

**Recent influence of climate and environment on
coniferous tree growth at treelines of the Northeastern
Tibetan Plateau**

**- divergent growth trends question traditional
dendroclimatology?**

Inauguraldissertation
zur
Erlangung des akademischen Grades
doctorum rerum naturalium (Dr. rer. nat.)
an der Mathematisch-Naturwissenschaftlichen Fakultät
der
Ernst-Moritz-Arndt-Universität Greifswald

vorgelegt von
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geboren am 30.11.1980
in Ningxia

Greifswald
06. March 2011

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Tag der Promotion: 12/10/2011

Abstract

Forests cover ~30% of the land surface and store ~45% of terrestrial carbon, contribute ~50% of terrestrial net primary production and can sequester large amounts of carbon annually. Recent climate change has affected the forest system comprehensively. Northern hemisphere elevational treelines are considered as a key environment for monitoring the effects of current anthropogenic climate change. Moreover, trees from these areas are also widely employed in paleo-climate reconstructions since it is generally assumed that the tree growth climate relationships can be calculated by an approximate simple linear regression. The stability of the tree growth climate relationship under current scenario is crucial for all tree ring based climate researches. It is important to investigate how trees respond to this rapid environmental change at altitudinal treelines. Tree cores from 21 treeline sites of three species (*Pinus tabulaeformis*, *Picea crassifolia*, and *Sabina przewalskii*) from Northeastern Tibetan have been conducted in this thesis.

The instable correlations between tree growth and climate are the general response pattern of trees from all study sites in NE Tibetan Plateau. *Picea crassifolia* is one of the three species which shows the most instable response to climate factors (mean monthly temperature and total monthly precipitation). *Picea crassifolia* trees from all upper treeline sites could be divided into two groups according to their responses to climate factor: one group benefited from recent warming and displayed an increasing positive correlation with growing season temperature; another group was stressed by warming induced drought and showed an increasing negative correlation with growing season temperature. *Pinus tabulaeformis* and *Sabina przewalskii* just showed instable and divergent responses to their main limiting climate factors but no clear trend was found which is limited by the few sample sites.

Corresponding to divergent responses of *Picea crassifolia* to mean monthly temperature, most radial growth of *Picea crassifolia* were inhibited by this climate change type drought, only few trees within same sites grew faster due to temperature increasing during recent decades. The divergence response mainly started in last 30 years in six of eleven sample sites over the Northeastern Tibetan Plateau. A clear spatial pattern exists that north-westerly drier sites showed a large percentage of trees per site with a negative correlation to temperature and mostly southerly moister sites showed more mixed responses with both negatively and positively responding trees within site. Concurrent with the regional pattern, a general trend is evident of low elevation sites showing mostly negative correlations with temperature and high elevation sites showing more mixed responses. As the hydrothermal conditions of the investigation area changed to a drier and warmer combination, drought stress on tree growth have been intensifying over time and expanding spatially from the middle to most of our study area during the last half century.

The *Picea crassifolia* tree growth climate relationship conducted on an elevational gradient with four different levels from upper treeline to lower treeline at the NE Tibetan Plateau. Results show that upper treeline where tree growth was limited mainly by temperature, show divergent growth trends and divergent responses in recent decades. Some trees show increasing positive and some increasing negative responses to growing season temperature during the last decades. Trees from lower treeline show a strengthening drought stress signal over time and no divergent growth trends within sites. Even though it is hard to completely rule out other contributing factors such as detrending methods or disturbance on the divergent response of trees within site, the spatial and temporal co-occurrence of large scale changes in climate and tree growth suggests a causal link between them. This potential ecological reaction of tree populations to changing environmental conditions shows an implications for using trees to reconstruct climate, since the indiscriminate use of tree ring data from sites showing opposite responses to

increasing warming could cause mis-calibration of tree ring based climate reconstructions, and over- or underestimation of carbon sequestration potential in biogeochemical models.

The physiological response of *Sabina przewalskii* tree growth to major limiting climate factors based on the Vaganov-Shashkin (VS) model indicated that precipitation during the early growing season, especially in May and June, has significant effect on tree growth, while temperature mainly affects tree growth by warming-induced drought and by extending the growing season in the NE Tibetan Plateau. Under current and projected climate scenarios, modeling results predict an increase in radial growth of *Sabina przewalskii* around the Qaidam Basin, with the potential outcome that regional forests will increase their capacity to sequester carbon. However, most *Picea crassifolia* trees growing at lower elevations than *Sabina przewalskii* might be continue stressed by the warming induced drought and might decrease radial growth in future.

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Chapter 1:

Introduction

1.1 Background and Motivation

Recent climate change is an important concern of the whole human society. Most areas of the world are experiencing a general warming trend, with the global mean surface temperature projected to increase by 1.4-5.8 °C over the next 90 years (IPCC, 2007). Meanwhile, recent climate change is also expected to cause progressively increased frequency and severity of drought events in the Northern Hemisphere (Shaver, 2000; IPCC, 2007). Recent studies indicate that this warming trend and its consequences are heavily accelerated by anthropogenic factors and are impacting nearly all ecosystems (Allen and Breshears, 1998; Walther et al., 2002; Parmesan, 2007; Harrison et al., 2010). Recent climate change can provide favorable conditions for some species but unfavorable conditions for other species (Walther et al., 2002; Llody et al., 2003; Wilmking et al., 2004; Hartmann, 2011).

Forests play an important role, not only in terrestrial ecosystems but also for the global carbon circulation (Sabine et al., 2004; Hassan et al., 2005). The recent climate change impacts virtually all chemical and biological processes of forest ecosystems (Holtmeier and Broll, 2007; Bonan, 2008). Treelines are dynamic zones of forests. They are considered as a key environment for monitoring the effects of current anthropogenic climate change (Camarero et al., 2000). The position of upper elevational treelines and polar treelines of the northern hemisphere are likely controlled by a temperature deficit (Fritts, 1976; Körner, 1998). These treelines are expected to benefit from the current warming trend with increased radial growth of existing trees, new tree establishment leading to a possible advance to higher elevations and more northerly latitudes and / or infilling of existing stands (Rupp et

al, 2000; Grace et al., 2002; Scheller and Mladenoff, 2005). However, due to the increasing warming but uneven precipitation distribution, drought can become a severe challenge for several other forest ecosystems (Breshears et al., 2005; Carnicera, 2011). Thus, it is important to investigate how trees respond to recent climate change, especially at treelines.

Calculating the tree growth climate relationship is a simple but effective approach to evaluate the linear response of trees to climate factors (Fritts, 1976). This method has been widely employed in dendroclimatological research because the relationship between climate and tree growth can be approximated by simple linear regression (Cook, 1990). Traditional dendroclimatological analysis assumes that trees from the same site have similar responses to the main limiting climate factors (Hughes, 2002). However, some tree ring chronologies from natural elevational and latitudinal treelines have been recently reported to show decreasing sensitivity to temperature (Briffa et al., 1998a; Solberg et al., 2002; Carrer and Urbinati, 2006; Lloyd and Bunn, 2007). Moreover, trees within sites responded to their limiting climate factors (e.g. to temperature) differently at these regions in recent decades (Wilmking et al., 2004, 2005; Pisaric et al., 2007; Zhang et al., 2008; Zhang and Wilmking, 2010). These phenomena indicate that dendroclimatological research should carefully assess the stability of tree growth climate relationships and the consistent responses of trees within a site. Hence it might not be so reliable to investigate how trees respond to recent warming by using traditional site chronologies. Alternatively, single trees instead of site chronologies should be employed to check the tree growth climate relationships over these areas.

Both meteorological records and current research show that a pronounced warming has taken place in recent decades at the Tibetan Plateau (Liu et al., 2006; ACIA, 2005). Mountain forests play a crucial role by providing ecological, economic and social services to natural systems and humankind (Führer, 2000). The elevational treelines from these areas are usually regarded as ideal areas to investigate the response of forest ecosystems to global climate change (Sun and Zheng, 1998; Holtmeier and Broll, 2005) since these areas are characterized by little

anthropogenic disturbance, and climate mainly controls the extent of tree growth there. Several tree ring based climate researches have been done in these regions (Lloyd and Bunn, 2007; Shao et al., 2009; Yang et al., 2010; Esper et al., 2010; Linderholm et al., 2010). This thesis focuses on the upper treelines of the NE Tibetan Plateau and contributes to the investigation of the dynamic relationship of trees response to recent climate change.

1.2 Objectives of this work

The main goal of this thesis was

- (1) to investigate the tree growth climate relationships of different coniferous species at elevational treelines in NE Tibetan Plateau under current climate scenario;
- (2) to investigate the question whether radial growth of these coniferous species benefits from recent warming or if divergent growth trends exist;
- (3) to investigate the physiological response of coniferous trees to recent climate change by a process based physiological model;

1.3 This thesis

This thesis consists of six main chapters, each of which represents an individual publication plus an introduction and brief synthesis chapter. Tree ring width data from 18 sites from upper treelines at Northeastern Tibetan Plateau, Northwestern China have been analyzed in this research.

Chapter 2 contains the analysis and discussion of the changing relationships between tree growth and climate in Northwestern China, which were based on tree ring width data of six sites. Three conifer species (*Pinus tabulaeformis*, *Picea crassifolia*, and *Sabina przewalskii*) from their upper and lower treelines at Qilian Mountains and Helan Mountains were analyzed.

Chapter 3 is a systematic investigation of dynamic relationships between growth of the endemic species *Picea crassifolia* and climate factors at upper treeline in the Qilian Mountains, Northeast Tibetan Plateau.

Chapter 4 discusses divergent growth responses of *Picea crassifolia* to the increasing temperature along an elevation gradient at the northeast Tibet Plateau.

Chapter 5 presents the physiological response of *Sabina przewalskii* to climate factors simulated by a process-based model around the northeastern Qaidam basin.

Chapter 6 summarized the main results and discusses them in the context of divergent growth trends and the general field of dendrochronology.

1.4 The author's contribution to the single publications

Chapter 2 (publication 1): I did all the data process, figures and the main text. M. Wilmking edited whole text especially the English expression, rewrote it in parts and helped in the analysis. X. Gou supported data collection.

Chapter 3 (publication 2): I collected all raw data in China and did all analysis and figures and wrote main text. M. Wilmking and I discussed, reworked and finished the whole article. M. Wilmking did all English editing and X. Shao supported data collection and involved in discussion.

Chapter 4 (publication 3): I did the data processing, data analysis and wrote the main manuscript. M. Wilmking and I discussed the results and rewrote parts of the manuscript. Dr. G. Wilmking helped with language editing.

Chapter 5 (publication 4): I did all analysis and wrote the main manuscript. M. Wilmking initiated the collaboration for the model script and cedited for clarity and content. X. Shao provided the tree ring data and Y. Xu provided one figure.

Chapter 2:

Changing relationships between tree growth and climate in Northwest China? ¹

Abstract

Recently, several studies have shown changing relationships between tree growth and climate factors, mostly in the circumpolar north. There, changing relationships with climate seem to be linked to emergent subpopulation behavior. Here, we test for these phenomena in Northwest China using three tree species (*Pinus tabulaeformis*, *Picea crassifolia*, and *Sabina przewalskii*) that had been collected from six sites at QilianMts. and HelanMts. in Northwest China. We first checked for growth divergence of individual sites and then investigated the relationship between tree growth and climate factors using moving correlation functions (CF). Two species, *Pinus* and *Sabina*, from two sites clearly showed growth divergence, not only in the late twentieth century as reported in other studies, but also over nearly the whole record. In divergent sites, one chronology shows more stable relationships with climate factors (usually precipitation). In non-divergent sites, nearly all relationships either vary in strength or become non-significant at one point. While this might possibly be related to increased stress on some trees due to increasing temperature, the exact causes for this shift in sensitivity remain unclear. We would like to highlight the necessity for additional studies investigating possible non-stationary growth responses of trees with climate, especially at sites that are used for climate reconstruction as our sites in Northwest China.

¹ This paper is published as Zhang Y, Wilmking M, Gou X. Changing relationships between tree growth and climate in Northwest China. *Plant Ecology*, 2008. DOI 10.1007/s11258-008-9478.

2.1. Introduction

Global warming is a great concern to human populations, as it has been shown to bring many threats, such as heat waves and warmer weather, spreading disease, earlier spring arrival, plant and animal range shifts and population declines, sea level rise, and frequent disaster etc. (Greenough et al., 2001; Kahn, 2005; Webster et al., 2005; Shepherd and Wingham, 2007; IPCC, 2007). In order to evaluate whether current global warming is unprecedented or not, it is essential to put this warming into a long-term perspective. Due to the limited time interval of instrumental climate records, many natural proxies have been used to conduct paleoclimatic reconstructions. Tree rings have been widely used to reconstruct the variability of many climate factors (e.g. temperature, precipitation), due to their annual resolution, wide spatial distribution and the possibility of using simple linear models of climate–tree growth relationships that seem to be easily verified and calibrated (Hughes, 2002).

It is generally assumed in dendroclimatological studies that the approximate relationship between tree growth and the limiting climate factor is stable over time (Fritts, 1976). However, many recent studies have reported problems with this assumption. Either formerly temperature sensitive tree ring chronologies have lost or decreased in temperature sensitivity (Jacoby et al., 1996, 2000; Briffa et al., 1998a, 1998b; Smith et al., 1999; Solberg et al., 2002), increased in sensitivity (Knapp et al., 2001; Wilmking et al., 2005) or even changed from positive to negative temperature sensitivity or vice versa (Wilmking et al., 2004, 2008).

In addition, temperature reconstructions in the northern hemisphere based on tree rings are often not able to follow the documented temperature increase in recent decades, thus leading to a widening gap (a divergence) between the temperature curve and the tree ring based temperature reconstruction. D'Arrigo (2008) has recently termed this phenomenon the 'divergence problem' in northern forests.

Meanwhile, even trees growing at the same site showed not only opposite response relationships with climate factors, but also diverging long term growth trends in the late 20 century, possibly diluting the climate signal when averaged to site chronologies (Wilmking et al., 2004, 2005; Driscoll et al., 2005; Pisaric et al., 2007). These growth trend differences have also been called “diverging”. To avoid possible confusion, we will use the term “growth divergence” for differences in growth trends between trees and “divergence problem” for the underestimation of recent temperatures by tree ring based climate reconstructions.

Neither the real reasons causing 1) the shift in tree growth response to temperature (or possibly other environmental factors), 2) the diverging between recorded and reconstructed temperature and 3) the diverging growth trends between neighboring trees nor the interaction between those three challenges are known. Some possible mechanisms have been proposed to explain these shifts in tree growth climate relationships, such as temperature-induced drought stress (Jacoby and D’Arrigo, 1995; Barber et al., 2000; Lloyd and Fastie, 2002), nonlinear thresholds or time-dependent responses to recent warming (D’Arrigo et al., 2004, Wilmking et al., 2004, Sergio Rossi et al., 2007), delayed snowmelt and related changes in seasonality (Vaganov et al., 1999), air pollution (Wilson and Elling, 2004; Yonenobu and Eckstein, 2006), and differential growth/climate relationships inferred for maximum, minimum and mean temperatures (Wilson and Luckman, 2002, 2003). In addition, there are also some other potential causes, for example, end effects during chronology development and biases in instrumental target data and its modeling (Cook and Peters, 1997; Melvin, 2004; Hoyt, 2006; D’Arrigo et al., 2008).

Whatever the reasons for the growth divergence or the divergence problem are, these phenomena seem to be limited to the high latitudes of the northern hemisphere (D’Arrigo et al., 2008). But do these divergences and changes in climate sensitivity only appear in the circumpolar northern latitudes or do they exist worldwide? Here we try to better understand the magnitude and extent of these phenomena by testing several sites in northwest China.

In northwest China, tree rings (width, isotopes, density) have been widely used in dendroclimatological studies at the alpine treeline (e.g. Yuan et al., 2003; Zhang et al., 1997; Shao et al., 2004, 2005; Gao et al., 2005). Several climate reconstructions have been conducted in the Qilian Mts. (Zhang et al., 1996; Wang et al., 2001; Gou et al., 2001), and the Helan Mts. (Liu et al., 2004, 2005), some extending back over 1000 years (Kang et al., 2002). However, no study has yet considered testing for growth divergence or the stability of the relationship between tree growth and climate over time in this region. A better understanding of the tree growth responses to climate in northwest China during the last century, however, is important not only for regional paleoclimatic studies, but also for forest carbon uptake simulations and future forest planning.

2.2. Materials and Method

2.2.1. Study area

For this study we sampled three regionally dominating tree species (two sites each) in the Qilian Mts. and Helan Mts.: 1) *Pinus tabulaeformis*, 2) *Sabina przewalskii* and 3) *Picea crassifolia*. The Qilian Mts. and Helan Mts. are two prominent mountains in Northwest China (Fig. 2.1). Each of them has their own typical topography and typical atmospheric systems. The Qilian Mts., located on the northern edge of the Tibet Plateau, have several peaks over 4000 m, and create a strong rain shadow effect for monsoons coming from the southeast. Our study area is situated in the eastern part of the Qilian Mts., a transitional area between temperate monsoons and continental climate. There, *Picea* and *Sabina* are two typical and widespread conifer species. The Helan Mts. are located in north central China where the arid northwest areas meet the Loess Plateau. They extend over 200 km from south to north, but only 15–60 km from east to west with peak elevations between 2000–3000 m a.s.l.. Located along the northwest margin of the East Asian Summer Monsoon, the Helan Mts. act as a barrier to the penetration of monsoon rainfall into northwest China. *Pinus* and *Picea* are two typical and widespread species in Helan Mts..

2.2.2. Climate data

Most of the meteorological stations in Northwest China were set up after 1950 and thus provide only a short climatic record. As a consequence, we used gridded data from the high-resolution $0.5^{\circ} \times 0.5^{\circ}$ gridded climate dataset CRUTS2.1 (Mitchell, and Jones, 2005) instead of the measured data for our analysis, fully aware that relationships between tree ring parameters and CRU data are usually weaker than with nearby station data, mostly because of the large scale smoothing applied in the CRU data sets (Mitchell and Jones, 2005). In order to evaluate the quality of gridded data over time, a 10 years moving standard deviation was employed. The moving standard deviation of precipitation data has an abrupt change around 1934, indicating a possible problem with the precipitation data prior to 1934. The moving standard deviation of temperature is stable over the whole time period. Therefore, in this study we used only gridded data from 1934 to 2000 (1934-1999 for sites of Helan Mts.).

The climate data of the nearest CRU grid cells were used in this study for the calculations of climate-growth relationship since the relationships between chronologies and climate data of the four grid cells around the sample sites were similar (data not shown).

2.2.3. Tree-ring sampling and cross dating

Increment cores of trees in the Qilian Mts. were collected in October 2000. 29 cores were taken from 16 living *Picea* trees growing between 2600~2900 m a.s.l. near the lower tree line and were herein named S1. All sampled trees were healthy and growing on an east-facing slope with moist soil (if compared to the other sampling sites). 41/39 cores were taken from 23/22 *Sabina* trees at two sites taken from the east Qilian Mts and named J1 and J2. All cores were taken from healthy trees growing at the upper limit of the forest at an elevation of about 2930-3100 m a.s.l. with thin gray cinnamonic soil.

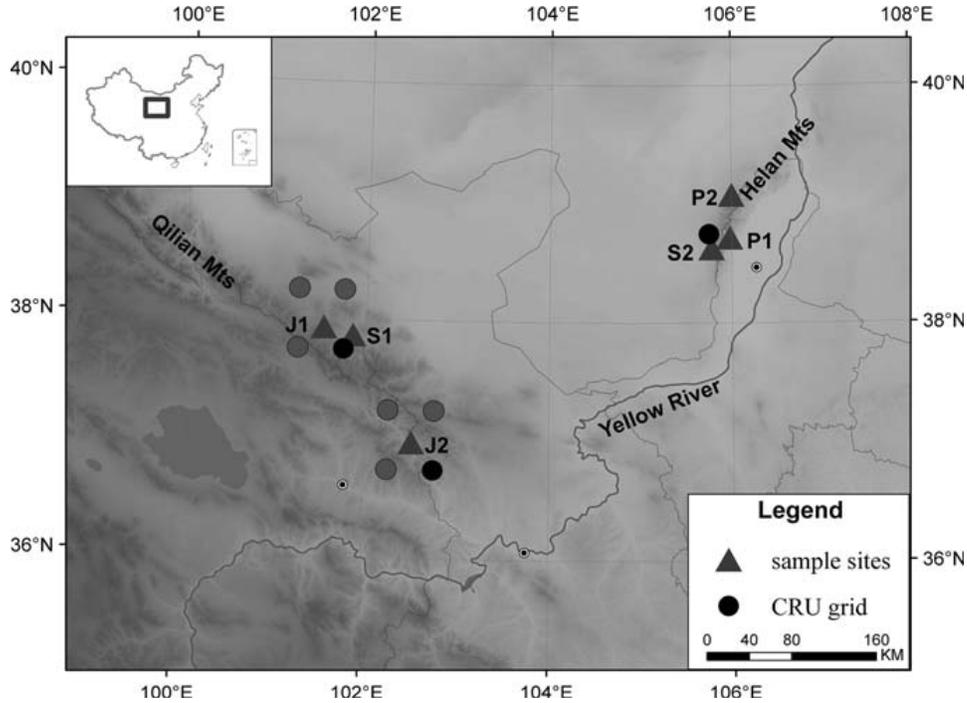


Figure 2.1 Map of the sampling sites (▲) in eastern Qilian Mts. and Helan Mts. as well as of the nearby grid data (●) from CRUTS2.1 (37°75'N, 101°75'E; 36°75'N, 102°75'E; 38°75'N, 105°75'E). The grey dots indicate the grid cells around the sampling sites which showed similar results.

The increment cores of Helan Mts. were collected in October 1999. 35 cores were taken from 18 living *Picea* trees growing above 2500 m a.s.l. at west slope of Helan Mts and were named S2. 68/41 cores were taken from 40/25 *Pinus* trees growing above 2000-2300 m a.s.l at two sites from Helan Mts. and named P1 and P2. P1 and P2 are at the east and west slope of the Helan Mts. respectively. The soil at both sites was thin and rocky. The dominant tree species in both forests sites was *Pinus*, typically found growing at an elevation between 1900-2350 m a.s.l. (Table 2.1).

Tree-rings were processed and cross-dated with standard dendrochronological techniques (Cook and Kairiukstis, 1990). Ring-width was measured on a Velmex system with a precision of 0.001 mm. The program COFECHA (Holmes, 1983) was employed to check the quality of visual cross-dating.

Table 2.1 Site information.

Site	Species	Latitude (N)	Longitude (E)	Elevation (m)	Slope
S1	<i>Picea</i>	37.87°	101.53°	2600~2900	east-facing
S2	<i>crassifolia</i>	38.63°	105.78°	2500	north-facing
P1	<i>Pinus</i>	39.08°	106.08°	2600	north west-facing
P2	<i>tabulaeformis</i>	38.72°	105.98°	2400	north west-facing
J1	<i>Sabina</i>	37.93°	101.53°	2930~3100	south-facing
J2	<i>przewalskii</i>	36.59°	102.31°	~3100	south-facing

2.3. Tree ring data processing

2.3.1. Divergent growth trends over time and chronology development

First, we used the raw data to calculate the growth trend of each tree for the last 40 years using linear regression. All series at each site were classified into two groups: one with increasing growth trend (slope, $b > 0$) and the other with decreasing growth trend ($b < 0$) (Pisaric et al., 2007). All series were then standardized with the program ARSTAN (Cook, 1985) using conservative negative exponential or linear regression. Due to the failure of conservative detrending in a few series (Table 2), they were standardized with the Hegershoff growth curve.

