn, 2008). This conservative fitting procedure assumes that most of the individual growth trend is age related growth (biological growth trend) (Biondi & Qeadan, 2008b), and was used to retain as much long-term variation resulting from climate as possible. The standardised ring-width records for each site were then used in the calculation of the mean chronology using the biweight robust mean, also in dplR. A residual chronology was also produced by removing first order autocorrelation (correlation between the growth of one year and that of the previous year) using autoregressive modelling.

All further calculations in this report are based on the residual chronology, unless otherwise stated. For each of the three sites one chronology was developed from the 7 trees with the highest inter-correlation. This allowed us to disregard cores which did not correlate well or were assumed to contain error, e.g. due to rotten sections. The chronologies were compared for the period 1850 to 2009. However, owing to intermittent temperature data until c. 1900 and a period of uncertainty on the cross-dating of several series all further analyses were conducted for the time from 1918 to 2009.

The statistical quality of each master series was assessed by calculating the expressed population signal (EPS), i.e. “the degree to which it represents the hypothetical perfect noise-free chronology” (Storch & Navarra, 1999). This was done using the ‘rwl.stats’ function in the dplR package. Furthermore the mean sensitivity of the chronologies was calculated using the ‘rwl.stats’ function of the same package. Mean sensitivity is a measure of year to year variability which indicates the strength of the climate signal present in the chronologies (Douglas 1928, cited by Biondi & Qeadan, 2008a).

Relationships of site properties, such as height of the trees and altitude were examined using correlation matrices and linear model fitting. In the special case of mean ring width linear mixed effect models were used (‘lme’ in the R package ‘nlmer’ (Pinheiro et al., 2009)), which allowed for non-independent samples in a nested design (included as random effects), i.e. two cores per tree as well as unequal variances due to temporal autocorrelation structure (lag 1). Due to non-uniform distribution of the residuals and strongly skewed frequency distribution (Figure 4), the ring widths were log-transformed in advance.

### **Climate relationships**

Climate data was obtained from NIWA Cliflo database (NIWA, 2010). The nearest climate station with long-term available data is Hokitika (1866-2009); 156km north of Mt. Fox at 39m a.s.l. Monthly climate data included total precipitation and mean temperature, minimum temperature, average cloud cover and number of frost days. Based on this data further indices were derived such as the sum of growing degree days, i.e. the sum of all daily temperatures that were above 5°C and mean temperature in the three warmest months. The 30 year standard climograph for Hokitika is plotted in Figure 2. Precipitation is high throughout the year, owing to the topographic situation of the site along the Southern Alps as an orographic cloud barrier. Temperature remains moderate, due to the typical dampening effect of a maritime climate.

We assume that the climate characteristics do not differ from low-land Hokitika station to our sites at higher elevation, apart from the absolute value of course. We compared 2009 1.5m air temperature from a data logger at a nearby treeline with the lowland climate station data. For monthly mean temperature we observed near perfect correlation of  $r=0.985$ , therefore we can be confident that the Hokitika weather station temperature data are relevant for use in this study. However, whether this holds true for precipitation data remains unknown and there might well be a difference, especially if rain is falling from low altitude clouds.

The tree-ring chronologies were then related to monthly precipitation and monthly mean temperature using the R package *bootRes* (Zang, 2009). First, correlation function and response function analyses were conducted to examine the relative importance of all included factors (Blasing et al., 1984). In both cases, explanatory factors were added as time-ordered series of monthly values and then related to the tree-ring series. 18 months, from previous January to current June, were included in the analyses, since climate in the previous growing season may also have an effect on the current year's growth. Correlation function results in estimates of Pearson's product-moment correlation coefficients, while response functions are multivariate estimates from a principal component regression model (Biondi & Waikul, 2004). In order to increase statistical robustness both functions were bootstrapped using 1000 bootstrap samples. Generally, correlation function analysis is considered more conservative regarding significant results (Blasing et al., 1984, Biondi & Waikul, 2004). Although this was not the case in our study, we report the results of the correlation functions, as they are generally considered less error-prone (Blasing et al., 1984).

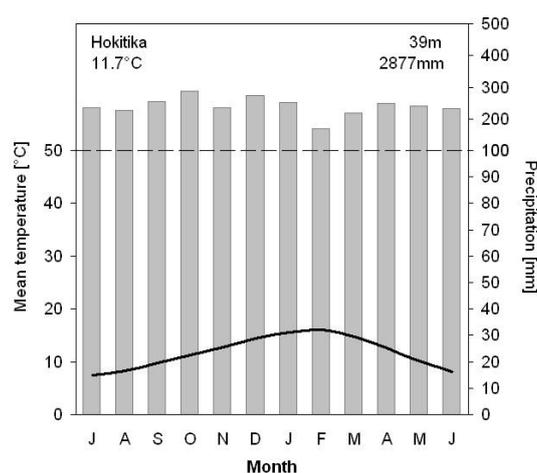


Figure 2. Climograph of Hokitika. 30 year averages derived from NIWA Cliflo (2010) data .