Chronologies based on the groups were built using traditional methods. Since we used raw data to judge the growth trend, the two chronologies (one with increasing and one with decreasing growth trend) were combined into one chronology, if the two groups showed a similar trend after detrending. Several descriptive statistics, commonly adopted in dendrochronology, were used to compare chronologies. These statistics include the mean sensitivity (MS) and standard deviation (SD) (to assess the high-frequency variations), the first-order serial autocorrelation (AC) (to detect eventual persistence retained after the standardization), the mean correlation between trees (Rbt) and the expressed population signal (EPS) (to estimate the amount of year-to-year growth variations shared among trees of the same chronology). To visualize the apparent growth divergence over time, we subtracted

the detrended tree ring width indices of the increasing chronology from the decreasing chronology where applicable.

2.3.2. Climate-growth relationships and their stability over time

After dividing all series into groups of increasing and decreasing growth trends and chronology building, we tested each resulting chronology for its climate growth relationship. First, simple correlation functions (CF) were employed. We then tested the stationary and consistency of these climate-tree growth relationships over time using moving CF (DENDROCLIM2002, Biondi and Waikul, 2004). A moving CF employs a fixed number of years progressively slid across time to compute the correlation coefficients (Biondi, 1997). Considering the length of recorded data and the reliability of sample size, we chose 48 year as the moving interval for each calculating analysis. Moving CFs produce a temporal set of coefficients for each predictor and coefficients not significant at the 95% confidence level are changed to zero. Here we just present the results of the moving correlations in detail because the moving CFs not only include the results obtained from simple correlation analysis, but they also provide a dynamic perspective on the evolution of tree responses to climate over time.

2.4. Results

2.4.1. Growth divergence and Chronologies

After calculating growth trends for all trees we found that sites J1 and P1 contained each one group with increasing and one with decreasing growth trends. Hence they were separated for chronology building (Fig. 2.2) and subsequently termed J1D and P1D (for decreasing) and J1I and P1I (for increasing). Trees from the other four sites did not divide in groups and thus showed no growth divergence and were subsequently combined into one chronology per site, resulting in a total of eight chronologies from the six sites. Time spans of the chronologies were different and we chose a fixed common period 1900-2000 to compare the quality of different chronologies. Mean sensitivity and first-order serial autocorrelation varied from

0.304 to 0.696 and from -0.004 to -0.124, respectively. All sites (except S1) exhibited low serial autocorrelation in their mean chronologies (in Table 2.2), which was mostly removed after autoregressive modeling of single series. Two useful parameters for evaluating the quality of a chronology are the mean inter-series correlation (Rbt, varied from 0.248 to 0.694) and the expressed population signal (EPS, varied from 0.811 to 0.988). The EPS values of the chronologies are greater than 0.85 except for S2 which has a 0.983 EPS value during 1920-1999 but low value during 1900 to 1920, since most trees of this site were younger than 100 years. The two Sabina sites (J1 and J2) had lower Rbt and EPS values, but all EPS values were above the accepted cut-off of 0.85 (Wigley et al., 1984).

Smoothing the chronologies with a 48-year spline showed that the two sub-chronologies from a site (J1D and J1I; P1D and P1I) had very similar short term variation but different long term trends (Fig. 2.2).

2.4.2. Influence of climate and the stability of the tree-ring growth climate relationships

2.4.2.1. Regional influences of climate on tree growth

Most chronologies show a strong, consistent and positive relationship with precipitation during the current growth season (Fig. 2.3). June precipitation was the key variable for tree growth in both mountain ranges. The strength of the positive correlations however varied over time except for J1D and J2.

2.4.2.2. Climate growth relationships of each species

First noticeable in the Pinus chronologies is the high climate sensitivity of P1I chronology, which shows significant correlation with several climate parameters. P1D and P2 have quiet similar relationships but less significant than P1I. The Pinus trees are generally limited by growth season (especially June) precipitation, but this relationship weakened and is not significant in recent years. September temperature of the growing season and October precipitation of the previous year had influence on all Pinus chronologies with a positive relationship but the relationships are not

stable during the calculated time period. During the growing season, temperature seems to play a limited role for tree growth with negative relationships, for example in August and March. These relationships are not stable over time. In P1I, two stable positive relationships between tree growth and prior October and December started from early 1980 and became stronger and stable in recent time. Also in P1I, there is a noticeable phenomenon that the precipitation seems to affect growth of P1I moving forward from July to May over time.

Table 2.2 Statistics of the eight chronologies. Hug.: series detrended by Hegershoff growth curve; MS: mean sensitivity; AC: first order autocorrelation; Rbt: the mean interseries correlation; EPS: the expressed population signal and the year from when EPS is consistently greater than 0.85.

Site	sub-chro	Sample size (cores / trees)	Hug .	Time interval	MS	AC	Rbt	EPS	EPS > 0.85
S1	S1	29/16	2	1840-2000	0.430	-0.124	0.601	0.945	1900
S2	S2	35/18	2	1869-1999	0.351	-0.006	0.496	0.811	1920
	P1I	8/6	0	1742-1999	0.648	-0.004	0.583	0.854	1850
P1	P1D	60/38	6	1700-1999	0.566	-0.067	0.615	0.988	1820
P2	P2	41/25	7	1739-1999	0.696	-0.013	0.694	0.983	1819
	J1I	18/13	0	1288-2000	0.351	-0.007	0.256	0.857	1865
J1	J1D	22/14	0	1590-2000	0.304	-0.034	0.248	0.868	1875
J2	J2	39/22	4	1740-2000	0.422	-0.043	0.341	0.952	1852

The Sabina chronologies are not consistent with each other. At the J1 site, both J1D and J1I have a strong negative correlation with June temperature, but while this relationship in both chronologies weakened over time, it recently dropped to non-significant in J1I. This weakening of the negative correlation with June temperature in J1I is concurrent with an emergent positive correlation with June precipitation. The positive correlations with prior November and December temperature and negative correlation with the precipitation of August and September in J1I also become stable and significant during the second half of the record. In J1D, the negative relationships with temperature of January and February gradually become stronger. At the J2 site, May temperature and September temperature affect tree growth with negative and positive relationships, previous December temperature

started to affect tree growth with a significant positive relationship which became stronger in the late 20th century.

In S1, the relationships between tree growth and current September temperature and June precipitation are positive, but the relationships dropped to non-significant at the end of the record. Instead a negative relationship between the S1 chronology and several monthly temperatures become significant at the end of the record. S2 has mainly stationary significant positive correlations with prior October and current June precipitation over time.

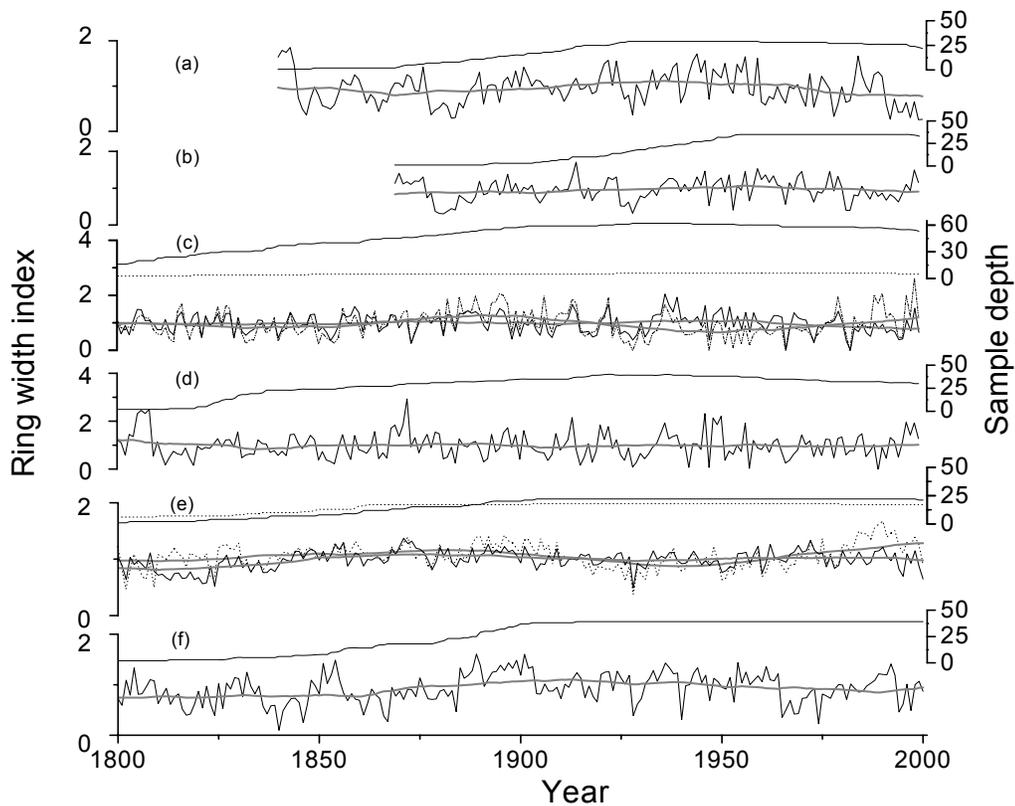


Figure 2.2 The standard ring-width chronologies, 48 years smoothing (thicker line) and their corresponding sample depth, (a) S1; (b) S2; (c) P1, continuous line P1I and dashed line P1D; (d) P2; (e) J1, continuous line J1I and dashed line J1D; (f) J2.

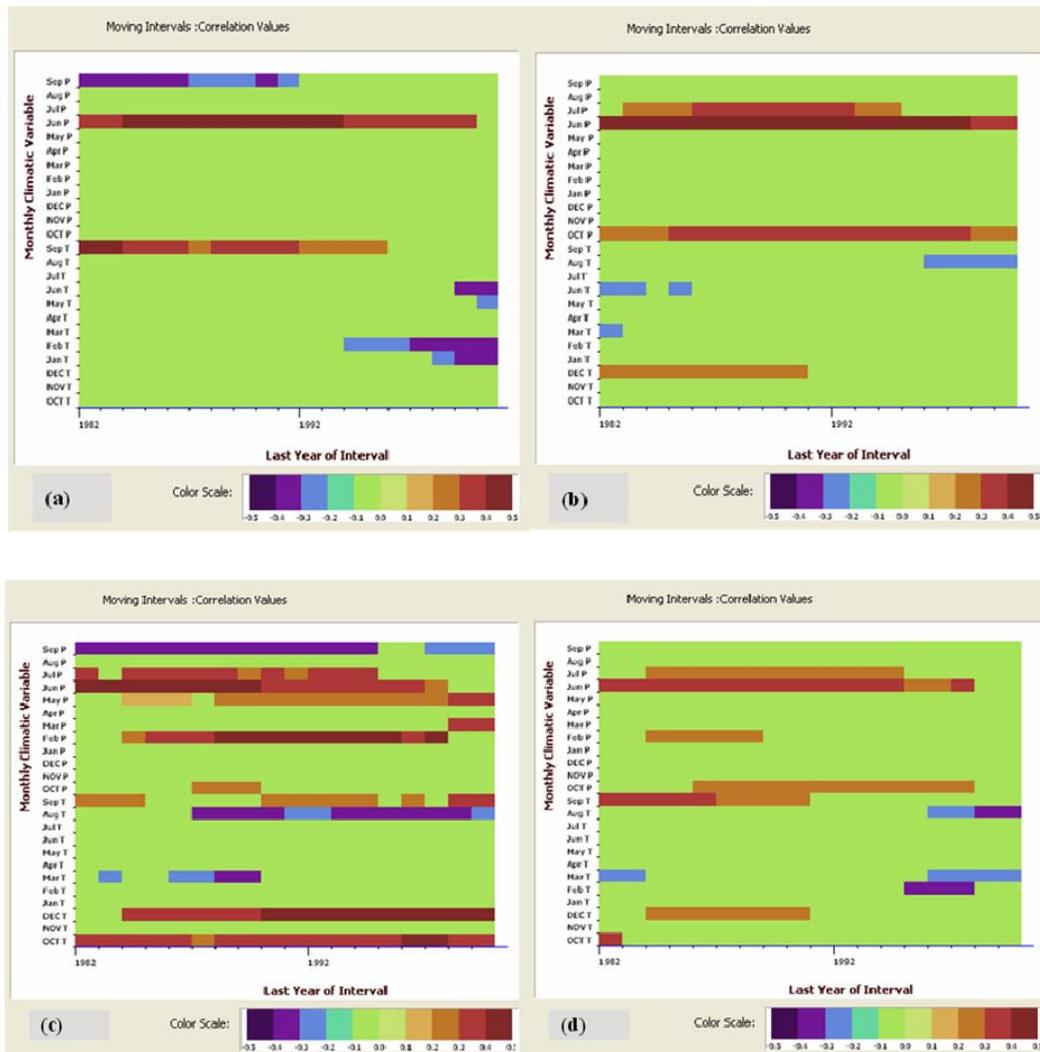


Figure 2.3 Moving correlations between climate variables (monthly mean temperature, (T) and monthly total precipitation, (P) and tree-ring chronologies (a) S1; (b) S2; (c) P1I; (d) P1D; (e) P2; (f) J1I; (g) J1D; (h) J2. Previous year October – current year September were used in the analyses.

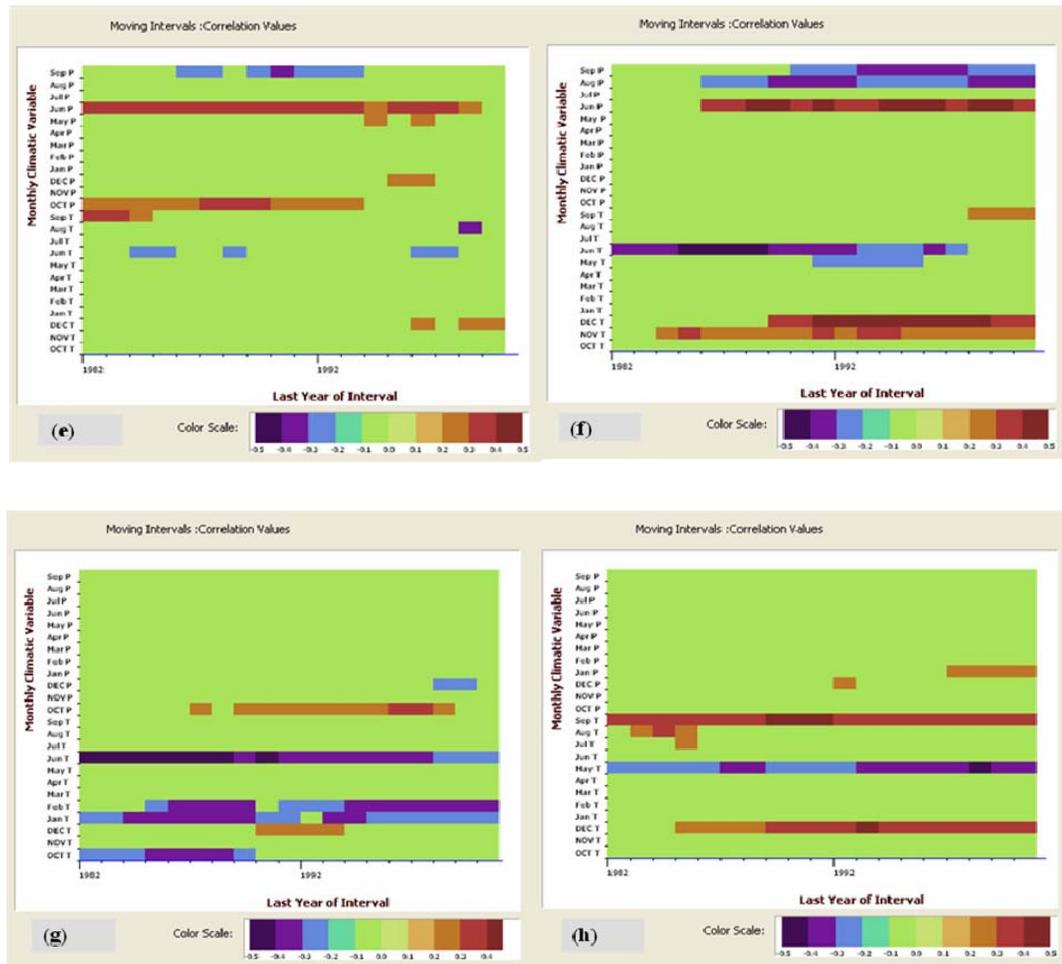


Figure 2.3 (continue)

2.4.2.3. Seasonalized pattern

For different seasons, trees from different sites (except J1D and S2) display similar relationships with temperature and precipitation (Table 2.3). In previous year autumn and early winter (from October to December), there is a positive relationship between tree growth and both temperature and precipitation. During winter, early spring and summer, last year have similar negative relationships with temperature but some positive relationships with precipitation. The response pattern to precipitation was generally opposite to the correlations with temperature during growing season (May, June, July), and September.

Table 2.3 The signs of significant moving correlation coefficients between chronologies and monthly climate factors (mean temperature, T, and total precipitation, P). All correlation coefficients were calculated based on a 48 year time interval and previous year October (P-Oct) – current year September were used in the analysis.

	T							P								
	P1I	P1D	P2	S2	S1	J1I	J1D	J2	P1I	P1D	P2	S2	S1	J1I	J1D	J2
P-Oct	+	+						–	+	+	+	+			+	
P-Nov						+										
P-Dec	+	+	+	+		+	+	+			+				–	+
Jan					–		–									+
Feb		–			–		–		+	+						
Mar	–	–		–					+							
Apr																
May					–	–		–	+		+					
Jun			–	–	–	–	–		+	+	+	+	+	+		
Jul								+	+	+		+				
Aug	–	–	–	–				+							–	
Sep	+	+	+		+	+		+	–		–		–	–		

2.5. Discussion

Recent studies show several problems with the development of tree growth climate relationships, e.g. growth divergence of subpopulations (Wilmking et al., 2004, 2008), the “divergence problem” or underestimation of current temperatures by tree ring based climate reconstructions (D’Arrigo et al., 2008) and changing relationships between tree growth and temperature variability (e.g. Carrer et al., 2006), most of them occurring circumpolar at high northern latitudes. Here we present evidence of growth divergence and instability of tree growth-climate relationships in three conifer tree species in northwest China. Two species (*Sabina* and *Pinus*) at two different sites show subpopulation behavior with growth divergence but the other sites do not. The growth divergences at these sites appeared not only in late 20th century but also about 1920 (Fig. 2.4) in both species at similar times but with differing amplitude. The largest divergences occurred in *Sabina* in the late 20th century, but in *Pinus* during the 1920s. The growth divergence here is different from the growth divergences shown in other studies (Wilmking et al., 2005; Pisaric et al., 2007), which only reported growth divergence in late 20th century. Unfortunately,

our sample size of different sites is inadequate to comprehensively address the question, if the growth divergence observed in this study is the result of a specific combination of site factors, such as elevation, slope and exposure.

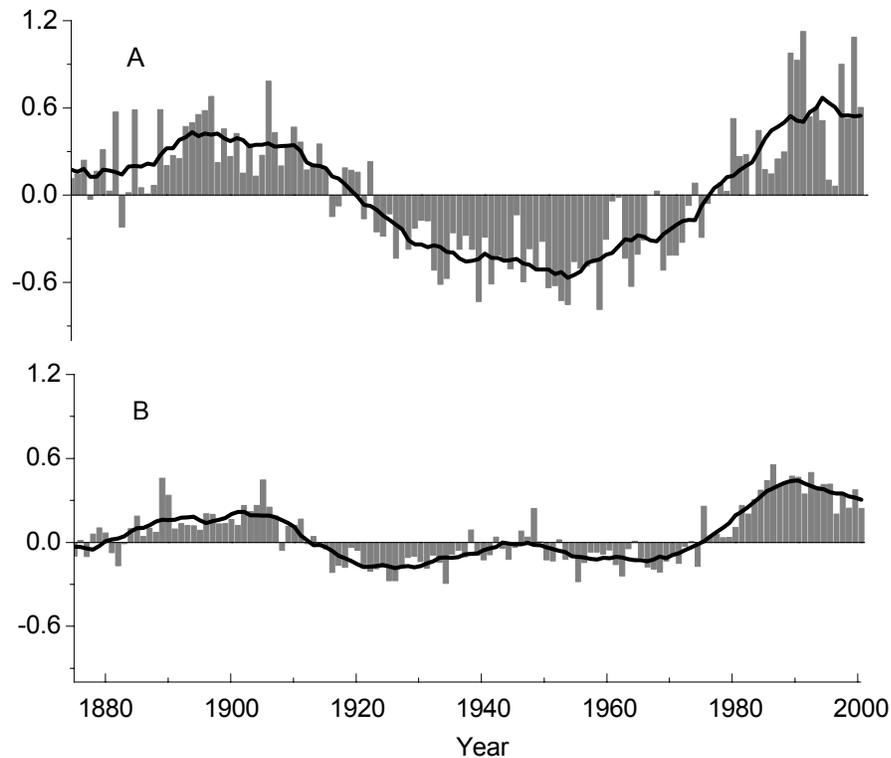


Figure 2.4 An index of growth divergence in P1 (a) and J1 (b) shows similar trends, but different amplitudes over the period 1934–1999. The thick lines are 11 years smoothing lines.

Although the growth responses to climate revealed by most chronologies support the common fact that growing season (especially June) precipitation is the main limiting factor for tree growth, there are still other phenomena: 1) Positive correlations between tree growth and previous year autumn temperature suggest that the warm October condition likely support trees to keep carbohydrate storage and perhaps increased foliage or wood production in the subsequent growing season (Julian et al., 2000; Schaberg, 2000). Previous studies indicate that temperate conifers have a positive carbon gain in warm winter days when their leaves are not frozen (Chabot and Hicks, 1982; Havranek and Tranquillini, 1995). 2) Negative relationship with temperature and positive relationship with precipitation during winter and early

spring (from January to March) might indicate the protection of snow cover at high elevation. At the alpine timberline, Oberhuber (2004) found that trees show a tendency to suffer from enhanced desiccation during winter–early spring periods with insufficient snow depth because of increased transpiration rates of needles and shoots, photo inhibitory stress and short-term fluctuations in shoot temperatures. 3) The warm autumn of the current year also has a strong effect on tree growth in most species. Trees seem to grow better during the warmer autumn. According to Shi (2008), temperature could play an important role on tree ring formation at the end of the growing season in arid and semi-arid areas, by prolonging the growing season.

The instable relationships over time between tree growth and climate factors might have been caused by different combination of climate factors (e.g. temperature, precipitation). Recent studies indicate there is an ongoing warming and drying trend for all seasons in north central China (Wang and Zhou, 2005; Zhai et al., 2005; Ma and Fu, 2006). Individual trees (especially Pinus and Sabina) might have become more sensitive to micro-site differences resulting in the breakdown of the uniform growth behavior at the sites and subsequent differing growth trends and climate sensitivity. One example is that the chronologies with increasing trend show more stable positive correlation with June precipitation than the chronologies with decreasing growth trend. The high correlations with prior winter and autumn of the current year appeared in both increasing chronologies during the calculated time period indicating that those trees could take advantage of the available conditions better than trees of the decreasing chronology. However, the decreasing trees started to become more sensitive to the temperature during the late spring and early summer which could be induced by more desiccation through increasing evaporation before the arrival of the summer monsoon (Ding, 1994). Furthermore, the positive correlation with precipitation, gradually moving forward from July to May in the PII chronology might also indicate the drying trend in the early growth season.

2.5. Conclusion

Recent studies discussed three major challenges to the field of dendroclimatology, 1) changing relationships between tree growth with climate over time, 2) emerging sub-chronology behavior at sites formerly considered suitable to build one chronology and (as a possible result) 3) the “divergence problem” or underestimation of recent warming trends by tree ring based climate reconstructions. Many of these studies were conducted either in the boreal zone or at altitudinal tree limit in Europe. Here we present evidence of the first two phenomena in mid-latitude NW China. Diverging growth trends were found in Pinus and Sabina sites, but not in Picea sites. The correlations between tree growth with climate factors at most sites are instable over time, as also indicated by switches from significant to non-significant or vice versa relationships with climate factors at different periods of the record. Non-divergent sites have more stationary relationships with climate factors than chronologies from divergent sites. There, decreasing chronologies show more stable relationships with climate than increasing chronologies, which are more sensitive to climate factors, indicated by the higher correlation scores.

For the future, we see a major need for additional work at two fronts, 1) to test more regions and species for the phenomena of changing climate growth relationships over time and 2) to better understand the mechanisms affecting growth from the level of the individual tree to the population through time. Only then can we safely proceed to use tree rings as robust source of paleo-climatic information.

Acknowledgments: We thank Dr. Jayendra Singh and Jinbao Li for discussing and help.

Chapter 3:

Dynamic relationships between *Picea crassifolia* growth and climate at upper treeline in the Qilian Mts., Northeast Tibetan Plateau, China²

Abstract

Knowledge of the spatial pattern and temporal relationships between tree-growth and climatic factors are important not only for the projection of forest growth under varying climate but for dendroclimatology in general. Here, we systematically investigated tree-growth climate relationships of *Picea crassifolia* at upper treeline in the Qilian Mts., northwestern China. 297 trees from eleven sites, covering a large part of the natural range of this species, show increasing and partly divergent correlations with temperature in the most recent decades. The dominant signal at all sites was a strengthening of negative correlations of annual radial growth with summer temperature. In a subset of trees at six sites, a strengthening positive correlation with summer temperatures existed as well. Wetter and high altitudes sites tended to show a higher percentage of trees that are positively correlated with warming temperatures, indicating that some individuals there may take advantage of warmer conditions. Divergent responses between the two sub-populations clustered by their response to climate factor were significantly stronger in the last 30 years compared to earlier time slices. In the same time frame, hydrothermal conditions of

² This paper is published as Zhang Y, Shao X, Wilmking M. Dynamic relationships between *Picea crassifolia* growth and climate at upper treeline in the Qilian Mts., Northeast Tibetan Plateau, China. *Dendrochronologia*, 2011, doi:10.1016/j.dendro.2010.11.001

the investigation area changed to a drier and warmer combination. Drought conditions, most likely affecting the radial growth of most *Picea crassifolia*, have been intensifying over time and expanding spatially from the middle Qilian Mts. to most of our study area during the last half century. While explanations such as methodological effects due to trend removal or human disturbance at the sampling sites might be able to explain the result at single sites, the spatial and temporal co-occurrence of large scale changes in climate and tree growth suggests a causal link between them.

3.1. Introduction

Recent climate change has been impacting nearly all ecosystems on earth. Most areas experience a general warming trend, with the global mean surface temperature projected to increase by 1.4-5.8 °C over the next 100 years (IPCC 2007). Mountain ecosystems, which are among the most fragile environment on the globe (Stone 1992), are projected to experience the most dramatic warming as well (e.g. Shugart et al., 1998). Since the position of upper elevational treelines is likely controlled by a temperature deficit (Fritts 1976; Körner 1998), upper treelines are expected to benefit from this warming trend with increased radial growth of existing trees, new tree establishment leading to possible upslope movement and / or infilling of existing stands (Scheller and Mladenoff, 2005).

However, some tree ring chronologies from natural elevational and latitudinal treelines are reported to recently show decreasing sensitivity to temperature, possibly resulting in the so called “divergence effect” (e.g. Briffa et al., 1998a; Solberg et al., 2002; Carrer and Urbinati 2006; Lloyd and Bunn 2007). Using single trees instead of entire chronologies to investigate tree growth climate relationships, divergent growth responses have been found during the last half century within treeline sites formerly considered suitable to build one chronology (Wilmking et al., 2004, 2005; Pisaric et al., 2007; Zhang et al., 2008; Zhang and Wilmking, 2010). When building sub-chronologies based on similarly reacting single trees from these sites, climate sensitivity actually increased (Wilmking et al., 2005; Zhang et al.,

2008). The reasons for a decrease or increase in climate sensitivity are discussed in the literature (D'Arrigo et al., 2007), with temperature induced drought stress suggested as the main cause for a reduction in sensitivity to temperature. Other hypotheses include threshold effects of growth to temperature (D'Arrigo et al., 2004; Wilmking et al., 2004), delayed snowmelt and related changes in seasonality (Vaganov et al., 1999), an increase in UV-B radiation (Briffa et al., 1998a, 2004), global dimming (D'Arrigo et al., 2007), methodological issues related to detrending procedures (Melvin and Briffa, 2008) or a combination thereof (Esper and Frank, 2009). Whatever the cause, variable climate growth relationships question the reliability of tree ring based climate reconstructions (D'Arrigo et al., 2007).

It is important to stress that not all trees show this divergent response to observed temperature (Briffa et al., 2004; Wilson et al., 2007). Most evidence of this phenomenon comes from the high northern latitudes (Cook et al., 2004, D'Arrigo et al., 2007) and only little evidence exists from other areas. Therefore, it is necessary to investigate the response of trees to recent warming, especially in the mid latitudes of the northern hemisphere where tree rings are an important proxy in paleoclimatic research.

The Tibetan Plateau area, where pronounced warming has taken place in recent decades (Liu and Chen, 2000; Liu et al., 2006), is usually regarded as an ideal area to study the response of forest ecosystems to global climate change (Sun and Zheng, 1998) and several dendroclimatic reconstructions have been published from the area (Wu and Shao, 1995; Zhang et al., 2003; Shao et al., 2005; Liang et al., 2006). The Qilian Mts., which are composed of a series of North-Eastern mountain ranges, occupy the northeastern Tibetan Plateau. Their permanent glaciers and perpetual snow cover are the main sources of inland rivers which are crucial for agriculture, ecology, and daily life of local people. Forests play an important role in regulating water flow of those rivers and provide a crucial natural proxy for studies of paleoenvironments (Wu and Shao, 1995).

Picea crassifolia is the dominant conifer species in the Qilian Mts. (Fig. 3.1), which are the centre of its natural range, and it has been widely used in dendroclimatology

and dendrohydrology (e.g. Kang et al., 2002; Tian et al., 2007). However, a comprehensive analysis of climate-growth relationships of individual trees and populations over a large area is missing. Thus, the objectives of this study were to examine the response of single *Picea crassifolia* trees and *Picea crassifolia* populations to recent warming over a large portion of its natural climatic envelope. We stress that our goal was neither to reconstruct past climate nor to test for a possible ‘divergence effect’ (a recent offset between tree ring based climate reconstructions and measured climate data), but rather to elucidate the spatio-temporal variability of recent *Picea crassifolia* growth and its possible environmental and ecological drivers.

3.2. Materials and methods

3.2.1. Tree ring data

We sampled *Picea crassifolia* at upper treeline over a large part of its natural range in the Qilian Mts. during 2005-2006 (Fig. 3.1). Increment cores were taken from dominant and co-dominant trees which appeared healthy and were relatively isolated at and close to their upper limit (Table 3.1). In total, 297 trees from 11 sample sites were collected in our study area. While sites from the central Qilian Mts. are higher in elevation and receive comparatively more precipitation, sites (e.g. j and k) from the outermost north-west distribution of *Picea crassifolia* are lower in elevation and are comparatively drier. At the highest site a on the mountains bordering of the Qaidam basin, orographic precipitation contributes enough moisture for tree growth. According to our sampling design we sampled trees from the central and north-western distribution of *Picea crassifolia* and omitted the eastern part of Qilian Mts. which is most heavily influenced by human activities.

All cores were processed following standardized methods (Fritts, 1976). After being glued into slotted wooden boards, cores were air dried and progressively polished with fine sandpaper until cellular structures were clearly visible. Tree-ring series were carefully cross-dated by visually comparing their growth patterns. Ring widths

were measured to 0.001mm precision using a LINTAB measuring system. The COFECHA program (Holmes, 1983) was employed to check the quality of visual cross-dating. The growth trend of each series was removed using ARSTAN (Cook, 1985) by conservative

Table 3.1 Sample sites and characteristics of closest climate stations.

Site	Latitude	Longitude	Elevation	Sample size(c/t*)	climate station	Latitude	Longitude	Elevation	Record length
W1(a)	37°02'	98°39'	3777	25/50	Dulan	36°18'N	98°06'E	3191.1	1954-2005
Q1(b)	38° 08'	100°24'	3357	24/48	Qilian	38°11'N	100°15'E	2787.4	1957-2005
SDL(c)	38°25'	99°56'	3304	31/31	Zhangye	38°56'N	100°26'E	1482.7	1951-2005
DDS(d)	39°03'	100°49'	2826	28/34					
XM1(e)	37°13'	103°11'	3000	27/43	Yongchang	38°14'N	101°58'E	1976.9	1951-2005
XM2(f)	37°13'	103°10'	3000	30/30					
KGM(g)	38°47'	99°44'	2900	24/30	Zhangye	38°56'N	100°26'E	1482.7	1951-2005
DYK(h)	38°31'	100°15'	3040	47/67					
XDH(i)	38°05'	101°24'	2755	23/43	Wuwei	37°55'N	102°40'E	1531.5	1958-2005
QKD(j)	39°23'	98°31'	2800	22/33	Jiuquan	39°46'N	98°29'E	1477.2	1951-2005
JG(k)	39°37'	97°51'	2852	16/29					

*(c: core; t: tree)

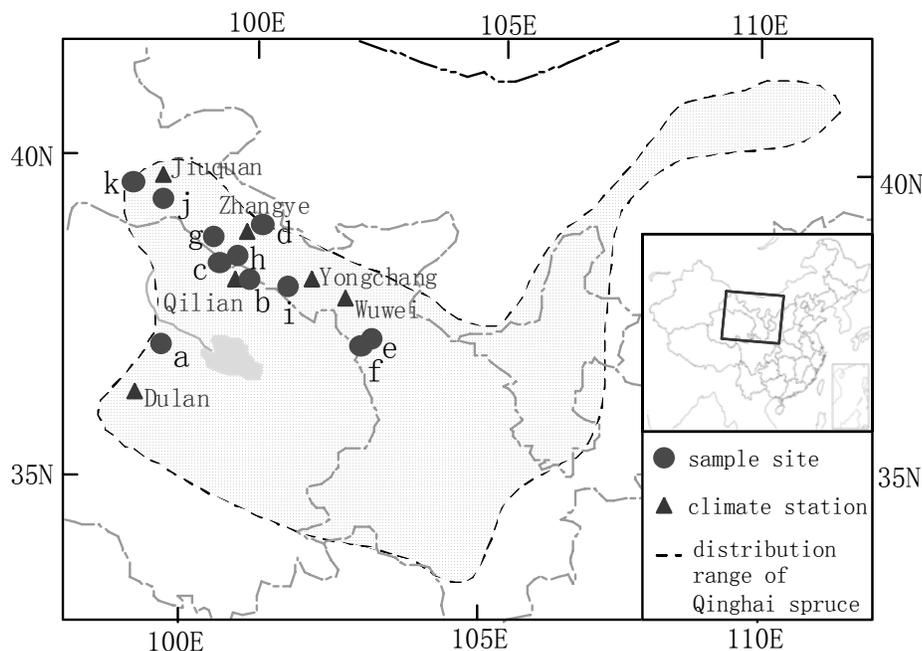


Figure 3.1 Natural range of *Picea crassifolia*, location of sample sites and the nearest climate stations.

detrending methods such as negative exponential function or linear regression ($k \leq 0$), a few series were detrended with a cubic spline with $2/3$ length of the series. We performed all analyses also on raw ring width data, as well as on tree ring indices and chronologies built using Regional Curve Standardization (RCS). Results did not differ substantially and are not shown here. After detrending, individual series of each tree were averaged into single tree indices. We also tested the effect of removed lag-1 autocorrelation in the tree ring series. Tree ring series were still significantly correlated to specific climatic parameters after removal of lag-1 autocorrelation (data not shown).

Table 3.2 Sample size of chronologies and sub-chronologies of each site.

Site	a	b	c	d	e	f	g	h	i	j	k
Site											
chronology*	11	23	30	28	27	18	24	24	22	20	15
Time-slice I	5/6	17/6	17/13	19/9	15/12	10/8	15/9	16/8	-	11/9	10/5
Time-slice II	5/6	16/7	15/15	16/12	16/11	10/8	14/10	12/12	20/2	19/1	10/5
Time-slice III	5/6	14/9	20/10	19/9	14/13	9/9	22/2	17/7	19/3	18/2	14/1

*Total number of trees at each site used to construct the main chronology (line 2) and number of trees in each respective sub-chronology in the three different time slices. Number of trees in sub-chronology 1 before and number of trees in sub-chronology 2 after the dash symbol (/).

3.2.2. Climate data

The circulation system over the Qilian Mts. area is complicated. The northwest parts are mainly affected by westerlies, the south and middle parts are mainly affected by the southerly monsoon and the northeastern parts are mainly affected by the East Asia monsoon (Ding, 1994). Generally, maximum temperature and maximum precipitation occur in summer. Monthly temperature and precipitation records were obtained from the six closest meteorological stations (Fig. 3.1). Although these are the closest stations to our sample sites, they are still a certain distance and elevation difference to the sampling sites (Table 3.1). Since most meteorological stations in Northwest China were set up after 1950, most records are no longer than 60 years. The significance of trends in annual temperature and precipitation from each station was evaluated by a Mann-Kendall trend test.

Since the network of climate stations was sparse, we also used gridded climate data from the high-resolution gridded climate dataset CRUTS2.1 (Mitchell and Jones, 2005) for our spatial analysis of hydrothermal conditions. Grid points between N 35°- 41° / E 96°-106° were used contributing climate data from 1951-2002. To obtain two periods of about equal length and since there is indication for a climate shift around 1976 in many parts of the northern hemisphere (Liu and Chen, 2000), we used 1951-1975 as a reference period to calculate the difference of annual average temperature and total precipitation (J-D) to the period 1976-2002.

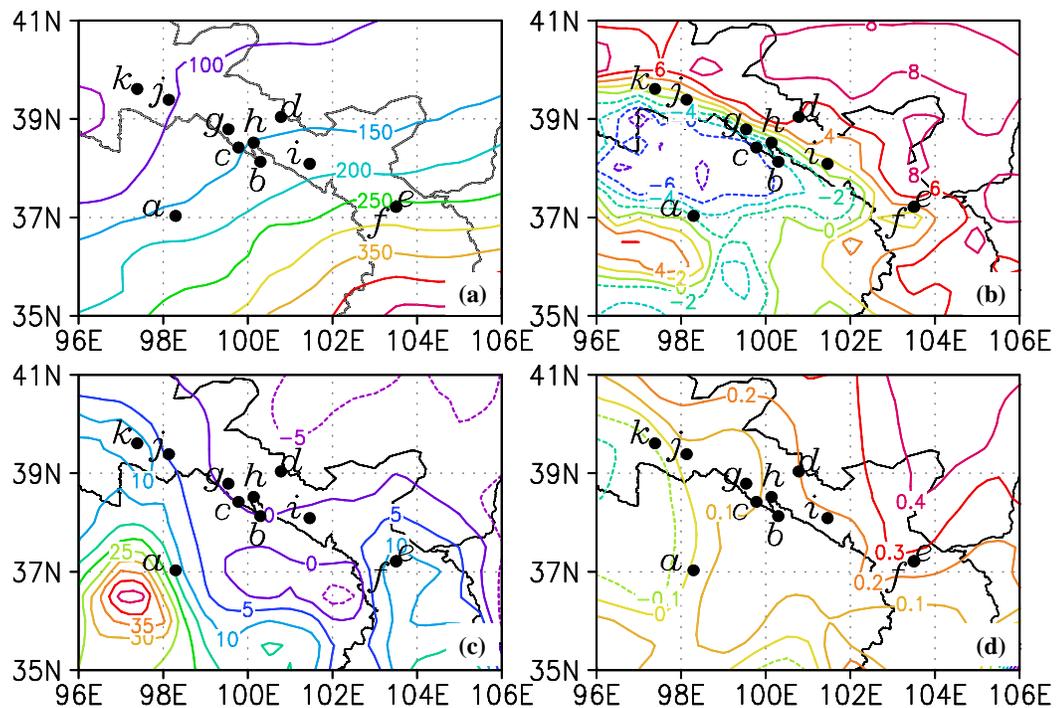


Figure 3.2 Regional climate conditions.

3.2.3. Response of radial growth to main climatic factors

We calculated 30 year moving correlations between single trees of a given sampling site and the main climatic factors mean monthly temperature (MMT) and total monthly precipitation (TMP) from September two years prior to growth to current growth year September. We then displayed correlation scores from three time slices to show how trees responded to climate factors over time. Generally, the first time slice is 1951-1982, the second time slice is 1962-1993 and third time-slice is 1974-

2005. Some sites have a different first time slice because of different start years of the climate records. In order to test 1) how these individual signals translated into a complete site chronology, 2) how a chronology composed of all different recent responses differed from chronologies composed of trees with similar recent responses, and 3) if the differences were significant, we clustered trees within each site into two groups using k-mean clustering. The clustering procedure was based on the correlation coefficients with MMT and was performed for each time slice separately. According to the clustering results, we then built two sub-chronologies for each time slice. To compare results, we also built a chronology composed of all trees within one site. All chronologies were built using ARSTAN with the biweight robust mean and we used the STD and RES chronologies. Then, we repeated the moving correlation analysis with the three resulting chronologies per time slice as was done for the single trees with climate parameters (see above). To test, whether the two samples correlation coefficients are equal, we used the z-transformation to test the hypothesis $H_0: \rho_1 = \rho_2$.

Since this area is heavily influenced by drought (Zheng, 1996), we also calculated correlations between the site chronology (all trees at a site) and each of the two sub chronologies of a site and a climate index (CI), used in (Barber et al., 2000). This CI seems ecologically more appropriate to test the influence of the combination of precipitation and temperature (hydrothermal conditions) on radial tree growth. This CI is composed of the following parameters:

$$CI = ((Yr0 (PPTgr)n - (TA-S)n) + (Yr-1 (PPTgr)n - (TA-S)n)) / 2$$

where $Yr0$ is the year of ring formation, $Yr-1$ is the year prior to ring formation, $(PPTgr)n$ is the normalized growth year precipitation, and $(TA-S)n$ is the normalized April-September temperature from the closest meteorological station to the site. Higher correlations between tree growth and CI indicate stronger moisture deficit caused by warming induced drought on tree growth.

To evaluate the shared variance of the sub chronologies network, we used a principal component analysis (PCA). PCA was performed based on the correlation

matrix during the common period 1917-2005. Members for each of the 22 sub-chronologies (2 per site) were selected based on the clustering procedure during the last time slice, because this time slice showed the most months with significant differences between the two sub-chronologies of each site. We then calculated correlations in three time slices (1952-1980; 1962-1991; 1973-2002) between the resulting PC1 and PC2 with a regional CI based on gridded climate variables.

3.3. Result

3.3.1. Characteristics of regional climate

The spatial distribution of total annual precipitation and average annual temperature based on gridded data shows clear regional hydrothermal differences (Fig. 3.2). Precipitation decreases from the south-east to the north-west. Temperature has a general decreasing trend from north-east to south-west, affected by the topography and elevation of the Tibet Plateau. Comparing 1951-1975 to 1976-2002 indicates a precipitation increase on the north-eastern Tibet Plateau and little change in other areas. The opposite trend is shown by mean annual temperature, with little change on the north-eastern Tibet Plateau and a trend of increasing temperature further north-east. When differentiated into non-growing season and growing season parameters, similar spatio-temporal trends emerged (data not shown).

The climate data recorded at the meteorological stations indicate that annual precipitation of each station shows no significant trend over the last 50 years, but mean annual temperatures show a significantly increasing trend starting between 1987-1997, depending on stations (see Appendix 3.2). Dulan station, as the highest station on the plateau, is the first to show the significant trend.

3.3.2. Instable responses over time: Individual tree level

At all eleven sites there is evidence of instable climate-growth relationships of the majority of individual trees over time, especially a stronger relationship of radial growth with MMTs in the last 30 years (Fig. 3.3). A strengthening negative correlation in some months of individual trees is common to all sites. A

strengthening positive correlation of individual trees in some months is evident mainly from six sites (Fig. 3.3 a-f).

In sites where trees had no significant correlation with temperature during the first time slice (such as sites a and d), trees displayed significant correlation with summer temperature during the last time slice. Sites where trees already had significant correlation with summer temperature (such as sites c, e and f), this correlation became stronger in the last time slice.

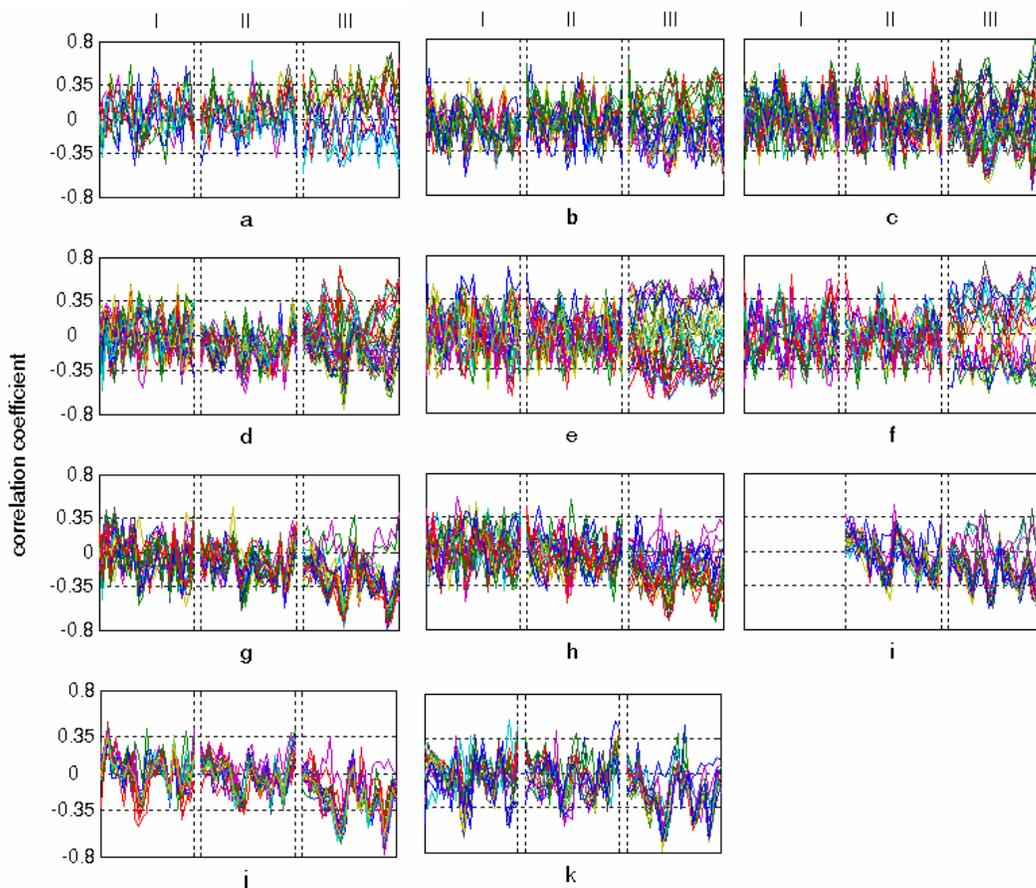


Figure 3.3 Single tree responses to mean monthly temperatures (MMT). Correlations between single trees of each site (a-k) and MMT from the nearest climate station in three different time slices (I-III). Each line represents a series of correlation coefficients of one tree with 25 MMTs starting from September 2 years prior to growth to current year September. Time slice I: 1951-1982; Time slice II: 1962-1993; Time-slice III: 1974-2005. The horizontal dashed line is the 95% significance level. The dominant signal at all sites is an increase in negative correlations of individual trees growth with MMT over time. In six sites (a-f), some individual trees show an increasing positive correlation to MMT, resulting in divergent responses within sites.