In addition, we examined annual-scale relationships with all climate variables by generalized least square linear model fitting ('gls' in the R package nlme (Pinheiro et al., 2009)). In contrast to generalized linear models, GLS allow for unequal variance, sample size & non-independent samples. The model was run using the maximum likelihood algorithm and specifying lag -1 autocorrelation structure. Stepwise backward model selection was then applied to identify the best significant model, where at each step the variable with the highest non-significant ( $\alpha=0.05$ ) p-value was dropped.

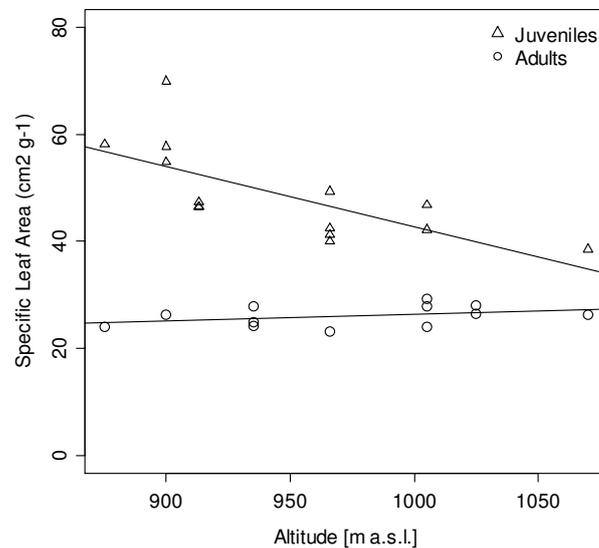
All mean values throughout the study are reported including their respective standard error.

## Results

### Site and tree characteristics

The sampled trees of which the corer had hit the centre revealed an average age of  $343 \pm 22$  years with the oldest tree dating back as far as 1388 AD. Both mean height of the tree (using linear models,  $R^2_{\text{adjusted}} = 0.82$ , slope =  $-0.05$ ,  $p < 0.001$ ) and mean height of the first branch ( $R^2_{\text{adjusted}} = 0.65$ , slope =  $-0.05$ ,  $p < 0.001$ ) decreased with increasing altitude. As expected the diameter at breast height (DBH) was linearly proportional to age ( $R^2_{\text{adjusted}} = 0.53$ , slope =  $0.1$ ,  $p < 0.001$ ) and height ( $R^2_{\text{adjusted}} = 0.47$ , slope =  $4.1$ ,  $p < 0.001$ ) of the tree. Further summary statistics can be found in Table 1.

As can be seen in Figure 3, the specific leaf area (leaf area per unit weight) of juvenile plants decreased significantly with altitude ( $R^2_{\text{adjusted}} = 0.45$ , slope =  $-0.11$ ,  $p < 0.01$ ). For foliage from adult trees, however, this did not hold true. Here, there was no significant change in SLA with altitude ( $R^2_{\text{adjusted}} = 0.05$ , slope =  $0.01$ ,  $p > 0.1$ ).



**Figure 3. Specific leaf area index of juvenile and adult foliage along an altitudinal gradient with corresponding linear trend line.**

**Table 1. Summary statistics of sampled trees per site. Arithmetic mean  $\pm$  standard error, where applicable.**

	FxA	FxB	FxC	FxD
# Trees*	8 (7)	10 (7)	8 (7)	1 (0)
# Cores*	19 (14)	18 (13)	21 (13)	2 (0)
Altitude [m a.s.l.]	866.5 $\pm$ 1.5	940.8 $\pm$ 2.1	1012.0 $\pm$ 2.2	1068
Mean Height [m]	13.6 $\pm$ 0.3	9.9 $\pm$ 0.4	7.2 $\pm$ 0.1	4.5
Height First Branch [m]	5.8 $\pm$ 0.2	4.1 $\pm$ 0.3	2.9 $\pm$ 0.2	0.5
Mean DBH [m]	65.3 $\pm$ 2.6	35.8 $\pm$ 2.7	47.2 $\pm$ 2.0	27
Mean Slope [°]	12.3 $\pm$ 1.6	31.1 $\pm$ 3.4	21.8 $\pm$ 2.7	52
Mean Aspect [°]	230.5 $\pm$ 4.1	314.2 $\pm$ 10.1	279.5 $\pm$ 9.9	350
Mean Age [yr]	427 $\pm$ 33	318 $\pm$ 24	403 $\pm$ 32	144

\*Total number of samples with numbers of samples used for chronology in brackets

### Tree ring chronologies

The standardized time series of all cross-dated cores over the period from 1850 to 2008 were visualized in Figure 7. Especially the diverse spectrum of responsiveness was apparent; e.g. core Fx26 vs. Fx22 in Figure 7c). Series inter-correlation, i.e. correlation with a master series assembled of the remaining cores, was moderate ( $0.52 \pm 0.06$ ,  $0.39 \pm 0.05$  and  $0.44 \pm 0.03$  for FxA, FxB and FxC respectively (Table 2).

The expressed population signal (EPS), a measure of sample correlation with its population, was used as a criterion for the quality of the chronology. The commonly applied criterion, brought forward by Wigley et al. (1984), where  $EPS > 0.85$ , was fulfilled for all three sites ( $0.912$ ,  $0.850$  and  $0.851$  for FxA, FxB, and FxC respectively).