Significant negative or positive correlations are mainly found in current and previous growing season temperatures (especially April, June, July and September). In sites e and f, almost all 25 months show significant positive and negative correlations in individual trees. More than half of the sites show a pattern of opposite response during the last time slice, meaning that some individual trees display significant positive relationships with individual MMTs and some trees show significant negative relationship with the same or other MMTs. No obvious change exists in the pattern of individual tree correlation with TMP (see Appendix 3.3).

Table 3.3 Correlation coefficients between the climate index (CI) and chronologies from all sites.

Chronology	Correlation coefficient	Subchro1	Correlation coefficient	Subchro2	Correlation coefficient
a	0.091	a1	0.209	a2	-0.249
b	0.016	b1	0.167	b2	-0.189
c	0.029	c1	0.188	c2	-0.511**
d	0.174	d1	0.338**	d2	-0.332**
e	0.043	e1	0.352**	e2	-0.314*
f	0.009	f1	0.390**	f2	-0.286*
g	0.633**	g1	0.636**	g2	0.105
h	0.363**	h1	0.477**	h2	-0.093
i	0.355*	i1	0.309*	i2	0.454**
j	0.571**	j1	0.519**	j2	0.162
k	0.628**	k1	0.589**	k2	-0.015

Significance levels are indicated by * = $P < 0.05$, ** = $P < 0.01$.

3.3.3. Divergent responses within sites: The sub-population level

Significant differences between the two sub-chronologies of each site (calculated for each time slice separately) and MMT mainly exist in the last 30 years (see Appendices 1 and 4). In the first and second 30 year time slices, some significant differences between the two calculated sub-chronologies at each site exist as well, but these are restricted to some specific months and sites and do not show a consistent pattern over all sites. Therefore we restrict our further analysis to the chronologies obtained by clustering correlation coefficients from the last time slice.

When using site chronologies (all trees from a site), five sites show significant positive correlation with CI (a sign of drought stress). Subchronology 1 (Subchro1) was composed of trees with negative correlations to MMTs during the last time-slice, sub-chronology 2 (Subchro2) was composed of trees with positive correlations to MMTs during the last time-slice. In general, subchro 1 show a drought stress signal (most of them significant). Subchro 2 show mainly the opposite signal, which will be obscured when only looking at site-chronologies.

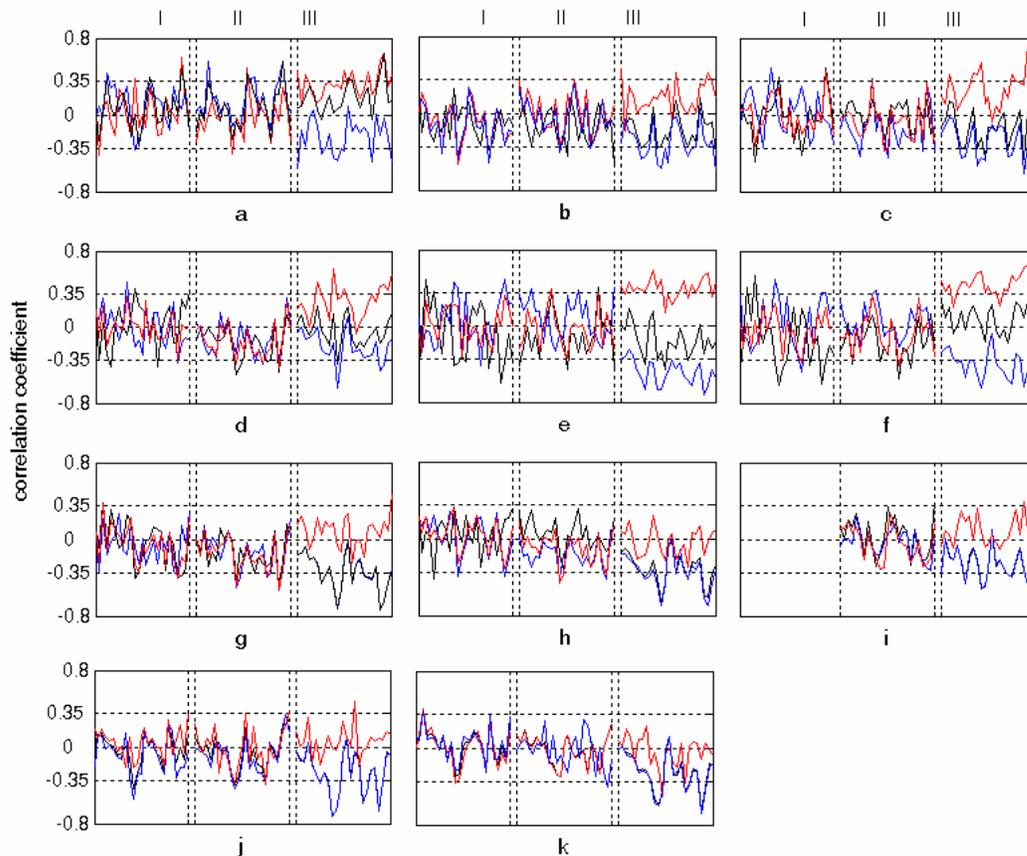


Figure 3.4 Sub-population responses to mean monthly temperatures (MMT). Correlations between sub-chronologies (STD), built from a clustering procedure during the respective time-slice, and MMT from the nearest climate station calculated for the three different time slices (I-III). The red and blue lines represent the respective sub-chronologies, the black line the respective site-chronology. Correlations were computed for a period of 25 MMTs, from September 2 years prior to growth to current year September. Time slice I: 1951-1982; Time slice II: 1962-1993; Time-slice III: 1974-2005. The horizontal dashed line is the 95% significance level. While the two sub-chronologies do not show strong differences in the first and second time-slice, divergent responses clearly exist in six sites (a-f) during the last time-slice. Significant correlation coefficients are shown in Appendix. 3.4.

In the last time slice, the resulting two sub chronologies show opposite trends in correlation with MMTs (Fig. 3.4), meaning that one sub-chronology mainly correlates positively or non-significantly and the other negatively to MMT. All but one site (site a) show a higher percentage of trees belonging to the cluster with negative correlations to MMT (Table 3.2). The chronologies composed of all trees at a site show either similar or less strong correlations with MMT when compared to the two sub-chronologies of the same site. The significant differences in correlation between the two sub-chronologies and MMT exist mainly in June/July of current and prior year. Several sites also show significant differences in April and September of the current year (Appendix 3.4).

The significant differences mainly exist in the correlation of climate with the STD sub-chronologies which contain low frequency variability. Only sites e and f show significant differences in the RES sub-chronologies.

3.3.4. Effect of moisture conditions on sub-populations

The correlations of CI with all chronologies show that the sub chronologies which respond more negatively to MMTs in the last time slice all have a positive correlation with CI. Eight (of eleven) are significant positive correlations (Table 3.3). The sub-chronologies which respond either positively or non-significantly to MMTs in the last time slice generally show a more mixed signal. Four have significant negative correlations with CI (c2, d2, e2 and f2), six have non-significant correlations (a2, b2, g2, h2, j2 and k2) and one (i2) shows a significant positive correlation.

3.3.5. Results of PCA

The PC1 and PC2 of the chronologies network were significant, representing 35.0% and 17.0% of the total variance respectively. Although the chronologies showed different loadings with PC1, all of them show positive correlation with PC1 (Fig. 3.5). Based on the correlation with PC2, sub-chronologies were separated into two groups, one of them showing positive, the other negative loadings with PC2. The two sub-chronologies from each site always belonged to the same group. Group 1

(positive loading with PC2) was composed of sites a, b, c, e, and f; group 2 was composed of sites d, g, h, i, j, and k.

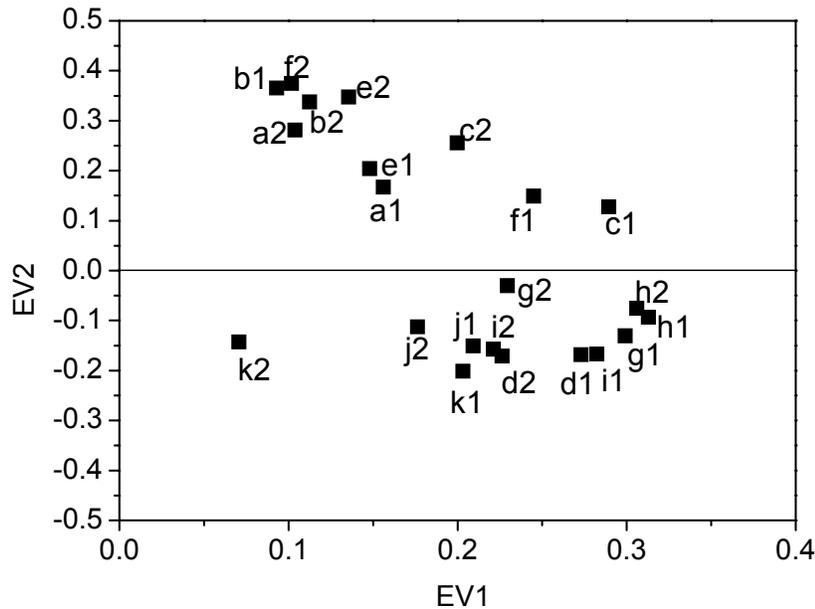


Figure 3.5 Factor loadings of all sub-chronologies in the PCA. While factor loadings of all sub-chronologies are positive with Eigenvector 1, differences exist in factor loadings with Eigenvector 2. Drier, low elevation sites have negative correlations with PC2, higher and wetter sites have positive correlations with PC2. Of those, generally sub-chronologies built of trees with positive correlations to MMT show higher correlations with PC2 (except site b).

3.3.6. Effect of hydrothermal conditions on the tree ring network over time

There are general significant positive correlations between PC1 and CI and significant negative correlation between PC2 and CI (Fig. 3.6). The positive correlations of PC1 with CI expanded during the three time slices investigated from the northeast to the southwest, reaching significance in the whole area covered by our chronology network in the last time slice. The negative correlations of PC2 with CI retreated from the main study area covered by our chronology network to the southwest during the three time slices investigated.

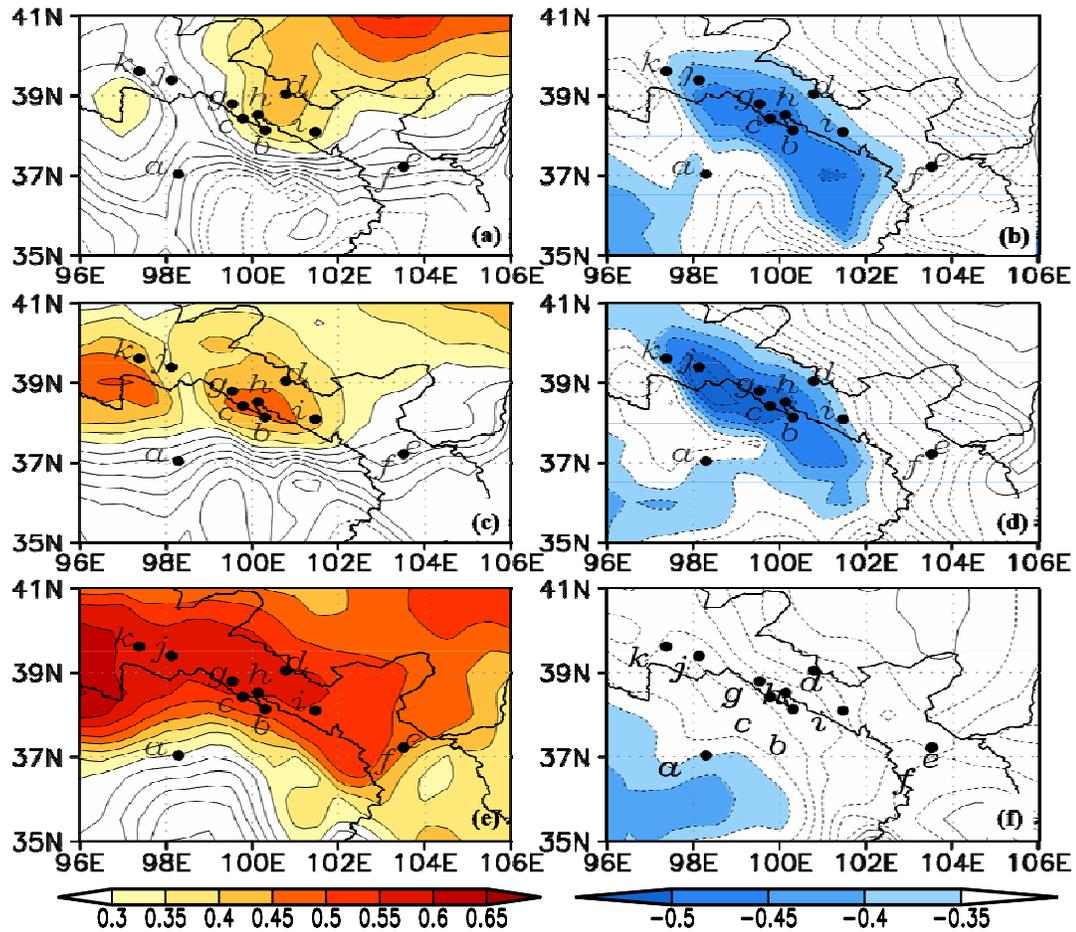


Figure 3.6 Spatial correlations between PC1 and PC2 with gridded climate index (*CI*). Correlations of PC1 (left) and PC2 (right) with regional *CI* show increasing influence of drought stress on our tree ring network over the last half century, concurrent with a retreat of conditions favorable to tree growth. The calculation periods were for (a) and (b) 1951-1982; (c) and (d) 1962-1993; (e) and (f) 1974-2005. Colored areas are significant at the $\alpha=0.1$ level.

3.4. Discussion

During the last years, there has been increasing evidence of changing climate-growth relationships of trees in many northern and alpine areas (Briffa et al., 1998a; Solberg et al., 2002; Wilmking et al., 2004; Carrer et al., 2006; Zhang et al., 2008, Zhang and Wilmking, 2010). Here we specifically tested the stability of climate growth relationships of *Picea crassifolia*, a mid-latitude elevational treeline species in China. All sampling sites, covering large parts of the range of this species, show evidence of increasing, and often significantly changing, correlations between temperature and annual ring width index during the last decades. This change was evident at the level of individual trees (Fig. 3.3) and the level of tree populations

(Fig. 3.4), and was most likely not the result of outliers or the detrending method (Esper and Frank, 2009), since non-detrended (raw ring-width) data showed practically the same results. The phenomena of 1) changing climate growth relationships and 2) divergent responses of individual trees and populations in recent decades therefore seems to affect not only high latitude areas (Cook et al., 2004), but also elevational treeline species in the mid-latitudes of Asia.

Three important questions need to be addressed in this context: 1) What are the reasons for recently changing climate-growth relationships of *Picea crassifolia* changing – ecological or methodological issues? 2) What does it mean for this region, if climate-growth relationships are changing? 3) What are the effects of these results on the field of climate reconstructions using tree rings?

3.4.1. What are the reasons for changing climate-growth climate relationships?

The north-eastern Tibet Plateau is a region influenced by drought and the main climate signal recorded by tree growth in this area is a negative correlation with temperature and/or a positive correlation with precipitation, a drought index or soil moisture (Shao et al., 2005; Yin et al., 2007; Tian et al., 2007). This is also the dominant signal in our tree ring series at all sites.

Drought conditions in this region have intensified over the last decades. First, looking at the station records reveal significant trends of increasing temperature over time, but no significant trends in precipitation (See Appendix 3.2). Second, the gridded climate data show a precipitation increase during the last 25 years only on the highest areas of the north-eastern Tibet Plateau and little change in the main study area (Fig. 3.2c), concurrent with temperature increases in the main study area and little change on the highest areas of the north-eastern Tibet Plateau (Fig. 3.2d). Thus all of our sampling sites have been influenced by increasing temperature and more or less stable precipitation pattern in the last decades, leading to an increase in moisture deficit and increased drought conditions (e.g. Zou et al., 2005).

The reaction of our tree-ring network to increasing drought conditions is twofold: On the one hand, we find an increase of negative correlations to temperature at all sites and in many of our sampled individuals over time. On the other hand, the sample area affected by drought conditions is increasing over time. This is evidenced by more and more sampling sites showing increasing positive correlations of the PC1 of our tree ring network with the regional CI (a sign of drought stress) and retreating negative correlation of PC2 with the regional CI (Fig. 3.6).

Interestingly we do not find an increase in positive correlation with precipitation in trees which show an increasing negative correlation to temperature over time, as has been documented in other studies (e.g. Gou et al., 2001; Shao et al., 2005; Yin et al., 2007; Tian et al., 2007). Most likely this is due to the precipitation data, which might not be ideally suited for larger areas, and the distance of our sampling sites from the climate stations. While temperature generally shows a more regional signal, precipitation, especially in mountainous areas, is far more affected by topography. The patchy nature of precipitation and the lack of spatial overlap between the precipitation and tree ring data might cause missing (increasing) correlations between precipitation and annual ring width in our study. .

While most individual trees at any given site show an increased negative correlation of annual growth with temperature over time, in six sites (a-f) the opposite signal of increasing positive correlation with annual growth over time can also be found in several individual trees (Fig. 3.3). Building chronologies from trees with differing responses shows that there is little to no overlap between trees which are negatively and positively correlated with temperature. In other words, it is possible to distinguish at least two distinct climatic responses of trees to increasing temperatures in these six sites (Fig. 3.4). One response is characterized by increased negative correlations to temperature and decreasing annual radial growth and the other response is characterized by increasing correlations to temperature and increasing annual radial growth in recent decades.

The method of using climate-growth correlations as the basis to build chronologies which show different climate signals has been suggested as to contain “circular

reasoning” (e.g. Büntgen et al., 2008). In this study, however, where we do not use the trees for e.g. climate reconstruction, we use this as simply maximizing the differences between groups for the sake of simplicity. Our first step, where we studied the response of each individual tree to temperature and precipitation over time (Fig. 3.3), contains no circular reasoning and already contains the main results (a clear pattern of changing correlations over time and opposing correlation coefficients in six sites). To better visualize these differences, and only after testing each individual tree did we proceed in the second step to chronology building by clustering technique. The largest significant differences between the two resulting sub-chronologies, calculated for each time slice separately, exist in the last time slice (1975-2005) (See Appendix 3.1). Only in this last time slice the two sub-chronologies show significant differences in correlation scores at all sites at the same time: During summer (June, July). This time slice (1975-2005) also shows the largest change in climate drivers (i.e. significant increase in temperature concurrent with no significant change in precipitation, see Appendix 3.2) and thus points to the possibility that the divergent reactions of individual trees and sub-chronologies might be the result of changing climate variables rather than the methodology used to build the chronologies.

Several other lines of evidence argue for a climatic driver for the occurrence of opposing growth responses: 1) A clear spatial pattern exists that north-westerly sites showed a large percentage of trees per site with a negative correlation to temperature and mostly southerly sites showed more mixed responses with both negatively and positively responding trees within site. 2) Concurrent with the regional pattern, a general trend is evident of low elevation sites showing mostly negative correlations with temperature and high elevation sites showing more mixed responses (Fig. 3.7). Drought conditions are more severe in the north-west of our study area and generally at lower elevations, most likely leading to the dominance of the drought stressed trees in the north-west and at lower elevations. *Picea crassifolia* at high elevation are limited mainly by temperature whereas trees from low elevation are limited by precipitation (Gou et al., 2005; Peng et al., 2007). Similar spatial pattern have been

observed at Alaska’s treelines, where a higher percentage of drought stressed trees was more common in the continental interior (Wilmking and Juday, 2005) and at low elevations (Wilmking et al., 2005). Research based on individual *Picea crassifolia* indicates that trees grown at higher elevation sites have a higher tendency to display divergent response to the main limiting factor than at lower elevation sites (Zhang and Wilmking, 2010). As in these studies, some individual trees in our study, mostly at high elevation sites or at sites receiving relatively more precipitation, seem to be able to benefit from increasing temperatures with increased growth.

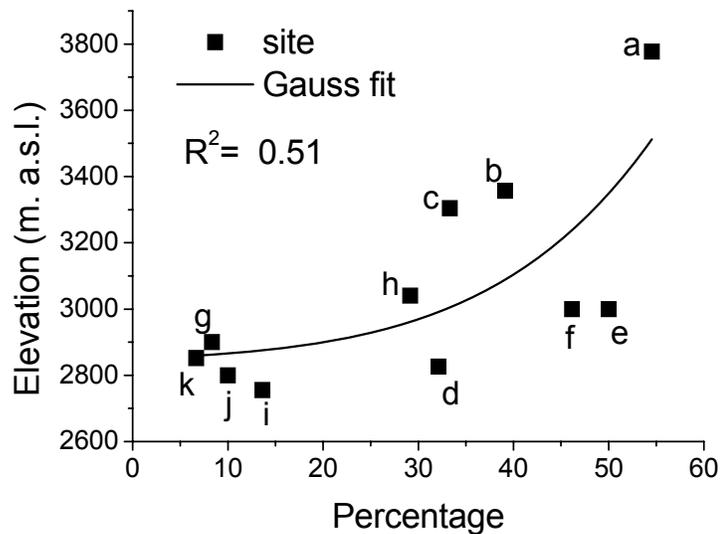


Figure 3.7 Relationship between elevation and the percentage of positive responding trees per site. As elevation increases, the percentage of positive responding trees within a site also increases, from less than 10% to over 50%.

There are several other potential reasons for some trees at a site to benefit from warming and some trees to react with decreasing growth to warming: 1) Methodological effects. We tested differing detrending procedures to avoid so called “end-effects” (Melvin and Briffa, 2008; Esper and Frank, 2009). However, our results of changing correlations of individual trees and sub-populations with temperature over time were similar when using undetrended raw data, traditionally detrended data (negative exponential or straight line fit), regional curve standardization or a cubic spline (50 years) (data not shown). Only in one site (d) could we detect the possible influence of methodology on the chronology building process. Thus methodological differences were unable to fully explain our results. 2)

Age effects: In our study no significant differences in age between the two sub-populations at each site existed (see Appendix 3.5). 3) Competition. While we cannot rule out below-ground competition as a contributing factor, no tree to tree competition seemed to exist in our sample sites. 4) Micro-site differences. Even though we considered each site homogenous with respect to soil type, elevation, aspect and slope, micro-site differences (e.g. soil moisture) could become more pronounced with time under changing environmental conditions and thus might be a factor for the differing growth responses (see also Wilmking and Juday, 2005). 5) Human influence. While we tried to avoid areas influenced by human activity, tree growth at sites e and f seemed to be influenced by compression wood possibly caused by a change in stand density (thinning). While this might have affected the divergent response within these two sites, it is very difficult to evaluate the absolute contribution of human interference. None of the other nine sites showed similar phenomena. 6) Genetic differences might play an important role. However, we do not have any information about our samples at this time, but a test of this hypothesis might be very worthwhile. Thus, while we can exclude some factors at this time, notably methodological ones, our results of opposing growth responses in *Picea crassifolia* at several sites of our study area in China are most compatible with a climatically driven explanation.

3.4.2. What does it mean for this region, if tree growth climate relationships are changing?

Negative correlations with temperature and an increase in temperature at the same time lead to reduced growth rates of affected trees. More than 70% trees from upper and near upper tree line in our study area had growth reduction after 1980 and only <30% trees had increased growth rates during recent years. Model based projections on regional climate change indicate that the current warming trend will increase in the future, while moisture precipitation will not change significantly (Liu et al., 2008, personal communication). Although there is a hypothesis that climate pattern will switch from warm-dry into warm-wet in northwest China (Shi et al., 2007), no

evidence exists so far since there is no increasing precipitation during the last 30 years in our study area, especially in northwest part (Zou et al., 2005). A future warming trend without a concurrent increase in precipitation could lead to higher occurrence of drought conditions and as a result also to more drought stress on *Picea crassifolia*. This species could be eliminated due to drought stress in some sites in the near future (e.g. sites k, j) as has been hypothesized for trees in other areas (Barber et al., 2000; Wilmking et al., 2004; Llody and Bunn, 2007). The key to this scenario is the question of successful recruitment, influenced by the relative abundance of drought stressed and non-drought stressed trees at a site, and the rate of change in environmental parameters. Scenarios of regional development and management of *Picea crassifolia* should be adapted to better consider the limitation posed by future increasing drought stress.

3.4.3. What are the effects of these results on the field of climate reconstructions using tree rings?

The Qilian mountain area is one of the early regions of dendroclimatological research in China (Zhuo et al., 1978). Several tree ring based climate reconstruction were successfully developed using ring width of *Picea crassifolia* (Gou et al., 2001; Kang et al., 2002). Underlying assumption of these and many other climate reconstructions is a stable relationship between tree ring index and climate factors. Here, we systematically investigated the response of *Picea crassifolia* to recent warming and found instable relationships in the vast majority of the cases. This is an important consideration for dendroclimatological research in this area and in general, since the current methodology of dendroclimatic reconstructions does not account for varying and changing relationships of tree growth and climate (Loehle, 2009).

Given our results of differing responses of individual trees within one site in the last three decades, we caution against the use of complete site chronologies in these cases. If we would ignore the differing responses of individual trees, the resulting site chronology would show a watered-down climate signal during the time slice of differing responses and might show a loss of sensitivity (Fig. 3.4, black lines). It is

somewhat of a coincidence that during the last decades, the so-called “divergence effect” has been introduced to the literature (D’Arrigo et al., 2007; Wilson et al., 2007), which describes the phenomenon of a loss of temperature sensitivity of formerly temperature sensitive sites. Our results from six sites (a-f) visually serve as an example for a possible explanation of a loss or change of temperature sensitivity of a site chronology without taking into account differing growth responses.

3.5. Conclusion

Our tree-ring network analysis of eleven *Picea crassifolia* sites showed instable correlation between annual radial growth and MMT during the last 50 years as the main signal in the Qilian mountains area, northwest China. Strengthening negative correlations of individual trees and tree-population at all sites with growing season temperatures indicate increasing limitation of growth by warming induced drought stress. The spatial signature of drought stress in *Picea crassifolia* has been increasing steadily during the last decades and is now influencing large parts of the natural range of this species, especially upper treeline environments.

At a subset of mostly higher and wetter sites, we also found increasing positive correlations of annual radial growth of individual trees and tree populations with growing season temperatures. This divergent response is significant only in the last 30 years concurrent with the significantly increasing temperature trends, indicating a climatic driver. While this phenomenon has so far been only reported from high latitudes, we present here the first large-scale evidence of diverging correlations of tree growth with climate at mid-latitude sites.

Our results indicate a potential ecological reaction of tree populations to changing environmental conditions. Even though we cannot completely rule out other contributing factors such as detrending methods or disturbance, we think that our results are best matched with a climatologically driven explanation. Our results would then have implications for using trees to reconstruct climate, since the indiscriminate use of tree ring data from sites showing opposite responses to

increasing warming could cause mis-calibration of tree ring based climate reconstructions, and over- or underestimation of carbon sequestration potential in biogeochemical models. It might be worthwhile to conduct a spatially comprehensive analysis of possible divergent responses of trees in areas where tree rings are used as the basis for climate reconstruction, since this phenomenon does not seem to be restricted to the high northern latitudes as previously assumed.

Acknowledgements

This work was supported by a Sofja Kovalevskaja Award by the Alexander von Humboldt Foundation, the German Ministry for Education and Research to M. Wilmking, who was also partly supported by a grant from the German Research Foundation (DFG Wi 2680/2-1). XM Shao was supported by a Special Program for Science and Technology Basic Research (Grant No. 2007FY220200).

Chapter 4:

Divergent growth responses and increasing temperature limitation of Qinghai spruce growth along an elevation gradient at the northeast Tibet Plateau³

Abstract

Divergent responses between tree growth and climate factors have been widely reported at high latitudes in the northern hemisphere. Here we show variable climate-growth relationships and divergent growth responses of Qinghai spruce (*Picea crassifolia*) along an elevation gradient at a mid-latitude site at the northeastern Tibetan Plateau, China. Trees from higher elevations, limited mainly by temperature, show divergent growth trends over time and two responses to climate: Some trees show increasing positive and some increasing negative responses to growing season temperature during the last decades. Trees from lower treeline show a strengthening drought stress signal over time and no divergent growth trends within sites. Our results indicate that single tree analysis might be a worthwhile tool to 1) uncover spatial-temporal changes in climate growth relationships of trees, 2) better understand future growth performance and 3) help overcome current limitations of tree ring based climatic reconstructions.

² This paper is published as Zhang Y, Wilmking M. Divergent growth responses and increasing temperature limitation of Qinghai spruce growth along an elevation gradient at the northeast Tibetan. *Forest Ecology and Management*, 2010. (260): 1076–1082.

4.1 Introduction

One of the main challenges in paleo-climatology is to uncover the relationships between climate proxies and their limiting environmental factors and to interpret this relationship by suitable mathematical and statistical methods (Briffa et al., 1995; Esper et al., 2002). This challenge is especially evident when applying biological proxies to climate reconstruction, since living organisms usually respond with non-linear relationships (e.g. optimum functions) to changing environmental drivers (Smith, 2008), which are difficult to model (Loehle, 2008). One of the prime examples is tree rings (Smith, 2008). Tree ring parameters have been traditionally analyzed as responding quasi-linear to e.g. changing climate variables, even though basic tree ring literature points to varying relationships over time, which can take non-linear forms (e.g. Fritts, 1976).

The traditionally applied approximate linear regression function between tree growth and climate factors has been widely applied in tree ring based climate reconstructions (Briffa et al., 2004; Jones et al., 2009). However, in the last decades, as temperature increases in many parts of the earth are not followed by subsequent changes in tree ring growth, mounting data has accumulated on the apparent changes of the relationship between tree growth and climate factors (Jacoby and D'Arrigo, 1995; Briffa et al., 1998a; Barber et al., 2000; D'Arrigo et al., 2004; Driscoll et al., 2005; Carrer and Urbinati, 2006; Lloyd and Bunn, 2007; Pisaric et al., 2007). Instable relationships between tree growth and climate factors (especially temperature) include the reduction, increase or loss of sensitivity, especially during the last decades (Biondi, 2000; Wilmking et al., 2004, 2005; D'Arrigo et al., 2007; Carrer and Urbinati, 2006; Zhang et al., 2008).

One first step to deal with the challenge of varying climate-growth relationships, and to possibly uncover the driver, is the study of single tree's correlation and responses to climate variables. For example, different treeline studies have found that trees growing at the same site responded to climate factors differently, especially in recent decades, and could be divided into different sub-groups according to their long-term

annual radial growth trends and responses to temperature (Wilmking et al., 2004, 2005; Pisaric et al., 2007; Zhang et al., 2008 and submitted). In these examples low-frequency variation between groups was different, while high frequency variation can be similar.

Among several hypotheses about the potential reasons for varying climate-growth relationships, possibly resulting in the “divergence problem” (D’Arrigo et al., 2007), increasing drought stress might be one of the main causes. Warming induced water deficit is or can become the main limitation on tree growth in many areas (Barber et al., 2000; Wilmking and Juday, 2005; Wilmking and Singh, 2008; Zhang et al., submitted).

In alpine areas, temperatures are usually decreasing with increasing elevation, while precipitation usually increases (Fu, 1983; Lin, 1995; Glickman, 2000). The elevational dynamics of forest growth reflects this with tree growth at upper treeline mainly limited by temperature, and tree growth at lower treeline mainly limited by precipitation (Larmache, 1974; Fritts, 1976; Tessier et al., 1997). Mountain gradients thus provide an ideal laboratory to study the effects of different hydrothermal combinations on tree growth. Systematic surveys of trees growing on a slope from lower to upper treeline could thus be helpful in uncovering the (possibly) dynamic relationship between tree growth and changing climate factors.

The Tibetan Plateau (TP) is an important place for studies on climate change effects, since it impacts the regional climate through its thermal and dynamic forcing mechanisms (Zheng, 1996). 20th century warming has been detected in most parts of this area comparable in response to the mean temperature instrumental records in the northern hemisphere (Liu and Chen, 2000). Since the 1970s, tree ring research has been conducted on the TP due to its large forests cover with only little anthropogenic influence (Wu and Lin, 1978). To date, many dendroclimatological and dendroecological studies have been published from this region (Wu et al., 1990; Zhang and Wu, 1992, 1997; Wu and Shao, 1995; Bräuning et al., 1994, 2001; Qin et al., 2003; Zhang et al., 2003; Shao et al., 2005; Gou et al., 2007; Huang et al., 2004;

Sheppard et al., 2004; Liang et al., 2006, 2008), but only few if any have considered in depth the possibility of instable climate-growth relationships.

Qinghai spruce (*Picea crassifolia*) is an endemic widespread tree species on the northeastern TP, widely used in previous dendroclimatological studies (Zhang and Wu, 1992; Liang et al., 2006). Recently, a systematic investigation on upper treeline Qinghai spruce showed instable relationships between tree growth and mean monthly temperature (Zhang et al., submitted). Essentially increasing negative correlations over time indicated increasing drought stress in the area, however, some treeline sites showed divergent growth responses with some trees increasing their (positive) correlations with mean monthly temperature while others followed the regional signal with increasing negative correlations (Zhang et al., submitted). But how do trees at different elevational levels react to a change in the respective climatic drivers: Temperature and precipitation? This is especially important when considering the future growth performance of tree species for forest management, and the (possibly different) distribution of a tree species, both regionally and locally.

In this study, we chose one slope where Qinghai spruce is growing in different hydrothermal conditions from upper treeline to lower treeline at the northeastern TP to investigate the following questions 1) What are the effects of changing climate conditions on Qinghai spruce trees at different elevational levels, 2) Are tree growth and climate correlations changing over time and if yes 3) what are the effects at the different elevations?

4.2. Materials and method

4.2.1. Tree ring data procession

All tree cores of Qinghai spruce were taken from the Qinghainan Mts. at the east margin of the Qaidam basin, more specifically in the Halihatu valley, North East TP (Fig. 4.1). The study site was located on a North East facing slope with inclinations between 15-35° and a soil depth of about 20-40 cm. The upper Qinghai spruce treeline in our study area is about 3780 m.a.s.l. with trees relatively widely spaced

(5-10 m apart) and hardly any crown to crown competition. The lower treeline extended to a small south-north V-shape valley bottom (~3450 m.a.s.l.). The forest coverage on the slope was about 60%. 23-25 tree cores were taken from upper treeline and lower treeline and two elevations in between (Table 4.1). Final sample size at each elevation is shown in Table 4.2. All tree-ring series were processed following the standard procedures of the International Tree Ring Data Bank (ITRDB), and cross-dated using COFECHA (Holmes, 1983). In our analysis we used a) raw ring width and b) series individually detrended using ARSTAN (Cook and Kairiukstis, 1990) with negative exponential curve or linear regression (negative slope or line through mean) fits. After averaging series from within the same tree, trees older than one hundred years were selected in following analysis to avoid the age effect from young trees.

Table 4.1 Sample sites and sample size.

Sample site	Latitude(N)	Longitude(E)	Elevation(m)	Slope	Sample size (tree/series)
W1	37°01.99′	98°39.342′	3777	25°~ 35°	25/50
W3	37°02.02′	98°39.401′	3727	28°~ 38°	24/48
W5	37°02.06′	98°39.467′	3614	~ 35°	24/48
W9	37°01.89′	98°39.757′	3495	~ 15°	23/46

4.2.2. Climate data

The continental arid climate pronounced in our study area is primarily influenced by the Westerlies. The meteorological station in Wulan (approximately 15 km from the study sites) with climate records since 1981 recorded the warmest and coldest months as July (mean of 15.68°C) and January (-11.38°C), respectively. Instead of the short record of Wulan meteorological station, we used the monthly climatic data of Dulan meteorological station (approx. 95 km southwest) (Fig. 4.1). The continuous climate record of Dulan station started in 1954 and the correlation of the mean monthly temperature (MMT) and total monthly precipitation (TMP) data with Wulan are of 0.928 and 0.771 (1981-2005), respectively. The Mann-Kendall test was applied to test the significance of trends in annual temperature and precipitation.

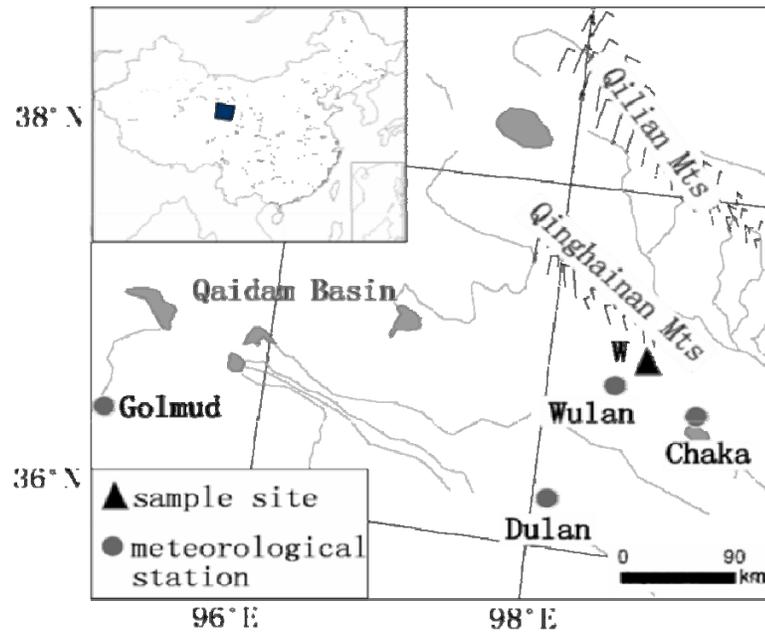


Figure 4.1 Location of sample sites and meteorological stations.

4.2.3. The response of single trees and building sub-groups

First, the climate-growth relationships of single tree series were calculated using 30 year moving correlations between single trees of a given sampling site and the main climatic factors MMT and TMP from September two years prior to growth to current growth year September of the closest meteorological stations (data not shown). For better illustration, we extracted correlation scores of prior and current growing season month (April-September) from three time slices to display how trees responded to climate factors over time. The first time slice consists of the first 30 years (1954 -1985) of the respective climate record and corresponding tree growth, the second time slice starts 10 years later, the third time slice covers the last 30 years of climate record and corresponding tree growth.

To highlight the general pattern of the single tree analysis, trees within each site were clustered into two groups, or sub-chronologies, based on the correlation coefficients with MMT in all three time slices. Sub-chronology.1 consists of all trees with mostly negative correlations to MMT, and sub-chronology.2 consists of all trees with mostly positive correlations to MMT. This was generated using the K-

mean clustering method. To compare results, we also built a chronology composed of all trees within one site. All three chronologies per site were built using a bi-weight robust mean (Cook, 1985) after detrending. To test for stationary and consistency of growth-climate relationships of the resulting separate sub-chronologies at every site, we correlated their indexed growth with growing season mean temperature (April-September, GST) and growing season total precipitation (April-September, GSP) using a moving window of 30 years.

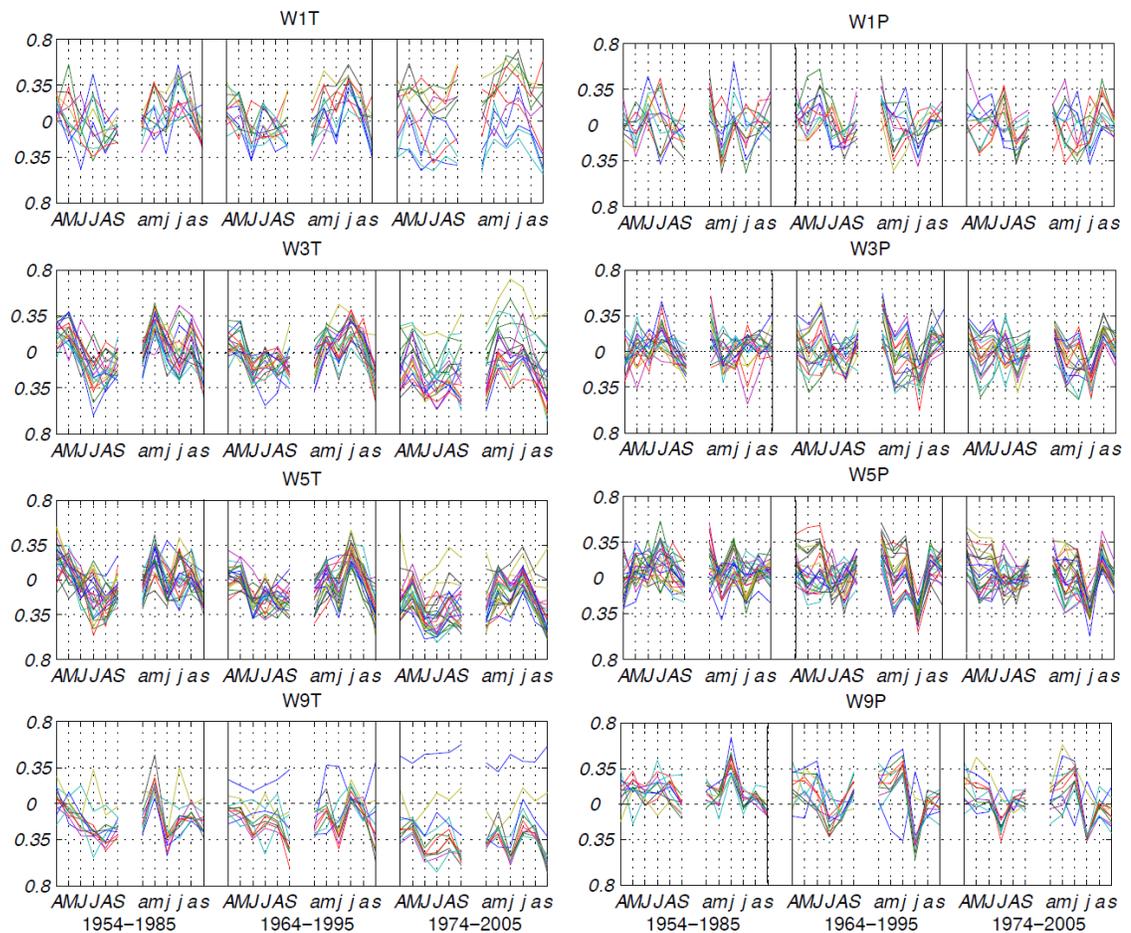


Figure 4.2 Correlations between single trees of all sites (W1, W3, W5, W9), mean monthly temperature (T, left), and total monthly precipitation (P, right) in three time slices. Each colored line represents a series of correlation coefficients of one tree with a climate factor in two growing season (prior and current); A - S are prior growing season April to September; a-s are current growing season April to September; horizontal dashed lines indicate significant level $\alpha=0.05$; different time slices show at the bottom of all figure.

4.3. Results

4.3.1. Growth responses of single trees to climate factors

All trees at all elevational levels on this slope showed instable correlations with MMT over time, and generally more stable correlations with TMP over time, with this general pattern (Fig. 4.2): 1) Trees from upper treeline were mainly limited by temperature, that is, tree growth correlated positively with current growing season MMT and negatively with current growing season TMP, e.g. May, July. 2) Trees from lower treeline were mainly limited by moisture with tree growth negatively correlated to MMT and positively correlated with TMP during the early growing season (May and June). 3) Trees growing at mid elevations showed gradually alternating intermediate responses to MMT and TMP which differed from upper and lower treeline trees. This general correlation pattern was strengthening over the investigation period.

Table 4.2 Chronology statistics.

Code	Sample size(tree /cores)	Ms	a.c.	R1	R2	PC1 (%)	Start year	EPS since1 900	Mean age (yr)	Mean ring width (mm)
W1	11(22)	0.152	0.752	0.214	0.817	34.41	1690	0.93	157	1.167
W1.1	5 (10)	0.127	0.748	0.48	0.884	59	1825	0.838	144	1.071
W1.2	6 (12)	0.165	0.767	0.283	0.758	39.55	1690	0.912	168	1.282
W3	18(32)	0.113	0.636	0.257	0.856	37.13	1790	0.91	176	0.751
W3.1	14 (25)	0.114	0.714	0.238	0.88	38.74	1790	0.954	183	0.748
W3.2	4 (7)	0.137	0.453	0.13	0.736	43.55	1808	0.862	151	0.761
W5	23 (42)	0.145	0.747	0.245	0.731	33.06	1627	0.955	199	0.675
W5.1	21(36)	0.147	0.741	0.22	0.733	29.76	1627	0.972	197	0.698
W5.2	3 (6)	0.183	0.669	0.307	0.7	51.52	1754	0.913	212	0.537
W9	11(18)	0.231	0.785	0.596	0.972	67.41	1835	0.95	106	1.713
W9.1	9 (16)	0.232	0.794	0.67	0.971	71.1	1835	0.95	107	1.73
W9.2	2 (2)	0.246	0.663	+	+	+	1887	0.512	98	1.579

Ms is the Mean sensitivity; a.c is the first order autocorrelation; R1 is the mean correlation between trees (Y variance); R2 is the mean correlation within trees; PC1 is the first principal component; EPS is the expressed population signal; Mean age of each group is the average of the measured ages of trees.