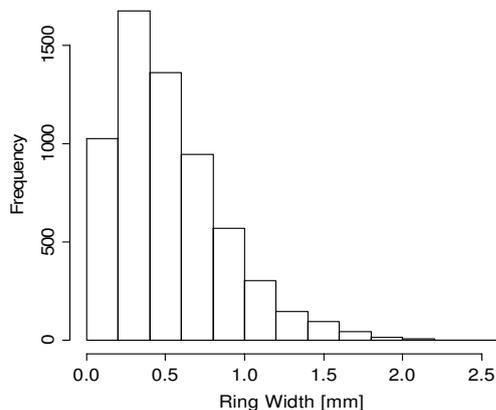
**Table 2. Ring width statistics of the three sites FxA, FxB and FxC. MeanRW: mean ring width, SD: standard deviation of ring width; MS: mean sensitivity; SI: series inter-correlation; AR: average 1<sup>st</sup> order autocorrelation, EPS: expressed population signal.**

Tree	MeanRW [mm]	SD [mm]	MS	SI	AR	EPS
FxA	0.59	0.30	0.24	0.52	0.80	0.91
FxB	0.48	0.24	0.23	0.39	0.79	0.85
FxC	0.49	0.25	0.26	0.44	0.78	0.85

We observed strong 1st order autocorrelation typically around 0.8, which was subsequently removed. That is to say growth in the previous year explained 80% of growth in the following year (Table 2). The effect of removal of 1<sup>st</sup> order autocorrelation is shown in Figure 8, where Figure 8a) shows the final master chronology of each site, standardized by removal of a possible negative exponential trend or the mean respectively and Figure 8b) shows the residual chronology on which further analysis was based. Optical examination showed a good concordance of the three master chronologies both in the standardized and in the residual chronologies.

The frequency distribution of the ring widths at all three sites was considerably skewed towards smaller ring widths. A histogram pooling FxA, FxB and FxC is plotted in Figure 4. It clearly shows that very small ring widths were most common, while there were only very few years showing a major increase in growth.

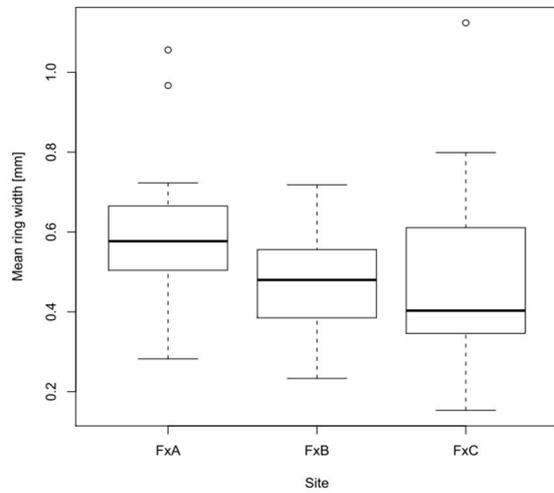
Although there was a decreasing trend in average mean ring widths with altitude, heterogeneity within sites increased (Fig 5) and thus the difference between sites became non-significant, as reflected in the results of the linear mixed-effects models (Table 3). Mean sensitivity of the trees was low (Fritts, 1976) with an average of  $0.26 \pm 0.01$  across sites. Also, it didn't change significantly with increasing altitude ( $R^2_{\text{adjusted}} = -0.03$ , slope =  $8.6E-05$ ,  $p > 0.1$ , Figure 6).



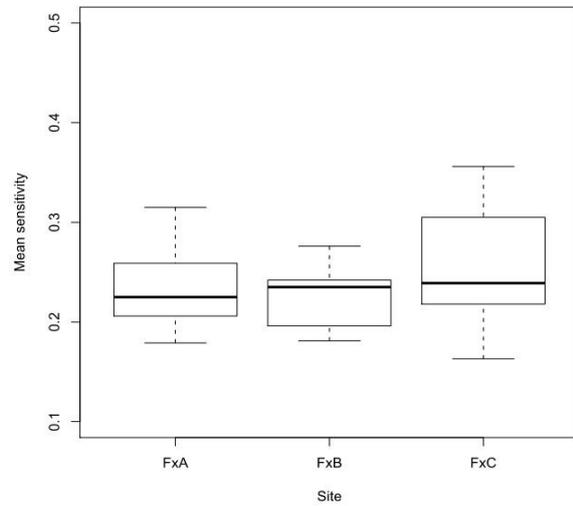
**Figure 4. Frequency distribution of annual ring widths of pooled data for all used cores across sites.**