Beside the general tree growth response pattern on our study slope, we also found a clearly divergent response to MMT during the growing season (prior and current year of growth) in the last time slice at the high elevations. At the highest elevation (W1) more than half of the sampled trees (6 of 11) showed an increasing significant positive correlation with MMT, resulting in divergent responses to warming temperatures. This response is mirrored in some trees at lower elevations as well, but significance levels are reached less often. No divergent responses to TMP were found in any sites.

4.3.2. Chronology statistics and sub-group growth trends

Table 4.2 shows the statistic of the chronologies built by all trees of each site (W1, W3, W5 and W9) and sub-chronologies built with groups clustered by their response to MMT. When we compared chronologies from the upper treeline site (W1), we obtained higher mean correlation between trees (R1) as well as higher values for the first principal component (PC1) by sub-dividing the trees into two sub-chronologies. At the next lower site W3, the combined chronology showed higher statistical values than either of the two sub-chronologies. Mixed signals were obtained for elevation site W5 with positive responding trees (W5.2) showing a higher R1 value. At the lowest elevation site (W9) it was not possible to generate two sub-chronologies as we only found 2 trees out of the 11 trees sampled, that showed a positive response to MMT. However, it was still worth generating the first sub-chronology W9.1 as the removal of the two positive responders increased the overall R1 signal.

Additionally, when comparing the first order autocorrelation (a.c.) values, we see once again a subdivision between site W1 and all other sites at lower elevations (Table 4.2). Sub-chronology W1.1 has a lower a.c. value than sub-chronology W1.2. At lower elevations these results are the opposite with all the negative responders (W3.1, W5.1 and W9.1) having higher a.c. values than the positive responding trees (W3.2, W5.2 and W9.2) respectively. The STD chronologies and sub-chronologies of all elevational levels are shown in Fig. 4.3. Trees from upper treeline (W1) diverged into two sub-groups showing different growth trends three times during their common period around 1910, between 1940 and 1960 and again in the last 10

years of the chronology between 1995 and the year 2005. The amplitude of the response on the last 10 years is however the largest one among all trees at all times. Divergence between sub-chronologies exists also in some other elevational levels at different times during the 20th century, but this behavior is mostly due to some outliers (and not half of the sample as in W1), as the chronology generated from all trees at an elevational level closely mirrors the negatively responding sub-chronology.

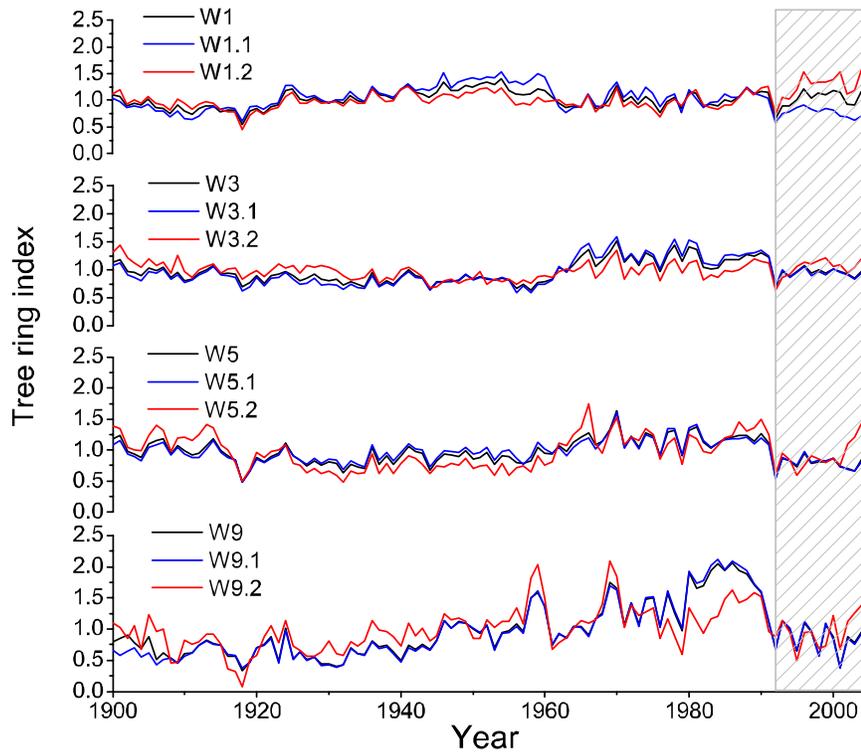


Figure 4.3 Standard chronologies at all elevational levels. The shadowed area is from 1975-2005. At each elevational level, two sub-chronologies (sub-chronology.1, blue line, sub-chronology.2, red line) and the chronology composed of all trees (black line) were compared. Real differences exist only at the highest elevation (W1).

4.3.3. Climate growth responses over time

Correlations with GST over time have changed at every elevational level (Fig. 4.4). As time progresses the strong positive correlation shown among trees from upper treeline (W1, Fig. 4.4 a) with GST increases until around the 1963 - 1993 period,

then correlations between GST and W1.1 decrease, and switch from positive response to negative. W1.2 continuously increases its positive correlation with GST reaching significance levels at the end of the analysis period. W3 (Fig. 4.4 b), the second highest site, shows a similar response pattern to GST as W1, but slightly differs in the strength of the correlation scores. At W5 and W9, the sub-chronologies show basically similar pattern. W5 (Fig. 4.4 c) shows barely positive correlations with GST before a maximum in the 1963 -1993 period, then both W5.1 and W5.2 switch their positive response into a strengthening negative response. At W9 (Fig. 4.4 d), both W9.1 and W9.2 show mainly negative response to GST with the exception of a non-significant response in the periods around 1963 - 1993 period. Then, the negative responses of both sub-groups are strengthening until the end of analysis period, when they reach significance levels with W9.1 showing slightly stronger correlations than W9.2. Correlations with GSP are mostly non-significant, but show a barely significant positive correlation at times at lower treeline.

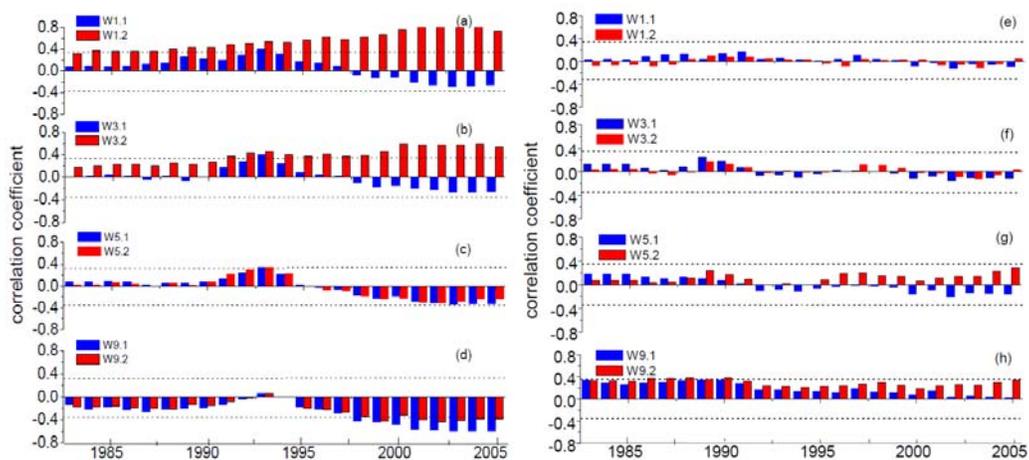


Figure 4.4 Moving correlations between different sub-groups and growing season mean temperature (GST, left a-d), and growing season total precipitation (GSP, right e-h). Dotted lines indicate significance at the level $\alpha=0.05$.

Elevation affects the percentage of trees responding positively to MMT, with higher percentages (55%) at treeline and decreasing percentages with decreasing elevation (18%) at W9 (Fig. 4.5).

4.4. Discussion

It has been recently shown in the literature that changing responses of trees to climate factors are widespread (Briffa et al., 1998a; D'Arrigo et al., 2007; Buentegen et al., 2008) and that it might be worthwhile to individually analyze single trees before they are used in building chronologies to understand the underlying ecological mechanisms (Wimking et al., 2004, 2005, Pisaric et al., 2007; Zhang et al., 2008). Most of this evidence has been focused on treeline areas in high and mid latitudes of the northern hemisphere. Investigation of single tree responses of Qinghai spruce at highest elevations shows that divergent growth trends and changing climate-growth relationships widely exist in the Qilian Mts. area (Zhang et al., submitted). Our results here show that trees growing at temperature limited sites display more divergent growth responses to increasing temperature during recent decades than trees growing at moisture limited sites.

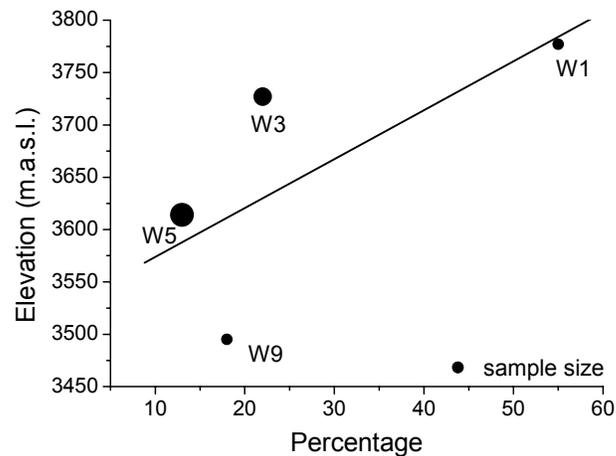


Figure 4.5 Relationship of the percentage of positive responding trees per site and elevation. The size of each dot indicates the total sample size of the site.

Many dendroclimatological studies at subalpine regions have shown that summer temperatures limit annual increment growth of trees at upper treeline (e.g. Peterson and Peterson, 1994; Oberhuber, 2004; Körner and Paulsen, 2004; Frank and Esper 2005). Working along elevational gradients on the TP, studies on tree growth

climate relationship using the traditional site chronology analysis have shown that trees at lower treeline have similar responses to those shown in our analysis, in that tree growth is mostly moisture limited (Gou et al., 2004; Peng et al., 2007). Moisture limitation at lower treeline fits the basic ecological assumptions (Lamarche, 1974; Hughes, 2002). However, Peng et al. (2007) in their study along an elevational gradient did not find tree growth limitation as a result of GST even at upper treeline. This might be due to two reasons: 1) Their upper treeline had the same elevation as our lower elevation study sites (around 3400 m.a.s.l.) and might not have contained trees with a temperature signal. 2) By using traditional site chronologies, Peng et al. (2007) might have suppressed the information contained in single trees as shown in our analysis.

Temperature limitation at upper treeline on the TP has been reported from other species as well, e.g. Qilian Juniper (*Sabina przewalskii*) at similar elevations as our site (Liang et al., 2006). However, the positive correlation of Qilian Juniper to GST at upper treeline in this region was not consistent among all of their research sites in the Qaidam basin. At some sites, only the moisture limited tree growth signals were reported (Liang et al., 2008; Zhu et al., 2008).

Traditionally, site chronologies are assumed to represent tree growth climate relationships at the local scale (Fritts, 1976; Hughes, 2002). However, due to the mounting evidence which shows two opposing growth responses among trees within one site, there is a need to uncover potential reasons for this differing growth response. One potential reason might be a rapidly changing environment. During the last forty years, the yearly average temperature of most areas in the TP increased with the rate of 0.2 to 0.4°C/decade (Ma and Li, 2003). Within the TP, Qaidam basin had the highest increase in temperature, without the equivalent increasing trend in total precipitation (Liu and Chen, 2000; Liu et al., 2006), possibly leading to a decreased moisture supply. Temperature is a key factor that regulates many terrestrial biogeochemical processes, such as soil respiration (Raich and Schlesinger 1992; Kirschbaum 1995), and plant productivity (Warren and Wilson, 1957), and plant nutrient uptake (Bassirirad et al., 2000). On the TP, higher elevations have a

more rapid increase in temperature than lower elevations (Liu and Hou, 1998; Liu and Chen, 2000). This might be a reason for trees at higher elevation to display subgrouping behavior. Furthermore, differences of micro-environment or genetical differences between trees from one site might be an important reason why trees display different responses under increasing warming during the recent decades (Wilmking and Juday, 2005; Wilmking and Singh 2008). Unfortunately, we neither have extensive environmental (such as soil layer depth, soil moisture status, nutrient supply, etc.), nor genetic information on every individual tree. Thus it is hard to come to a conclusion at this point in time of why individual trees display opposing responses. More in situ work should be done to test these hypotheses in the future.

In general, we would recommend to every dendrochronological study the collection of as much environmental information as possible. For example, not only should a core or two be retrieved from every individual tree, but also the exact tree position noted by GPS for later use in a geographical information system. Tree specific measurements such as diameter at breast height and tree height should be recorded, as well as possibly crown diameter or other allometric parameters. If at all possible, measurements should be carried out in plots, where ideally all trees are cored, but at least their position within the plot recorded to enable us to look at e.g. possible competition, regeneration, and stand dynamics, which all potentially influence a climatic signal. In addition to tree related data, spatial environmental data of the plots and especially right around the sampled trees (e.g. soil type, rooting depth, drainage class, slope angle, moisture status or understory vegetation etc.) will be extremely valuable in any later analysis and most likely enable us to better address the ecological foundation for diverging growth trends.

An alternative possibility next to an ecological explanation to explain divergent growth trends might be the method used to detrend the tree ring data. In this study we used traditional detrending techniques such as negative exponential curves and straight line fits, which have been shown to possibly artificially inflate the last portion of the tree ring series (so called “end-effect”), especially when ring width is very small (Cook and Peters, 1981). This inflation is mainly due to the constraint of

the curves to negative slopes and thus 1) an underestimation of the last years of growth which 2) gets inflated by the method to calculate the tree ring index (division). One could thus construct an argument that the smallest ring widths at the highest elevations (W1, the location where divergent growth trends are recorded in our sample) should be theoretically most affected by end-effects when compared to other elevations. Therefore we visually checked each detrending curve to assess if the raw data at the end of each series was “undershot” or if the increased indexed growth in the last years especially in the W1.2 chronology was a true characteristic of the undetrended growth curve. In 9% of the cases, increases in the detrended tree ring series might have been a result of the detrending method, which in turn means, that 91% of the tree ring series were detrended with an adequate method. In addition, average ring width along the elevational gradient and between sub-chronologies of the same elevational level does not vary significantly. Taken together we show that our results are to a very large degree not affected by methodological “end-effect” issues and as such an ecological explanation for our results seems the most likely.

Comparing the growth trends of both sub-chronologies over time, the most evident divergent response appears in last few decades even among those trees that once had similar growth responses (Fig. 4.4). The higher PC1 scores of individual sub-chronologies compared to the combined chronology of each sites indicate that some critical information might be lost if trees are not individually studied (and then grouped), especially at the temperature limited upper treeline. As stable and consistent correlation of tree growth to climatic factor are the current foundation for tree ring based climate reconstruction and the projection of future tree growth. Climate reconstructions and forest growth projections will need to take this analysis into account, which shows that the sub-group behavior seems closely related with changing climate factors. If these divergent sub-groups response to climate factor are in the future neglected, we will not only loose the information which is recorded by tree growth but could mis-estimate the climate variability of past times and the tree growth in the future.

4.5. Conclusions

Our analysis of *Picea crassifolia* from the same slope but from different elevational levels showed instable correlation between annual radial growth and MMT during the last 50 years. Formerly positive correlations with GST switched to negative correlations at every elevational level. However, at upper treeline and just below, a subset of trees responds with increasing positive correlations to GST, leading to divergent growth trends of sub-chronologies and divergent correlations with GST. It seems that at temperature limited sites (e.g. upper treeline), trees have higher tendency to display divergent response to the main limiting factor than at lower elevation sites, where tree growth is mainly influenced by moisture stress. Here, we call for more spatially comprehensive analyses of possible divergent growth responses of trees, especially at temperature limited sites before tree rings are used as the basis for climate reconstruction.

Acknowledgment: We thank Prof. Xuemei Shao for her support and informative discussions, Dr. Gabriela Antunez de Mayolo Wilmking for her kind English editing, Tianyu Li, Dr. Yonghong Zheng and Yan Li for field assistance. This work was supported in parts by DFG WI2680/2-1 and National Basic Research Program of China (Grant No. 2005CB422002)

Chapter 5:

Process-based modeling analyses of *Sabina przewalskii* growth response to climate factors around the northeastern Qaidam Basin⁴

Abstract

Sabina przewalskii is the longest living endemic tree species in the northeastern Tibetan Plateau, and has been widely employed in tree ring based climate research in China. However, most dendroclimatic reconstructions have been primarily based on empirical relationships between tree growth and climate factors identified by statistical assessment. To date, the physiological relationships between tree growth and their limiting climate factors have not been properly assessed. Here, we simulated the physiological response of *Sabina przewalskii* tree growth to major limiting climate factors based on the Vaganov-Shashkin (VS) model. The VS modeled results validated the relationships between tree ring and climate factors constructed by statistical models, both approaches suggesting that precipitation during the early growing season, especially in May and June, has significant effect on tree growth, while temperature mainly affects tree growth by warming-induced drought and by extending the growing season. Under current and projected climate scenarios, our modeling results predict an increase in radial growth of *Sabina*

⁴ This paper is in press as Zhang Y, Shao X, Xu Y, Wilmking M. Process-based modeling analyses of *Sabina przewalskii* growth response to climate factors around the northeastern Qaidam Basin. Chinese Science Bulletin.

przewalskii around the Qaidam Basin, with the potential outcome that regional forests will increase their capacity to sequester carbon.

5.1. Introduction

Tree ring indices (width, maximum latewood density and isotope etc.) play a crucial role in paleoclimatic research (Mann and Jones, 2003; IPCC, 2007). Several millennial climatic reconstructions at regional and hemisphere scale have been developed by this proxy (Mann et al., 2008, 2009). Tree ring indices are useful in revealing historical climatic variation and in projecting future climate change (Jones et al., 2009). One common approach in dendroclimatology is to approximate the relationship between tree growth and climate factors by a linear regression function (Fritts, 1976; Hughes, 2002). However, as temperatures have increased in many parts of the Earth during the last century, a phenomenon called “divergence” between tree growth and climate factors has been reported from the Northern hemisphere circumpolar area and from mountain area in the mid-latitudes of the Northern Hemisphere. This phenomenon encompasses the divergence between tree ring based reconstruction and measured data (Jacoby and D’Arrigo, 1995; Briffa et al., 1998a; D’Arrigo et al., 2007), the divergence of tree growth and their main limiting climate factors (Oberhuber 2004; Carrer and Urbinati, 2006) and the divergent growth responses of trees within sites (Wilmking et al., 2004; Wilmking and Juday, 2004). All of these divergences indicate that the statistically approximated linear relationship might not universally apply between tree growth and their limiting climate factors. Tree ring based climate reconstructions based on statistical models might over- or underestimate climate history, highlighting the need for a systematic physiological analysis of tree growth-climate relationships.

Physiological tree growth models are process-based models based on linear and non-linear relationships between tree growth and climate factors. Among such models, the Vaganov-Shashikin (VS) model is the most popular and widely used (Vaganov et al., 1996; Fritts et al., 1999). The VS model focuses mainly on the relationships between cambium activity and its limiting climate factors. The model is based on the

following hypotheses: (1) External influences mainly affect the cambial zone, specifically, the linear growth rate of cambial cells. (2) The external factors are temperature, light and soil moisture. (3) The principle of limiting factors is employed in the calculation of growth rates i.e. growth rate at a certain time of a season cannot be higher than that allowed by the most limiting factor. (4) The variations of growth rate in the cambial zone mainly pre-determine the anatomical characteristics of the tracheids being formed (e.g. radial diameter, cell wall thickness). (5) The model simulates variations in growth rate and tree ring structure resulting from current climatic changes (within the season). However, the model simulates the climatically induced tree ring width and structural variations only. Compared to other models, e.g. TREERING2000, that explicitly treats photosynthesis, respiration and the partitioning of assimilates (Vaganov et al., 2006), its applicability is limited. Despite such limitations, the VS model remains the most popular process based physiological model on account of its simplicity and its proven success in simulating coniferous tree growth in North America and Siberia (Anchukaitis et al., 2006; Evans et al., 2006). In China, the VS model successfully simulates the growth of *Pinus tabulaeformis* from Helan Mts and *Pinus armandii* from Huashan (Yin and Wu, 1995; Shi et al., 2008; Vaganov et al., 2011), and was hence an obvious choice for the simulation of radial tree growth in our current study species.

Sabina przewalskii is an endemic conifer species on the northeastern Tibetan Plateau (Qinghai Forest, 1993). It is the most important forest component because of its long age, drought endurance, and wind resistance. Several millennia-long tree-ring width chronologies of *Sabina przewalskii* have been compiled (Zhang et al., 2003; Shao et al., 2005; Liu et al., 2006) and employed in regional precipitation reconstruction. However, the tree growth climate relationships underlying these reconstructions were mainly assessed by statistical models, and no process based physiological validation has been undertaken to date. In this study, we simulated *Sabina przewalskii* growth and its main limiting climate factors by the physiological process model (VS model) to test (1) how trees physiologically respond to variations in their main limiting factors, (2) whether results are comparable to this relationship as

derived by statistical models, (3) how this relationship has varied in the past and what it predicts for the future.

5.2. Material and methods

5.2.1. Tree ring data

Thousands of *Sabina przewalskii* tree cores from seven sites have been collected from Zongwulun Mt. and Shalike Mt. around the northeastern Qaidam basin (Fig. 5.1). Increment cores were taken from dominant and co-dominant trees which appeared healthy and which were isolated at or close to their upper limit of around 3500–4000 meter above sea level (m a.s.l.) (Shao et al., 2005). All cores were processed following standard methods (Cook and Kairiukstis, 1990). All series have been employed to reconstruct the millennial precipitation in the Delinsha region. After comparing the relationship between the sites, we chose DLH3 (N37°27′05″, E97° 32′33″) as a typical site representative of all seven sites to simulate the regional physiological process of *Sabina przewalskii* to its main limiting climate factors.

DHL3 is the closest sample site to Delingha city, in which the meteorological station is located. 56 cores from 28 trees appeared healthy and isolated were sampled at a northwest facing site with slope around 20°, 50 cm soil layer at 3920 m.a.s.l. Following precise crossdating, chronologies were developed using the ARSTAN program (Shao et al., 2005). Nine pointer years were selected from 11 trees according to the annual precipitation and common wide rings and narrow rings. Wide rings developed in 1959, 1989, 1993 and 2002, while narrow rings were formed in 1957, 1966, 1979, 1995 and 1998. Cell numbers of each pointer year were counted by image analysis. First, the mean xylem cell numbers from five files were counted in each ring of every pointer year on each selected tree. The cell number of a given pointer year is the average of all standardized mean cell numbers of each tree in that year (Cook and Kairiukstis, 1990).