**Table 3. Results of the LME models. ~Site: model including site as factor, ~1 : null model.**

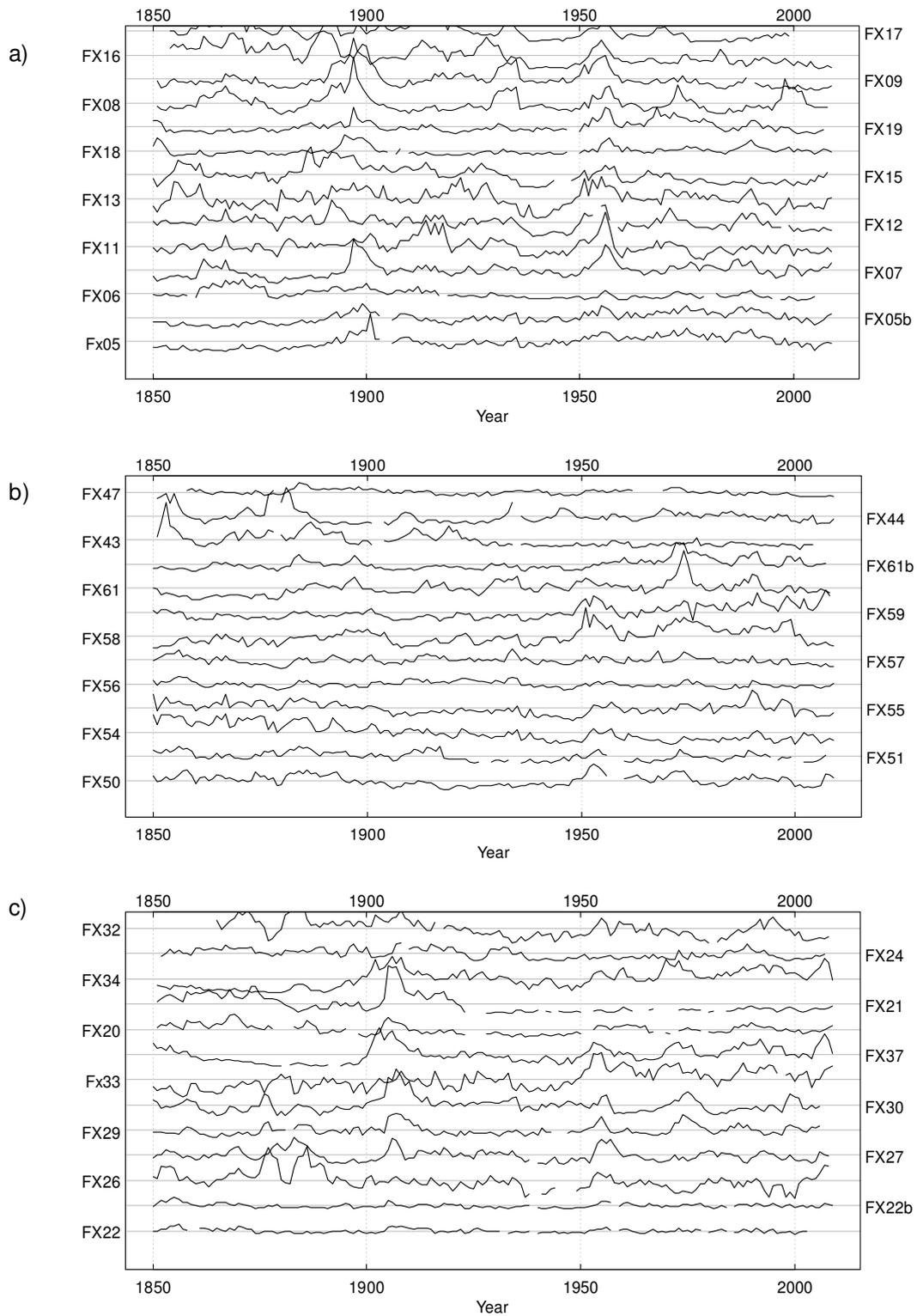
Model	Df	logLik	AIC	$\Delta$ AIC	Rank	P
~ 1	6163	-2142.603	4295.206		1	
~ Site	6163	-2141.741	4297.482	2.276	2	0.422