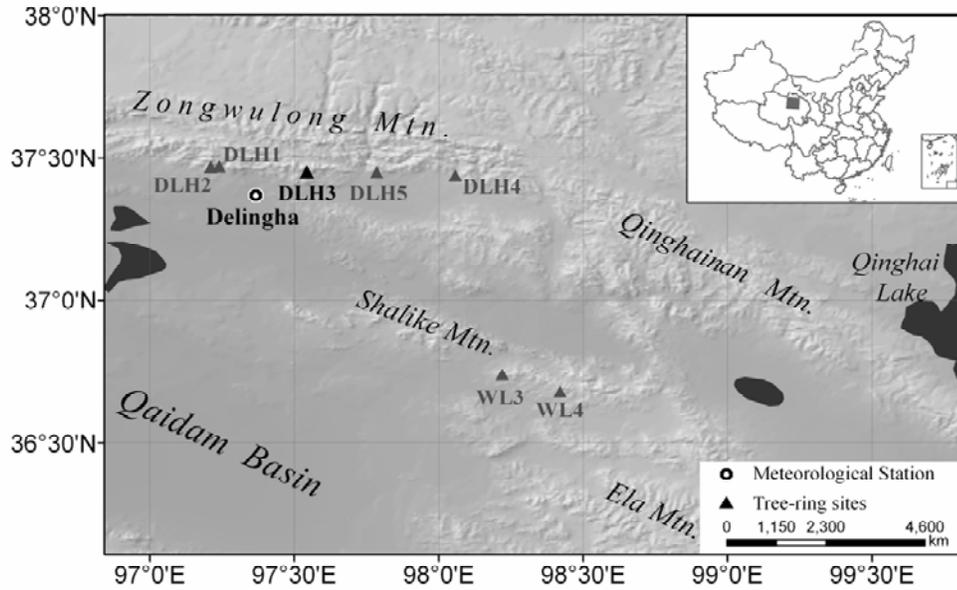


Figure 5.1 Sample site and meteorological station.

5.2.2. Climate data

The continental arid climate pronounced in our study area is primarily influenced by the Westerlies. The average monthly and daily temperatures and precipitation data from the meteorological station in Delingha (Figure 1), which holds climate records dating from 1955 (1956 in our analysis because some data from 1955 are missing) have been used in this study. The Mann-Kendall test was applied to test the significance of trends in annual temperature and precipitation. Because the elevation of the meteorological station (2981.5 m) is lower than that of the sample site (3920 m), a lapse rate (0.56°C/100m) was applied to interpolate the measured temperature from Delingha station to our sample site. No interpolation was performed on the precipitation data.

5.2.3. VS model

In the model, the seasonal growth of a tree is assumed depended on three main factors:

$$Gr(t) = GrE(t) \times \min[GrT(t), GrW(t)], \quad (1)$$

where $GrE(t)$, $GrT(t)$ and $GrW(t)$ are the partial growth rates, calculated independently from solar irradiation, temperature and water content in soil.

Calculation of solar radiation on tree growth. $GrE(t)$ is calculated from eq. (2), where φ is latitude, θ is sun slope angle, and ϕ is day length.

$$GrE(t) = \sin\varphi\sin\theta + \cos\varphi\cos\theta\cos\phi. \quad (2)$$

Here the transmittivity of the atmosphere and the eccentricity of the Earth around the sun are ignored.

Calculation of temperature on tree growth. In the model, tree growth starts when accumulated temperature is equal to T_{beg} . A piecewise linear function is employed for calculation of temperature on tree growth. There is no growth when temperature is less than a given minimum temperature. The growth rate increases linearly up to the first temperature optimum (T_{opt1}). Growth rate is stable between T_{opt1} and the second temperature optimum (T_{opt2}) inclusive. The growth rate decreases linearly between T_{opt2} and a limiting temperature (T_{max}), beyond which growth ceases.

Calculation of soil moisture on tree growth. Similarly to $GrT(t)$, $GrW(t)$ is calculated by a piecewise function with four parameters W_{min} , W_{opt1} , W_{opt2} and W_{max} . Daily water in soil (dW) is determined from a water balance equation:

$$dW = f(P) - Er - Q, \quad (3)$$

where $f(P)$ is daily precipitation, Er is daily water loss in soil by transpiration and Q is runoff. $f(P)$ is calculated as

$$f(P) = \min[kl \times P, P_{max}], \quad (4)$$

where P is the actual daily precipitation and kl is the part of precipitation falling into soil.

There are two ways to evaluate and define the parameters in the model. All parameters can be derived from experimental information prior to calculation. Alternatively, approximate starting values of parameters can be used in initial

calculations and the simulated results are then compared with the observed tree ring chronologies, as the first step in an iterative model-improvement process. In this study, both approaches have been applied. Parameters such as the depth of root system, wilting moisture and maximum daily precipitation falling into soil were defined by observed information. The other parameters were determined using the iterative approach. Start values used here were the same as those in previously-published studies (Vaganov et al., 2011).

5.3. Results

5.3.1. Climate condition in study area

The continental arid climate is pronounced in the study area, which is characterized by a typical inland aridity. The warmest and wettest month is July. Throughout the past 50 years, the highest recorded temperature in July was 20.5°C and the maximum precipitation was 36.1mm. The main source of soil moisture is precipitation. According to climate data recorded at Delingha meteorological station, annual mean temperature and precipitation have increased significantly during the last half century ($P < 0.0001$). Temperature increased mainly during autumn and winter (Jan., Feb., Sep., Nov. and Dec.), while precipitation increased mainly in July ($P = 0.0008$), January ($P = 0.01$) and June ($P = 0.09$). These results suggest an upward warming and wetting trend in this region.

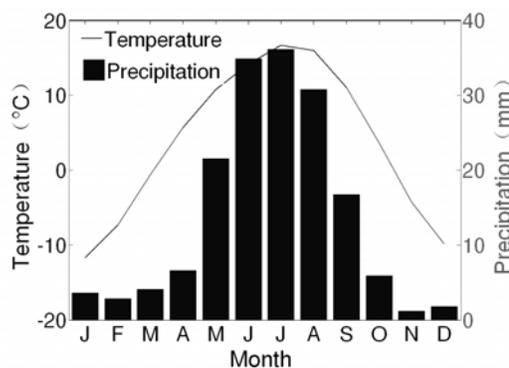


Figure 5.2 Monthly temperature and precipitation recorded in Delingha meteorological station.

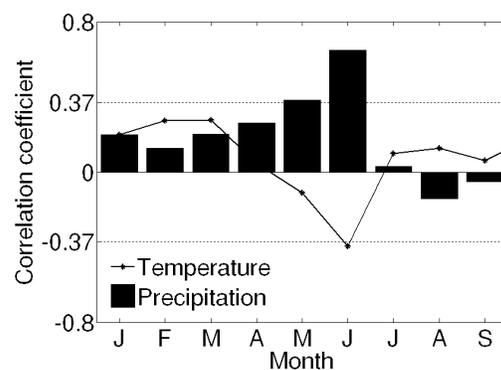


Figure 5.3 Correlations between DLH3 chronology and monthly temperature and precipitation.

5.3.2. Statistical analysis

The standing and environment of *Sabina przewalskii* is similar at northeastern Qaidam Basin. The climate information recorded by trees sampled within this area is coincident also. According to correlations between chronologies after removing growth trend and retaining most of the low frequency signals (Table 5.1) (Shao et al., 2005), it is clearly seen that trees from these sites have been coherent at both low and high frequency (first difference) during the last thousand years. The highest correlation (0.827) is between DLH1 and DLH2, the lowest (0.598) is between DLH1 and WL4. Correlation relationships of these two pairs are significant at first difference with correlation coefficients 0.919, 0.696 respectively. DLH3 shows high correlation relationships with all other sites. Hence we used DLH3 to represent all the other sites in the following analysis.

Trees at the DLH3 site have high common variance. The mean sensitive is 0.4 and miss ring rate is 1.238%. The ring width chronology is 1599 yrs, AD404-2002. The statistical model shows that DLH3 ring width chronology correlates positively with precipitation of current May ($R=0.38$, $P<0.01$) and June ($R=0.65$, $P<0.001$) and negatively with temperature of current June ($R= -0.39$, $P<0.01$, Fig. 5.3).

Table 5.1 Correlations between chronologies of all sample sites (AD 1005-2001).

	DLH1	DLH2	DLH3	DLH4	DLH5	WL3	WL4*
DLH1	1.00	0.919	0.855	0.734	0.797	0.735	0.696
DLH2	0.827	1.00	0.887	0.785	0.853	0.780	0.749
DLH3	0.679	0.783	1.00	0.784	0.852	0.753	0.733
DLH4	0.621	0.737	0.724	1.00	0.873	0.759	0.773
DLH5	0.686	0.787	0.771	0.837	1.00	0.788	0.776
WL3	0.610	0.727	0.689	0.728	0.792	1.00	0.895
WL4	0.598	0.710	0.691	0.733	0.776	0.890	1.00

* Lower left corner is annual correlation coefficients, top right corner is first difference correlation coefficients (Shao et al., 2005).

5.3.3. Process model analysis

Model parameters. Tree ring model parameters used in our final simulation are listed in table 5.2. Model parameter testing revealed that *Wopt1*, *Tmin* and *Topt1* are the

most sensitive parameters to tree growth (Fig. 5.4). The correlation between the observed and calculated values of tree ring width increases as W_{opt1} increases in the range $0.1 < W_{opt1} < 0.18$. This trend disappears for values of $W_{opt1} > 0.18$. No obvious change is observed when other parameters are changed (e.g. T_{opt2} , W_{opt2})

Table 5.2 Numerical value of model parameters.

Model parameter	Description	Value
Tmin	Minimum temperature (°C)	4
Topt1	The first temperature optimum(C)	14.6
Topt2	The second temperature optimum (°C)	22.0
Tmax	Limiting temperature (°C)	31.0
Wmin	Minimum soil moisture (wilting moisture; v/v)	0.04
Wopt1	The first optimum of soil moisture (v/v)	0.18
Wopt2	The second optimum of soil moisture (v/v)	0.8
Wmax	Limiting soil moisture (v/v)	0.9
Tbeg	Temperature sum determining growth start (°C)	60
Pmax	Maximum daily precipitation falling into soil (mm)	20
Droot	Depth of root system (mm)	500
k1	Part of precipitation falling into soil (dimensionless)	0.86
k2	The first coefficient for calculation of transpiration (mm/day)	0.12
k3	The second coefficient for calculation of transpiration (1/degree)	0.175
kR	Coefficient of water infiltration from soil (dimensionless)	0.001

Model behavior: inter-annual and intra-annual simulations. We first assessed the ability of the VS model to simulate inter-annual tree ring formation. The observed and simulated annual tree ring indices of the analyzing period, 1956-2002, are plotted in Fig. 5.5. In general, good agreement is observed at annual and at inter-annual scale. The correlation between observed and simulated series during the analysis period is 0.681 ($P < 0.001$). Xylem cell numbers of pointer years also match well between actual and simulated data, with correlation 0.73 ($P < 0.01$). Comparing model result and observed data of single trees, the highest correlation is 0.92 ($P < 0.001$) and the lowest is 0.50 ($P < 0.01$).

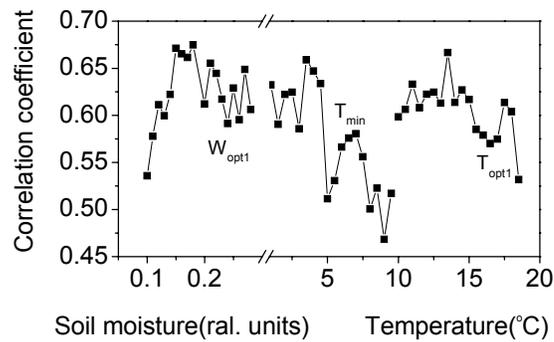


Figure 5.4 The sensitivity range of model parameters

Influence of climate factors on ring width formation. The difference between a wide ring year and narrow ring year is caused mainly by moisture limitation (Fig. 5.6). A high annual radial growth (wide ring formed) results when the moisture is abundant and temperature is not high during the beginning of the growing season (May to June). On the contrary, small annual radial growth (narrow ring formed) results when moisture is reduced during the beginning of the growing season, although the growth rate due to temperature is high at the same time. According to the observed climate record, no large differences of annual precipitation (greater than 100mm) exist between pointer years, excepting 1957 (during which the annual precipitation was 70mm). The main difference between years results from the accumulation of precipitation from January to June, especially in April, May and June. In years when a wide ring is formed, the precipitation during April-June is around 150mm, about 50% to 75% of the annual total precipitation. In years with narrow rings formed, the precipitation during April-June is less than 50mm, a mere 28% of annual precipitation. Meanwhile, there is no difference in temperature during this period between all pointer years.

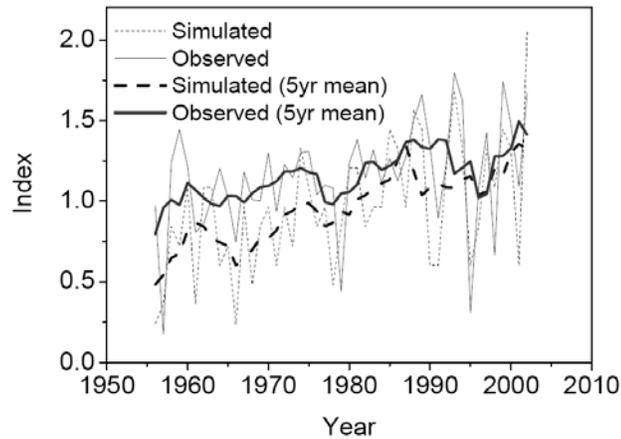


Figure 5.5 Observed and simulated tree-ring width indices, DLH3, 1956–2002. Annual (thin lines) and 5-year mean (thick lines) correlations are $R = 0.68$ and $R = 0.81$, respectively, both significant at the 99% level for the effective numbers of degrees of freedom.

Effects of growth start and end dates on cell numbers and tree ring widths. According to our model simulation (Fig. 5.7), the start date of the growing season falls within the range of the 114th to the 218th day of each calendar year (corresponding to end of April to beginning of August). The end date of the growing season falls within the range of the 234th day to the 284th day (corresponding to end of August to beginning of October). The length of the growing season of *Sabina przewalskii* has expanded in recent years. In the last half of the analyzing period, the start date is advanced by 9 days, and the end date delayed by 6 days, compared to the first half part of the analyzing period. Correlation coefficient for the observed tree ring index series and the start date series is -0.611 , which is significant at the 0.001 level. There is no significant correlation between the observed tree ring index series and the end date series.

5.4. Discussion

The VS model has been successfully employed to simulate, evaluate and interpret the tree growth-climate relationship of several conifer species for a variety of environmental conditions in the northern hemisphere (Evans et al., 2006; Vaganov et al., 2006; Shi et al., 2008; Vaganov et al., 2011) Here, the VS model performed well in simulating the growth-climate relationship of *Sabina przewalskii* in a dry, high-altitude area. High correlations between observed and simulated values indicate that

the VS model could simulate the radial growth of *Sabina przewalskii* well at both the annual radial growth and at the cell level. Hence, it can be used with confidence to evaluate the physiological relationship between *Sabina przewalskii* tree growth and its major limiting climate factors.

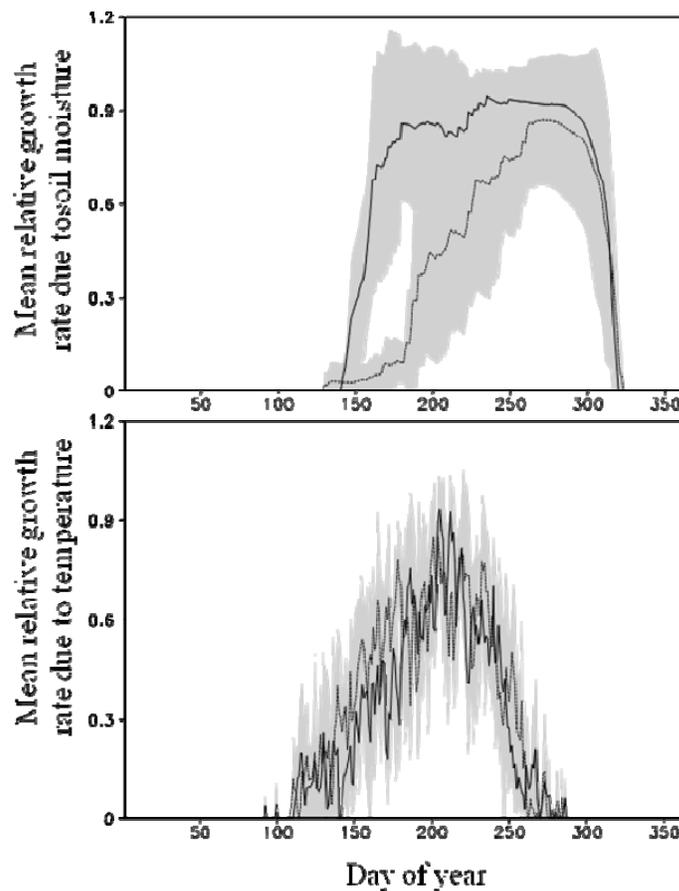


Figure 5.6 Modeled mean growth rate due to soil moisture (top) and mean temperature (bottom) in pointer years of wide rings (black line) and narrow rings (gray dashed line). The shaded areas in the top figure are the mean plus/minus one standard deviation.

Physiologically, different species growing in different environments respond differently to climate factors, as does the same species growing in different environments. Consequently, parameters in the model are characterized by different species and sites. Our values of W_{opt1} , T_{min} and T_{opt1} are lower than those used in the simulation of *Pinus tabulaeformis* from Helen Mts (Shi et al., 2008). (for which

$Wopt1 = 0.4$, $Tmin = 5^{\circ}\text{C}$, $Topt1 = 20^{\circ}\text{C}$). Reasons for this difference might be related to the habitat of *Sabina przewalskii*. *Sabina przewalskii* grow mainly on sunny slopes of mountains surrounding Qaidam Basin, where more solar radiation is received than on other slopes and trees can start growth at lower temperature. Meanwhile, trees are expected to utilize all available moisture to grow in this arid area, especially given the high evaporation induced by enhanced solar radiation. On the other hand, parameters values used in the simulation of *Sabina przewalskii* are similar to those of some conifer species at boreal tree line (e.g. Yakutia, $Tmin = 4^{\circ}\text{C}$, $15^{\circ}\text{C} < Topt1 < 20^{\circ}\text{C}$) (Vaganov et al., 2006). This finding could be explained by the high and cold climate condition of the Tibetan Plateau, which is similar to that found at high latitudes.

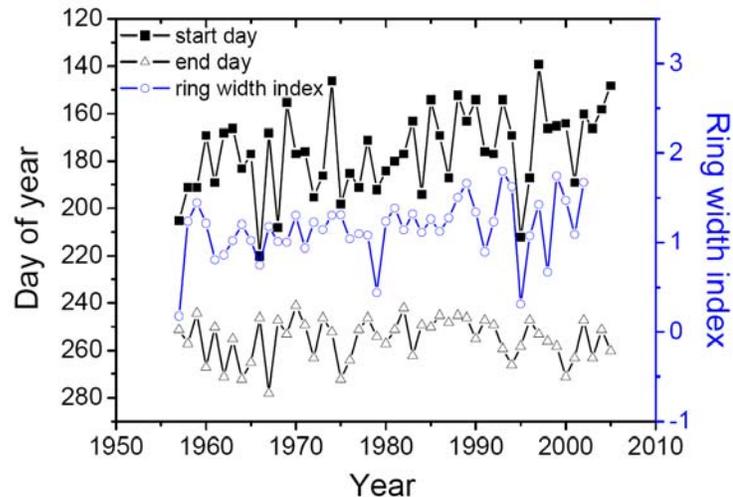


Figure 5.7 Modeled changes of the start date and the end date of the growing season and ring width index.

The climate conditions during the first part of the growing season greatly influence ring width formation at mid- and high latitudes (Vaganov et al., 2006; Rossi et al., 2007; Zhang et al., 2008). Precipitation during the beginning of the growing season is crucial for radial growth of *Sabina przewalskii*. This is reflected in results from the statistical model, which reveal a positive correlation with precipitation during May and June, and a negative correlation with temperature in June. In the physiological model, wide ring formation and more xylem cell growth is associated

with years of increased precipitation during May and June (e.g. 1989, 1993 and 2002). The effect of temperature is lower than that of precipitation on the radial growth of *Sabina przewalskii* in our study. Temperature mainly affects tree growth indirectly by warming-induced drought at the beginning of the growing season. Although temperature has increased during the last century in our study area and the growing season has extended, the influence of temperature on growth rate has not changed over this period.

The divergences phenomenon between tree growth and main climate factors is one of the most important research interests in dendroclimatology ((Jacoby and D'Arrigo, 1995; Briffa et al., 1998a; D'Arrigo et al., 2007). It has been reported not only at high latitudes in the northern hemisphere (Briffa et al., 1998a; D'Arrigo et al., 2007) but also in mountain areas of Eurasia (Carrer and Urbinati, 2006; Zhang et al., 2008). The divergence between tree growth and growing season temperature is potentially driven by warming-induced moisture stress (D'Arrigo et al., 2007; Wilmking et al., 2004; Wilmking and Juday, 2004). The crucial role of precipitation on the radial growth of *Sabina przewalskii* in Qaidam Basin has been demonstrated in both statistical models and a physiological model. However, according to our research, recent warming has not affected the tree growth climate relationship in recent decades.

During the past 50 years at Qaidam basin, significant temperature increases have occurred mainly in autumn and winter, while precipitation has increased primarily during summer and winter (Ma and Li, 2003; Li and Yang, 2007; Li et al., 2008). This change of hydrothermal condition is advantageous to tree growth. Comparing the growth rate in two parts of the analyzing period (Fig. 5.8), the growth rate due to precipitation (GrW) in the second part is greater than that in the first part. No obvious change in growth rates due to temperature (GrT) has occurred between the two time intervals. The total growth rate (Gr) is accelerated in summer and is also affected by moisture condition, consistent with observations that the mean ring width in the last half of the analyzing period is wider than that of the first half. Recent studies have projected an ongoing warming and wetter trend in northeastern

China (Shi et al., 2003). The results presented here suggest that this trend has already begun in the Qaidam Basin. Under current and projected climate conditions there will be an increase in radial growth of *Sabina przewalskii* around the Qaidam Basin. An important potential outcome of this prediction is that regional forests may enhance growth and increase their capacity to sequester carbon.

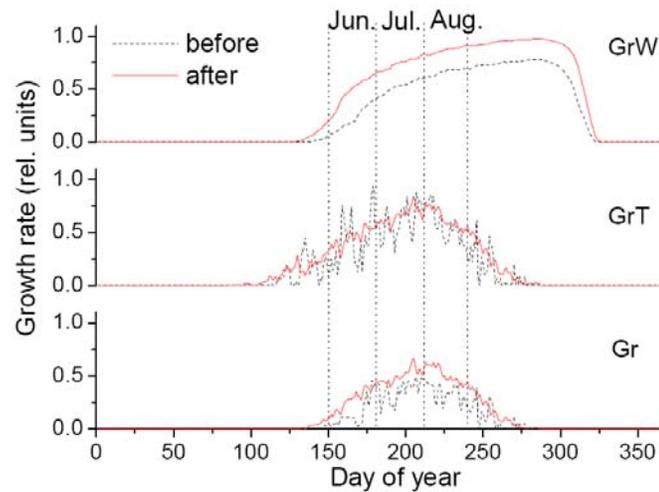


Figure 5.8 The growth rate during two parts of the analysis period, before is 1956-1980 and after is 1981-2005.

5.5. Conclusion

Using the VS model, we simulated the physiological response of *Sabina przewalskii* tree growth to its major limiting climate factors. Results show that this model can successfully simulate the radial growth of *Sabina przewalskii* at both ring width and at cell level, and can reveal the effects of different climate factors on tree growth at different stages. Precipitation during the early growing season, especially during May and June, has significant effect on tree growth, while temperature mainly affects tree growth by warming-induced drought. No change has been found in tree growth climate relationships over the last half century. However, the growing season of *Sabina przewalskii* has been extended as a result of recent warming. The radial growth has also increased, because of higher precipitation at the beginning of the growing season during recent decades. Our modeling results also suggest future

favorable growth conditions for *Sabina przewalskii* around the Qaidam Basin, leading to a potential increase of local carbon sequestration.

Acknowledgement: We thank the two anonymous reviewers for their valuable comments that helped to improve and to clarify our manuscript, Prof. Michal Evans for his support on VS model. This work was supported in parts by National Basic Research Program of China (Grant No. 2010CB950101) and National Natural Science Foundation (No 40671194).

Chapter 6:

Discussion and Conclusions

Many studies have investigated how elevational and boreal treelines trees respond to recent warming (Batchelet and Neilson, 2000; Bonan, 2008). One main finding was that recently instable correlations with climate factors widely existed at elevational and boreal treelines (Biondi, 2000; Briffa et al., 1998a; Wilmking et al., 2004, 2005; Carrer and Urbinati, 2006; Pisaric et al., 2007). In this study, instable tree growth climate relationships have also been found in three coniferous species (*Pinus tabulaeformis*, *Picea crassifolia*, and *Sabina przewalskii*) on the NE Tibetan Plateau using both statistical and physiological process based models at elevational treeline.

Divergent responses of trees within sites have been mainly reported around the circumpolar arctic (Wilmking et al., 2004, 2005; Pisaric et al., 2007). Few correspondent phenomena have been reported from mid-latitude areas where comprehensive tree ring based researches have been conducted (D'Arrigo et al., 2007; Bunn et al., 2011). Here I present the first large-scale evidence of diverging correlations of tree growth with climate at mid-latitude sites in Asia. The endemic species *Picea crassifolia* displayed similar divergent response within site to the summer temperature in most of our study sites, compared to the circumpolar north. However, the start of this divergent response of *Picea crassifolia* in the Northeastern Tibetan Plateau is later than that of *Picea glauca* in circum arctic by approximately two to three decades (Wilmking et al., 2005; Llody and Bunn, 2003), but close to that of other conifer species in the semiarid Western United States (Hughes, 2002; Bunn et al., 2005).

Several hypotheses have been discussed about the potential reason of the 'divergence' defined in D'Arrigo (2007). However, concerning the reason of the

within site divergent response of single trees, the micro-topographic differences should be the most potential causes. Current sampling strategy in dendroclimatology is to collect a certain number of increment cores or cross-sections from trees within a site. A stable and robust common signal is supposed to be achieved by a sufficient number of trees which are sharing a homogenous site (Fritts 2001; Hughes 2002). The homogenous site refers to factors such as slope, aspect, substrate, and stand history etc. However, most tree cores are collected from trees growing on high mountains dominated by complex terrain. Individual trees growing at the same site always occupy discrete microenvironments particular to their own location due to the micro-topographic differences of the landscape (Fritts 2001). Although they share the same macro-climate condition, which might reflect their similar responses to the same growth-limiting factor or set of factors, the micro-topographic differences influence how the tree records climate in its particular setting. In our cases, trees once responded similarly to their main limiting climate factor (e.g. temperature). As temperature kept increasing, it did not only cause different response mechanism of tree growth directly but might alter the function of other factors on tree growth. The micro-topographic differences of individual trees might be magnified by this warming and consequently caused the different responses of individual trees within the same site.

Recent researches indicate that even in relatively small areas the complexity of terrain in high mountain system can alter the responses of individual trees to their limiting climate factors (Bunn et al., 2011). To be specific, trees have different responses to climate factors due to elevational differences (LaMarche, 1974), but recent studies found that divergent responses of trees to climate factors existed only between a small elevational difference (e.g. 150 meter) within same site during recent decades (Salzer et al., 2009; Bunn et al., 2011). Similar results have also been found on *Picea crassifolia* in our study area. Both spatial and elevational analyses show that the higher the elevation the more the divergent response within sites. Elevational differences play a prominent role on this within site divergent response. Meanwhile, trees growing in the high, dry and cold subalpine of the semiarid

Western United States also have markedly different response to the same climate factor due to the micro-site difference (Villalba et al., 1994; Bunn et al., 2005). The topographic factors of individual trees which have important effect on tree growth (slope, aspect, substrate etc., Liang et al., 2006; Daly et al., 2008) might also affect the tree growth climate relationship under current warming scenarios. Hence, more detailed analyses should be done along the topographic position of individual trees to see if and how other micro-topographic factors modify the tree growth climate relationship in the future.

The climate change related drought caused slow growth, die off and defoliation of trees as has been found in most temperate forests and some boreal forests (Breshears et al., 2005; Lloyd and Bunn, 2007; Carnicer et al., 2011). The decreasing of radial tree growth of the endemic species *Picea crassifolia* due to warming induced drought also widely existed at elevational treelines of the NE Tibetan Plateau. The spatial signature of drought stress in *Picea crassifolia* has been increasing steadily during the last decades and is now influencing large parts of the natural range of this species, especially upper treeline environments. Recent climate researches found that most northern China has experienced severe and prolonged dry periods since the late 1990s (Zou et al., 2005). Since the Qilian Mts. areas are relatively dry areas, frequent drought stress in recent decades has become more serious (Dai et al., 2005). Regional net primary productivity and net ecosystem productivity has been reduced severely (Xiao et al., 2009). Global climate models project widespread summer drying in mid-latitude regions during the current century (Solomon et al. 2007). Such drying may have larger impacts on the terrestrial carbon dynamics in the Northeast Tibetan Plateau regions.

In comparison with the most stressed trees at upper elevational treelines, some *Picea crassifolia* trees from the same sites could still take advantages of this warming environment. The strengthening positive correlations between *Picea crassifolia* and MMT indicate that those trees will continue to benefit from warming under current scenarios which coincided with former observation (Piao et al., 2006). Only trees growing at certain elevation could benefit from recent warming but trees from low

elevations were mainly limited by moisture stress (Salzer et al., 2009). However, all significant correlations of tree growth we have investigated are correlated to temperature. Correlations between tree growth and precipitation are not significant. The potential reason might be related to the climate data what we have. Temperature generally shows a more regional signal. Precipitation, especially in mountainous areas, is far more affected by topography. Moreover meteorological stations of this area are generally located near or in cities. Precipitation recorded of these stations might not be ideally suited to estimate its direct impact on annual radial tree growth because of its patchy and complicated nature and the distance from the sampling sites.

Generally, the statistical models are employed to access the tree growth climate relationships due to the assumption that the transfer function designed using recent observations takes into account all climate factors that might have a significant effect on ring growth in the reconstructed period and all combinations of values of the predictor variables for the reconstruction period are represented in the calibration period (Hughes, 2002). Since instability of the tree growth response to climate variables has been widely reported not only in high latitudes but in mid-latitudes also in recent decades (D'Arrigo et al., 2007; Bunn et al., 2011; Zhang et al., 2011), the process-based tree ring climate model could be of considerable help in checking the stability of the statistical transfer function in dendroclimatology (Vaganov et al., 2006). The VS model has fully proved the relationship set up by statistical models that the radial growth of *Sabina przewalskii* growing at the NE Tibetan Plateau is mainly limited by moisture (Shao et al., 2005). Meanwhile, the instable response of tree growth has been interpreted as an increasing positive correlation relationship between tree growth and precipitation and a warming-induced drought stress during the last half century. The VS model is well suited for the simulation of conifer growth dynamics in the varying and changing climate of Northeastern Tibetan Plateau. In addition, the modeling results also suggest future favorable growth conditions for *Sabina przewalskii* around the Qaidam Basin, leading to a potential increase of local above-ground carbon sequestration.

The stable and consistent correlation of tree growth to climatic factors is the current foundation for tree ring based climate reconstruction and the projection of future tree growth (Hughes, 2002). Climate reconstructions and forest growth projections will need to take this analysis into account, since the indiscriminate use of tree ring data from sites showing opposite responses to increasing warming could cause miscalibration of tree ring based climate reconstructions, and over- or underestimation of carbon sequestration potential in biogeochemical models. If these divergent subgroups responses to climate factors are in the future neglected, we will not only lose the information which is recorded by tree growth but could mis-estimate the climate variability of past times and the tree growth in the future. Therefore, additional work should be conducted at three aspects, 1) to test more regions and species for the phenomena of changing climate growth relationships over time and 2) to better understand the mechanisms affecting growth from the micro-site of each individual tree to the population through time, 3) to deeply investigate the tree growth-climate relationship of the divergent response trees by more process based physiological simulations and analysis. Only then can we safely proceed to use tree rings as robust source of paleo-climatic information and to evaluate the impact of recent warming on the forest ecosystem and the future global carbon sequestration.

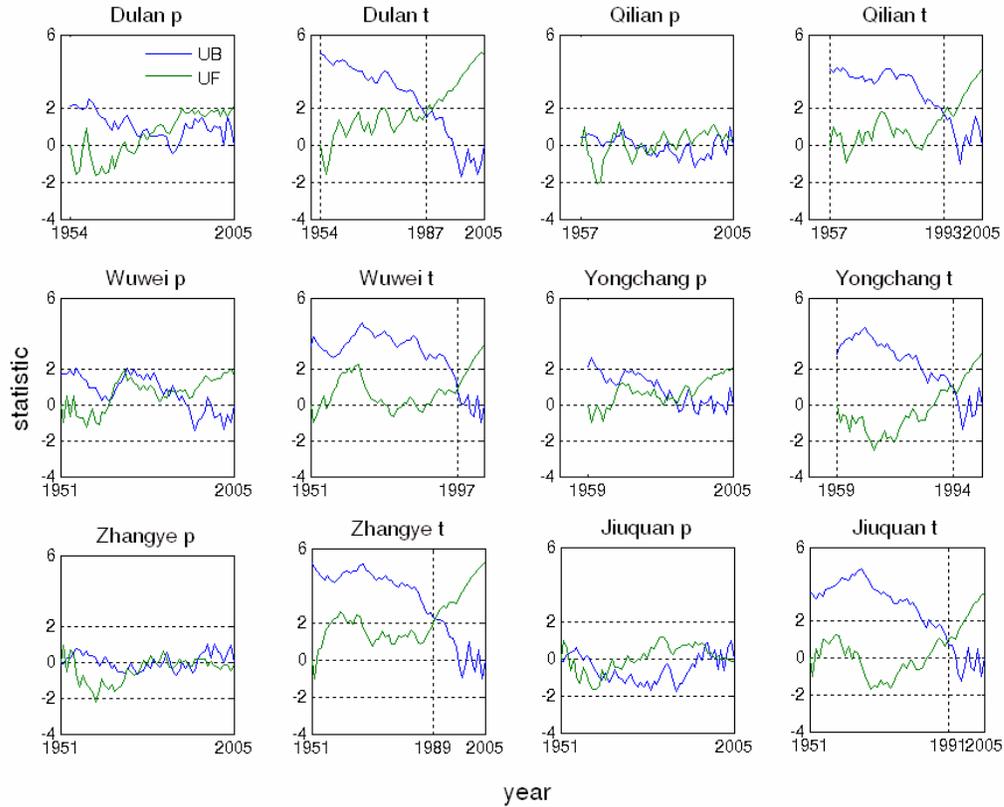
Supporting material:

Appendix 3.1 Test of significant differences of correlations with mean monthly temperature (MMT) between sub-populations of each site.

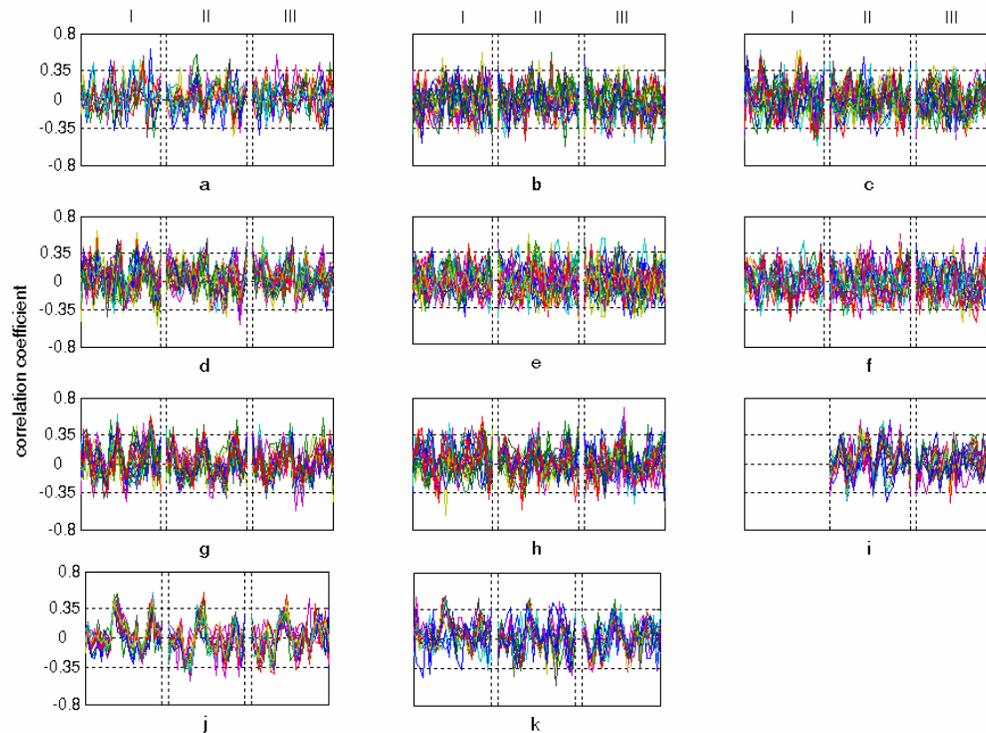
	t-2				t-1												t											
	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S			
3-1 (first time slice)																												
a					√																							
b																												
c					√												√											
d					√						√		√				√											
e					√						√	√		√			√							√	√		√	
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i																												
j																												
k																												
3-2 (second time slice)																												
a				√																								
b														√				√										√
c																												
d																												
e	√			√										√									√				√	
f																			√									
g																												
h				√																								
i																												
j																												√
k																												
3-3 (last time slice)																												
a	√	√					√	√		√	√	√	√		√			√	√				√	√		√	√	√
b										√	√		√											√	√	√	√	√
c						√	√	√		√	√	√					√	√	√				√	√	√	√	√	√
d							√			√	√	√						√	√				√	√	√	√	√	√
e	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
f	√	√	√		√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
g										√	√								√				√	√			√	
h																												√
i							√					√							√				√	√				√
j										√														√				
k												√						√						√				

Correlation scores of 25 months starting with September (S) of two years prior to growth (t-2) to current year (t) September were used to test significant differences between two sub-populations at each site in three different time slices. The Symbol ($\sqrt{}$) indicates significant differences (at the 95% level) in the corresponding month. Most differences between the two sub-populations at a site exist during the last time slice, e.g. consistent across all sites in summer temperatures of the year of growth (J, J).

Appendix 3.2 Test of significant trends in climate factors from the climate stations



The Mann-Kendall test revealed significant increasing trends in annual temperature (t) in the last decades. Vertical dashed lines indicate start of significant trends. No significant trends in precipitation (p) exist. The UF is forward sequence and the UB is backward sequence.

Appendix 3.3 Single tree responses to total monthly precipitation (TMP)

Correlations between single trees of each site (a-k) and TMP from the nearest climate station in three different time slices (I-III). Each line represents a series of correlation coefficients of one tree with 25 TMPs starting from September 2 years prior to growth to current year September. Time slice I: 1951-1982; Time slice II: 1962-1993; Time-slice III: 1974-2005. The horizontal dashed line is the 95% significance level. Compared to the correlations with MMT there is no obvious change, neither in trend of the correlations nor in opposing responses.

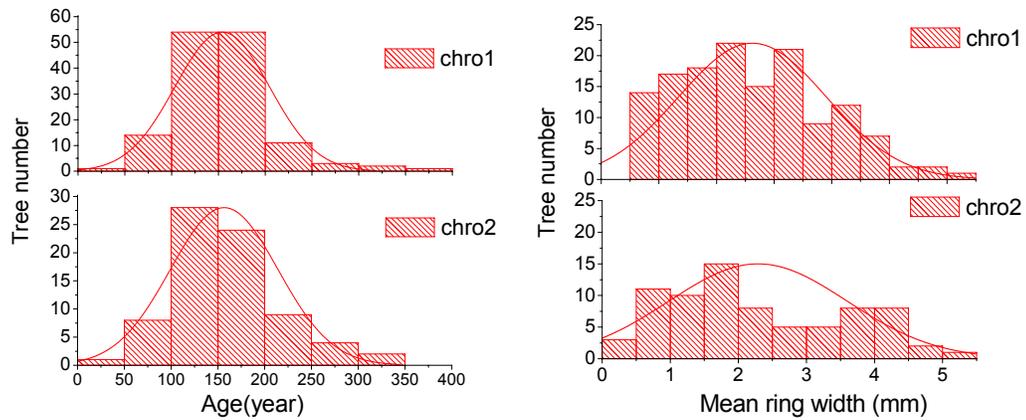
Time slice 2 (1962-1993)

	t-2				t-1								t													
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	
a				0.35										0.44									0.55			
a1				0.55																		0.36		0.55		
a2										-0.41				0.48		0.38	0.39									
b											-0.37		-0.45						-0.37							-0.55
b1											-0.41								-0.37							
b2															0.36											
c																										
c1						-0.43			0.38															-0.38		
c2												-0.38	-0.35												-0.39	
d											-0.51	-0.42							-0.37					-0.47		
d1	0.04																	-0.39						-0.36		
d2											-0.39													-0.43		
e																					0.4				-0.44	
e1	-0.42			0.39																					0.41	
e2									0.38																	
f											-0.36								-0.42							
f1									0.35	0.39																
f2																										
g											-0.5	-0.39							-0.39	-0.36				-0.5		
g1												-0.42														
g2												-0.49							-0.38					-0.53		
h																										
h1												-0.42													-0.41	
h2												-0.46	-0.36												-0.37	
i																									0.39	
i1																										
i2																										
j											-0.4								-0.36							
j1											-0.43	-0.35							-0.36							
j2											-0.38			0.35					-0.4						0.38	
k																										
k1																										
k2																									-0.41	

Time slice 3 (1974-2005)

	t-2				t-1								t													
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	
a														0.38	0.37							0.45	0.64			
a1	-0.56						-0.41	-0.35		-0.45	-0.48	-0.36	-0.39							-0.49					-0.5	
a2	0.45		0.42										0.47		0.47			0.45				0.58	0.65			0.43
b						-0.37				-0.37							-0.35								-0.42	
b1						-0.48	-0.44	-0.38		-0.53	-0.57	-0.37	-0.52				-0.45	-0.37	-0.36				-0.36		-0.6	
b2	0.46														0.41								0.43			
c						-0.35				-0.35		-0.45					-0.37					-0.46				
c1						-0.45	-0.43			-0.54	-0.45	-0.47					-0.44	-0.42				-0.62			-0.38	
c2			0.42						0.43	0.42	0.54							0.42	0.35				0.72			
d											-0.38											-0.47	-0.4			
d1											-0.64											0.43	0.45	0.39	0.56	
d2						0.48	0.35			0.61			0.41													
e							-0.41			-0.37		-0.46					-0.36									
e1	-0.35				-0.47	-0.54	-0.67	-0.38	-0.38	-0.67	-0.67	-0.54	-0.49	-0.36	-0.45	-0.4	-0.54	-0.58	-0.62	-0.46	-0.4	-0.72	-0.62	-0.47	-0.54	
e2	0.42		0.46	0.36	0.41	0.38	0.36	0.46	0.59	0.39	0.49					0.48		0.43	0.35	0.44	0.53	0.56			0.46	
f						-0.37	-0.35	-0.53	-0.35		-0.51	-0.64	-0.48				-0.47	-0.56	-0.6			-0.62	-0.46		-0.37	
f1						0.38	0.48	0.47	0.42	0.49	0.58	0.58	0.36	0.43		0.38	0.41	0.38	0.55	0.48	0.53	0.63	0.65	0.53	0.5	
f2	0.49	0.38	0.45																							
g							-0.46	-0.38		-0.47	-0.72	-0.52			-0.47		-0.38	-0.39	-0.41			-0.73	-0.64	-0.45		
g1							-0.47	-0.38		-0.48	-0.72	-0.52			-0.47		-0.38	-0.4	-0.42			-0.74	-0.65	-0.45		
g2																									0.48	
h						-0.36	-0.39	-0.35		-0.41	-0.66	-0.47			-0.37		-0.42					-0.58	-0.61	-0.36		
h1						-0.36	-0.42	-0.4		-0.48	-0.7	-0.46			-0.37		-0.41					-0.62	-0.69	-0.46		
h2																										
i	-0.35						-0.46				-0.5	-0.48					-0.36	-0.39					-0.48	-0.5		
i1	-0.35						-0.47				-0.52	-0.49					-0.37	-0.39					-0.47	-0.49		
i2																						0.4				
j							-0.38			-0.72	-0.67	-0.44					-0.59	-0.48				-0.66	-0.36			
j1							-0.38		-0.35	-0.72	-0.67	-0.45					-0.57	-0.47								
j2															0.48											
k										-0.54	-0.59	-0.46					-0.46	-0.37				-0.66	-0.42			
k1												-0.51					-0.36									
k2										-0.57	-0.6	-0.44					-0.47	-0.39				-0.68	-0.45			

Appendix 3.5 Histograms of age and average growth rate (mean annual ring width) of two sub-populations. No significant differences in age (left) or average growth rate (right) exist between the populations built of negatively (chro1) and positively (chro2) responding trees. Here we show only an average over all sites, individual sites show the same pattern of no significant differences (data not shown).



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Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch – Natur-wissenschaftlichen Fakultät der Ernst-Moritz-Arndt-Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.

Ferner erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die darin angegebenen Hilfsmittel benutzt habe.

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Acknowledgements

Four years ago, I rejected another offer and decided to come to Greifswald. Now I am glad I made such decision. It was a precious time. What I have learnt and experienced will equip me for life. First of all, thanks go to my supervisor Prof. Dr. Martin Wilmsking. I still remember he taught me how to compose a scientific paper word by word, sentence by sentence. He was always supportive and gave generously of his time. He is so nice not only at work but in daily life. To me, he is not only a great scientist and supervisor but also a nice friend. I appreciate what I have learnt and got from him.

Thanks Martin (M) and Ilka for helping my thesis.

Thanks Ilka, Julia, Inke, Marina, Michal, Martin, Jens and all present and former members of the group 'Ecosystem Dynamics'. Because of them, I really like this group very much and enjoy the time we spent together. Thanks Ilka, for taking care of me when I carried my baby girl. Thanks Gabby, she's always warm and nice. Thanks my friends Rui, Xin, Bingyu, Oli, Meli for accompanying me in Greifswald. Because of them, I could always find a place to go whatever I was happy or blue.

This work was mainly supported by a Sofja Kovalerskaja Award by the Alexander von Humboldt Foundation, the German Ministry for Education and Research to M. Wilmsking, who was also partly supported by a grant from the German Research Foundation (DFG Wi 2680/2-1).

To my parents and brothers, without their support I would not be where I am.

To my husband and friend, Jie Ma, with his support and encourage I could finish all these things.

To my little angel, Fiming, for broadening my life and happiness.