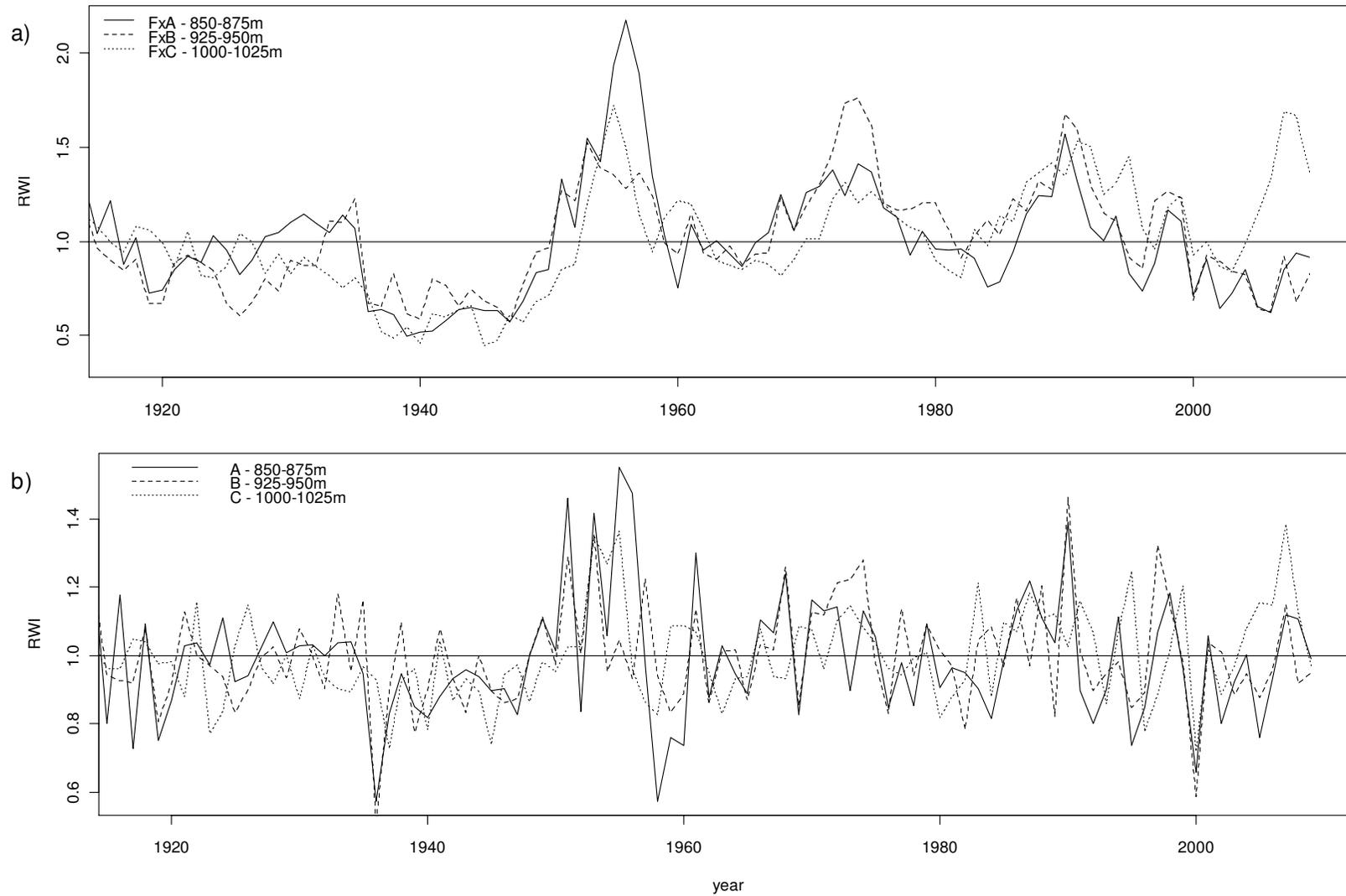
**Figure 5. Summary statistics for mean ring width of all three sites with FxA being the lowest and FxB the highest site. Horizontal bar: median, box: 1<sup>st</sup> and 3<sup>rd</sup> quartiles, whiskers: maximum and minimum respectively, dots: outliers.**



**Figure 6. Mean sensitivity per site. Horizontal bar: median, box: 1<sup>st</sup> and 3<sup>rd</sup> quartiles, whiskers: maximum and minimum respectively.**



**Figure 7. Cross-dated ring series of the individual cores which were then used to derive one master series per site. Ring width is standardized on the mean ring width per core. a) FxA b) FxB, c) FxC.**



**Figure 8. a) Standardized master series of all three sites, obtained by removal of negative exponential trend b) Residual master series of all three sites obtained from a) but removed 1<sup>st</sup> order auto correlation**

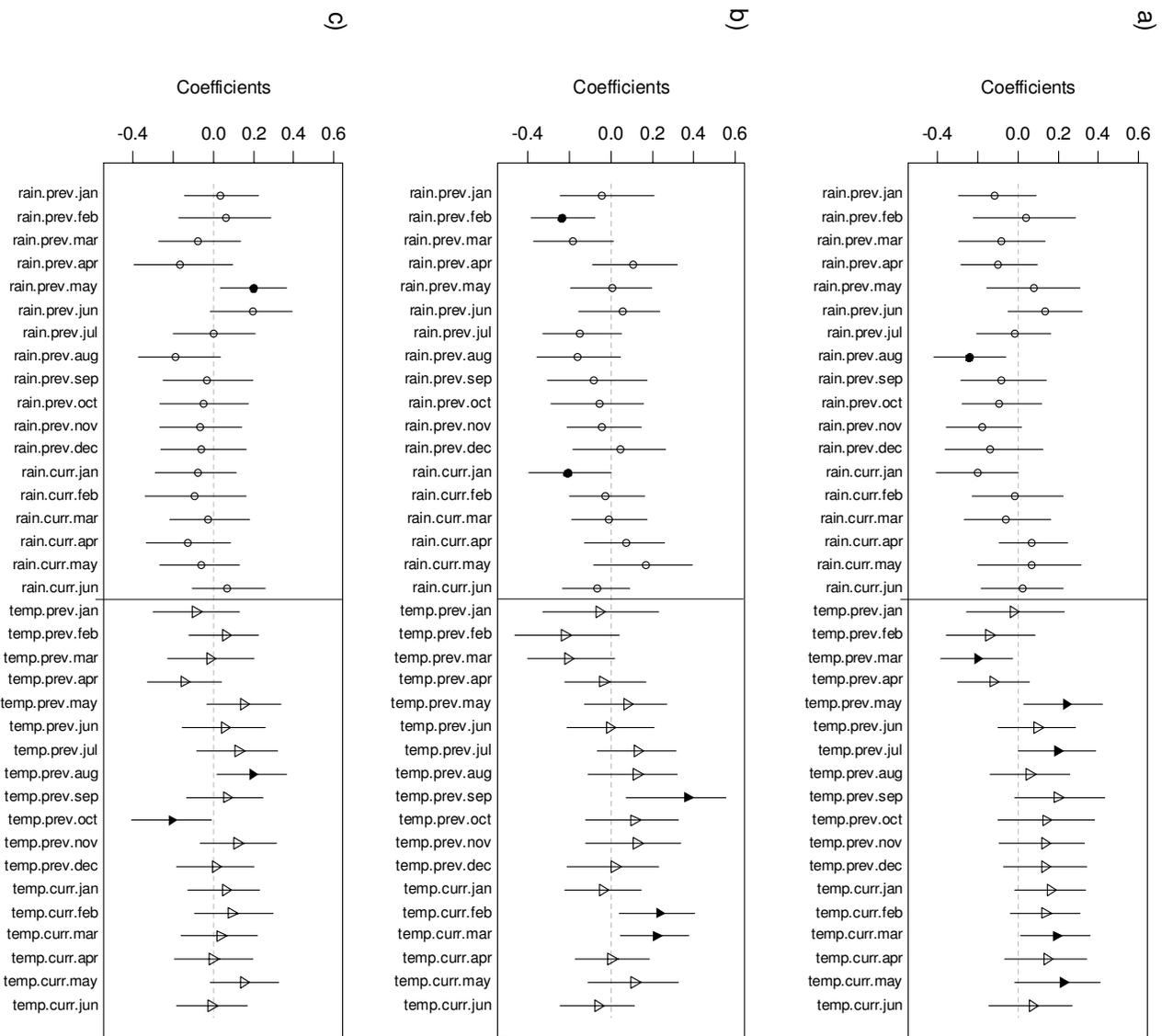
## **Growth - climate relationships**

The correlation functions showed several significant yet low correlation coefficients between the residual tree ring widths and climate data (Figure 9). For the lowest site FxA rainfall during current growing year had consistently negative correlation coefficients, however, only winter rainfall in August was significant. Moreover, correlation coefficients of mean temperature at the end of the previous growing period indicated a negative relationship with growth, but were significant only for mean temperature in the previous March. In addition, mean temperature was positively correlated with growth throughout the growing year. Correlations for mean temperature in previous winter's May and July as well as in March and May of the current growing season were significant.

On the mid altitude site FxB tree growth was significantly negatively correlated both with rainfall in February of the previous growing season and with mean temperature in previous March. Temperature had mostly positive coefficients, which became significant in September, March and April of the current growing season.

In contrast to the lower sites, the highest altitude site FxC showed positive correlation with rainfall in preceding May. Mean temperature in August was positively correlated, while mean temperature in October showed a significant negative correlation with tree growth.

The generalized least square models, which were used to test for the influence of a wide range of variables on an annual scale, consistently eliminated many climate variables, including number of frost days, growing degree days and average cloud cover. After removal of first-order autocorrelation for site FxA, only annual rainfall and mean temperature remained as significant factors (Table 4). Going higher up in altitude for site FxB only mean temperature remained significant, whereas for the highest site FxC no significant explanatory factor was left (Table 4). Incorporating significant factors from correlation function analysis into the initial factorial design of the GLSs did not alter the outcome, since the respective factors were removed during model selection procedure as non-significant.



**Figure 9. Correlation of the current function relating residual ring widths with monthly mean temperature and precipitation of the current growing year and the previous growing season. a) FxA, b) FxB, c) FxC. Circles denote correlation coefficients for precipitation, triangles represent temperature. Filled symbols denote significant coefficients ( $\alpha=0.05$ ), error bars show 95% confidence intervals.**

**Table 4. Results of the GLS models on residual chronologies (RWres) and climatic factors: significant factors. Rain: total annual precipitation, MeanT: mean annual temperature.**

Site	Model	df	Factor	$\beta$	SE	t
FxA	RWres ~ Rain + MeanT	92	Rain	-8.9E-5	4.7E-5	-2.40*
			MeanT	0.085	0.032	2.74**
FxB	RWres ~ MeanT	92	MeanT	0.091	0.030	3.03**
FxC	-	92	-	-	-	-

\*p &lt; 0.05 \*\*p &lt; 0.001

## Discussion

Along an altitudinal gradient on the West Coast of New Zealand, the physiognomic appearance of *Libocedrus bidwillii* trees resembled the commonly found trend in forests towards treeline: decreasing total tree height and height of branching with increasing altitude (e.g. Jarvis et al., 1989, Paulsen et al., 2000, Massaccesi et al., 2008).

However, this study suggests that this decrease in stature doesn't take place at the cost of annual growth (measured by mean annual ring width), which remained constantly low throughout the altitudinal gradient (Figure 5, Table 2). This reinforces the findings of Paulsen et al. (2000) who found no decrease in ring width for the conifers *Pinus cembra* and *Picea abies* along an altitudinal gradient towards treeline in the European Alps.

Generally, specific leaf area (SLA) decreases with altitude as environmental stress increases and leaves are becoming more robust, i.e. thicker and denser (Körner et al., 1986, Jan et al., 2009). However, in this study, only the SLA of juvenile plants decreased with altitude, while that of adult trees remained constant (Figure 3). Our results suggest that juvenile trees might actually be more sensitive to climate than adults. Hence, juvenile recruitment can not be excluded as limiting factor towards the upper end of the range. However, once trees are established, they perform equally well on all sites with slow and highly inert growth rates. This result calls for examining juvenile chronologies across the same altitudinal range in a future study to shed light on whether juvenile growth towards the tree-line becomes more sensitive to climate. Should this be the case, range shifts or extensions with increasing temperatures could take place through increased juvenile recruitment.

The finding that mean sensitivity does not increase with altitude (Figure 6) contrasts with the expected pattern, where trees are most sensitive to environmental conditions along their range limits (Fritts, 1976, Kullman, 1993, Cullen et al., 2001), however, it is not unique (Wang et al., 2005, Peng et al., 2008).

This lack of sensitivity towards the upper end of the range is also revealed by the growth-climate relationships, which showed some correlation at lower altitude yet almost none at the highest site (Table 4, Figure 9). Correlation function analysis revealed a few significant months for rainfall and temperature (Figure 9). Even though significant, correlation coefficients were low at all times. Positive temperature anomalies in late winter and spring seem to favour growth in the following growing period at all three sites. Additionally, warmer temperatures in February and March for site FxA and FxB are positively correlated with growth. Summarizing, this could be interpreted as an overall positive response of growth to a prolonged growing season. However, including the number of growing degree days in the models, as an indicator of growing season length, does not yield significant results. GLS models are considered less robust than the bootstrapped correlation function, but the lack of bootstrapping would likely result in more significance in the GLS models and a remaining non-significant effect of growing season length on annual width increment.

The models showed that total annual precipitation is negatively proportional to growth at the lowest site but not higher up (Table 4). This could possibly be due to water logging in the soil, which is unlikely on steeper slopes at higher elevation, or due to reduced irradiation caused by increased cloud cover during rain events. Alternatively, there may be increased precipitation at lower altitudes only, if cloud base is just above the lowest site. Percentage cloud cover data was available from Hokitika (and was non-significant in our analyses), but owing to lacking cloud height registration this cannot be tested.

Mean annual temperature seems to have the same positive growth effect at sites FxA and FxB, however not at FxC at the upper range limit (Table 4). Again, this suggests that climate sensitivity towards the upper end of the range is even decreasing. Thus, given the presented data, it is unlikely that adult *Libocedrus bidwillii* trees will be able to profit from warmer temperatures or changing rainfall regimes at the tree line, yet juveniles may show a different pattern. However, this does not exclude an increase in growth or range shifts and extensions owing to other environmental changes. Increased partial pressure of atmospheric CO<sub>2</sub> for example has been reported to stimulate conifer growth in the Swiss Alps (Handa et al., 2006).

There are also further environmental factors which were not considered but could play an important role near treeline, such as disturbance regime, especially wind and snow or soil fertility (Daniels & Veblen, 2003).

Given the current study, it has to be concluded that either climatic conditions are not the limiting factor for *Libocedrus bidwillii* or that the species is simply growing so slowly to endure this harsh environment that it is unable to respond to improved conditions such as increasing temperature. The latter has been conceptualized by Grime (1974) as a “stress-tolerant strategy”: stress tolerators live in extreme environments and scarcely available resources, where productivity and reproduction are very low, but individuals cope with it by growing slowly and being long-lived. This could apply to other slow-growing New Zealand tree-line conifer species like *Podocarpus hallii*, *Halocarpus biformis* or *Phyllocladus alpinus* as well. Further studies will examine this in detail. Considering the evidence presented, a range shift or extension of *Libocedrus bidwillii* due to climate change is unlikely, unless it enhances juvenile recruitment. However fast and high growing invasive species like *Pinus contorta* stand by to make for a shift of the New Zealand tree-line, leaving the native tree-line behind.

## **Acknowledgements**

I want to thank Ellen Geraad for being a superb supervisor, for steady and engaged input, most interesting discussions and for being a great field work companion.

---

## References

- Bigler C. (1996) CrossdateR - A visualization tool to assess the quality of crossdated tree-ring series. [http://www.fe.ethz.ch/people/cbigler/crossdater/index\\_EN](http://www.fe.ethz.ch/people/cbigler/crossdater/index_EN)
- Biondi F., Qeadan F. (2008a) Inequality in Paleorecords. *Ecology*, **89**, 1056-1067.
- Biondi F., Qeadan F. (2008b) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, **64**, 81-96.
- Biondi F., Waikul K. (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303-311.
- Blasing T.J., Solomon A.M., Duvick D.N. (1984) Response functions revisited. *Tree-Ring Bulletin*, **44**, 1-15.
- Bunn A.G. (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**, 115-124.
- Cullen L.E., Palmer J.G., Duncan R.P., Stewart G.H. (2001) Climate change and tree-ring relationships of *Nothofagus menziesii* tree-line forests. *Canadian Journal of Forest Research*, **31**, 1981-1991.
- Daniels L.D., Veblen T.T. (2003) Regional and Local Effects of Disturbance and Climate on Altitudinal Treelines in Northern Patagonia. *Journal of Vegetation Science*, **14**, 733-742.
- Fritts H.C. (1976) *Tree Rings and Climate*, London, Academic Press.
- Grace J., Berninger F., Nagy L. (2002) Impacts of Climate Change on the Tree Line. *Ann Bot*, **90**, 537-544.
- Grime J.P. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26-31.
- Haase P. (1990) Environmental and Floristic Gradients in Westland, New-Zealand, and the Discontinuous Distribution of *Nothofagus*. *New Zealand Journal of Botany*, **28**, 25-40.
- Halloy S.R.P., Mark A.F. (2003) Climate-Change Effects on Alpine Plant Biodiversity: A New Zealand Perspective on Quantifying the Threat. *Arctic, Antarctic, and Alpine Research*, **35**, 248-254.
- Handa I.T., Körner C., Hattenschwiler S. (2006) Conifer stem growth at the altitudinal treeline in response to four years of CO<sub>2</sub> enrichment. *Global Change Biology*, **12**, 2417-2430.
- Holmes R.L. (2007) COFECHA. v.6.0.6.  
<http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html>
- Jarvis P.G., Grace J., Hutchings N. et al. (1989) Tree Lines [and Discussion]. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **324**, 233-245.

- Jan Q., Keming M., Yuxin Z. (2009) Leaf-trait relationships of *Quercus liaotungensis* along an altitudinal gradient in Dongling Mountain, Beijing. *Ecological Research*, **24**, 1243-1250.
- Körner C., Bannister P., Mark A.F. (1986) Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia*, **69**, 577-588.
- Körner C., Paulsen J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713-732.
- Kullman L. (1993) Tree Limit Dynamics of *Betula pubescens* ssp. *tortuosa* in Relation to Climate Variability: Evidence from Central Sweden. *Journal of Vegetation Science*, **4**, 765-772.
- Massaccesi G., Roig F.A., Pastur G.J.M., Barrera M.D. (2008) Growth patterns of *Nothofagus pumilio* trees along altitudinal gradients in Tierra del Fuego, Argentina. *Trees - Structure and Function*, **22**, 245-255.
- Niwa (2010) CliFlo: NIWA's National Climate Database on the Web. Retrieved 01.03.2010 from <http://cliflo.niwa.co.nz>
- Norton D.A. (1983) Population-Dynamics of Subalpine *Libocedrus-Bidwillii* Forests in the Cropp River Valley, Westland, New-Zealand. *New Zealand Journal of Botany*, **21**, 127-134.
- Norton D.A. (1984) Tree-growth-climate relationships in subalpine *Nothofagus* forests, South Island, New Zealand. *New Zealand Journal of Botany*, **22**, 471-481.
- Norton D.A. (1985) A dendrochronological study of *Nothofagus solandri* tree growth along an elevational gradient, South Island, New Zealand. In: *Establishment and Tending of Subalpine Forest: Research and Management*. . (eds Turner H., Tranquillini W.) pp Page. Birmensdorf, Switzerland, Swiss Federal Institute of Forestry.
- Norton D.A., Schönenberger W. (1984) The Growth Forms and Ecology of *Nothofagus-Solandri* at The Alpine Timberline, Craigieburn Range, New-Zealand. *Arctic and Alpine Research*, **16**, 361-370.
- Paulsen J., Weber U.M., Körner C. (2000) Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arctic Antarctic and Alpine Research*, **32**, 14-20.
- Peng J.F., Gou X.H., Chen F.H., Li J.B., Liu P.X., Zhang Y. (2008) Altitudinal variability of climate-tree growth relationships along a consistent slope of Anyemaqen Mountains, northeastern Tibetan Plateau. *Dendrochronologia*, **26**, 87-96.
- Pinheiro J, Bates D., Debroy S, Sarkar D., Team R.D.C. (2009) *Linear and Nonlinear Mixed Effects Models - R package version 3.1-96*. v.R package version 3.1-96.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. v.2.9.1. <http://www.R-project.org>

- Reif A., Allen R.B. (1988) Plant communities of the steepland conifer-broadleaved hardwood forests of Central Westland, South Island, New Zealand. *Phytocoenologia*, **16** 145 - 224
- Savva Y., Oleksyn J., Reich P.B., Tjoelker M.G., Vaganov E.A., Modrzynski J. (2006) Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland. *Trees-Structure and Function*, **20**, 735-746.
- Stokes M.A., Smiley T.L. (1968) *An Introduction to Tree-Ring Dating*, Chicago, University of Chicago Press.
- Storch H.V., Navarra A. (eds) (1999) *Analysis of Climate Variability - Applications of Statistical Techniques*, Berlin, Springer.
- Voortech Consulting (1999) *Measure2X.v.3*.
- Wang T., Ren H.B., Ma K.P. (2005) Climatic signals in tree ring of *Picea schrenkiana* along an altitudinal gradient in the central Tianshan Mountains, northwestern China. *Trees-Structure and Function*, **19**, 735-741.
- Wardle P. (2008) New Zealand forest to alpine transitions in global context. *Arctic Antarctic and Alpine Research*, **40**, 240-249.
- Wigley T.M.L., Briffa K.R., Jones P.D. (1984) On the Average Value of Correlated Time Series, with Applications in Dendroclimatology and Hydrometeorology. *Journal of Applied Meteorology*, **23**, 201-213.
- Zang C. (2009) *bootRes: Bootstrapped Response and Correlation Functions.v.0.2*.