

Qinghai spruce (*Picea crassifolia*) growth–climate response between lower and upper elevation gradient limits: a case study along a consistent slope in the mid-Qilian Mountains region

Bo Wang^{1,2} · Tuo Chen¹ · Guoju Wu^{1,2} · Guobao Xu¹ · Youfu Zhang³ · Haining Gao⁴ · Yong Zhang⁴ · Qi Feng⁵

Received: 5 March 2015 / Accepted: 18 August 2015 / Published online: 25 January 2016
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Abstract Tree-ring width chronologies are important records of climate change. Mounting evidence suggests that tree-ring climate response is elevation dependent. In this study, even-aged Qinghai spruce (*Picea crassifolia* Kom.) chronologies from six sites along a consistent slope in the Qilian Mountains region were selected to investigate altitudinal variability of growth–climate response. Results showed that growth–climate response of this species at different elevations was limited by identical factors. In the Qilian Mountains, *P. crassifolia* tree-ring growth was limited primarily by drought conditions which are determined by precipitation and temperature in the Qilian Mountains along the entire elevation gradient, exhibiting a positive correlation with PDSI in growth season, a positive correlation with precipitation in May and a negative correlation with the maximum temperature in June. Moreover, *P. crassifolia* recruitment dynamics coincided well with the

temperature variations, suggesting that recruitment rates at different elevations were all primarily influenced by temperature. What was noteworthy was that the great decrease in the mean sensitivity and standard deviation of chronologies directly indicated that *P. crassifolia* climate–growth response weakened at higher elevations. Furthermore, tree-ring–climate correlation coefficients, and spatial correlation fields of tree-ring width indices to regional climate factors also significantly decreased at higher elevations, indicating that *P. crassifolia* climate–growth response at higher elevations was weaker than that at lower elevations. Additionally, response of *P. crassifolia* recruitment dynamics to changes in temperature decreased with increasing elevation, confirming results from chronology and response analyses that showed that *P. crassifolia* climate–growth response weakened at higher elevations.

✉ Tuo Chen
chentuo@lzb.ac.cn

Bo Wang
wangbo900824@lzb.ac.cn

¹ State Key Laboratory of Cryospheric Science, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Donggang West Road No. 320, Lanzhou 730000, China

² University of Chinese Academy of Sciences, Beijing 100049, China

³ Henan University of Science and Technology, Luoyang 471003, China

⁴ Hexi University, Zhangye 734000, China

⁵ Key Laboratory of Inland River Ecohydrology, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

Keywords Tree-ring · Altitude · Qinghai spruce · A consistent slope · The Qilian Mountains

Introduction

Owing to its high resolution and reliability, tree-ring width chronologies are valuable proxy records of past climate changes. Moreover, tree-ring reconstructions provide considerable insight into mechanisms related to climate change (Briffa and Cook 1990). The Qilian Mountains region, on the edge of the Tibetan Plateau, represents a climate transition zone from monsoon to continental. Its distinct natural environment and abundant forest resources make it ideal for dendroclimatic research. A number of dendroclimatic studies have been conducted in this area to date (Kang et al. 2003; Liu et al. 2009; Wang et al. 2001; Yang et al. 2005).

Although various researchers have worked in the area, however, disagreements still persist on whether Qinghai spruce (*Picea crassifolia* Kom.) growth rates are limited by precipitation or temperature in the Qilian Mountains (Gou et al. 2005; Wang et al. 2001; Zhang and Wilmking 2010).

An increasing number of studies have indicated that altitude is a significant factor influencing tree-ring to climate response (Mäkinen et al. 2002; Wilmking and Juday 2005). For example, complex non-linear relationships between altitude and tree-ring chronology sensitivity to climate were observed in previous studies for different areas (Kienast et al. 1987; Norton 1985; Peng et al. 2007; Yang et al. 2013). At the same time, such studies reported linear relationships between climate–growth response and elevation (Brookhouse and Bi 2009; Gou et al. 2005; Peng et al. 2008; Wang et al. 2005). Moreover, He et al. (2013) concluded through correlation and response function analyses that *Juniperus tibetica* elevation in the southern Tibetan Plateau had no significant effect on tree growth–climate relationships. Consequently, as suggested in the above, the relationship between tree growth–climate response and elevation remains undefined. According to previous studies, climate–tree growth relationships are significantly influenced by topography (Bunn et al. 2005; Leonelli et al. 2009; Liang et al. 2010) as well as tree age (Carrer and Urbinati 2004; Linán et al. 2012; Wu et al. 2013). However, the influence of topography and tree age has received only limited attention in previous studies on altitudinal variability of climate–growth relationships (Brookhouse and Bi 2009; Gou et al. 2005; Peng et al. 2008). To avoid effects of landform and tree age variation on results in the current study, six tree-ring width chronologies of even-aged *P. crassifolia* stands growing along a single slope were selected for investigation.

Age structure can also be used to analyze relationships between climate and tree regeneration. Various studies have been conducted on population structure, spatial distribution patterns, and *P. crassifolia* regeneration near the upper tree-line in this area (Li et al. 2012; Zhang and Jiang 2006). However, only limited research on the response of *P. crassifolia* density to climate change and the altitudinal variation of this response has been conducted. For this study, in order to investigate the response of *P. crassifolia* density to climate change and its altitudinal variation, age structure was established to analyze density changes at different elevations (Gou et al. 2012; Rozas 2003).

What is more, given its high sensitivity to climate change in addition to other advantages, alpine timberlines were always thought to be ideal to reconstruct variabilities of climate factors. However, according to several previous studies, trees growing at alpine timberlines of some tree species (e.g., *Sabina przewalskii*, *Juniperus tibetica*) were

not the most sensitive ones to climate changes (Yang et al. 2013; He et al. 2013). Current study on altitudinal variability of *P. crassifolia* growth–climate response from its lower elevation gradient limits to the upper elevation gradient limits may tell us whether *P. crassifolia* at alpine timberlines is most sensitive to climate changes and ideal to climate reconstruction or not, which is of fundamental significance on dendroclimatology and may provide clues on climate reconstruction using *P. crassifolia* in the mid-Qilian Mountains region.

The objectives of this study were (1) to detect whether *P. crassifolia* growth at different elevation gradients was limited by identical climate factors; (2) to investigate whether differences existed in *P. crassifolia* growth response (including tree-ring growth and forest recruitment) to identical limiting climate factors; (3) to validate whether *P. crassifolia* at alpine timberlines are the ideal ones for climate reconstruction or not.

Materials and methods

Study area and sampling strategy

This study was conducted in the Dayekou Reservoir Water Park (Zhangye City, Gansu Province, China) located in the mid-region of the Qilian Mountains (Fig. 1). According to records (1951–2012) from the nearest meteorological station (Zhangye Station, 100.37°E, 38.56°N, 1480 m AMSL), mean yearly temperature in study area was 7.24 °C; and the mean monthly maximum temperature was in July (Fig. 2a). Mean annual total precipitation was 129.9 mm; and mean annual total vaporization was 77.8 mm. Precipitation was primarily concentrated between May and September which can be seen as a wet season (Fig. 2a). Then, the vaporization was greater than precipitation in February to April, October and November which can be seen as a relative dry season (Fig. 2a). In summary, climate condition in study area showed as a typical semi-arid climate type which represents a climate transition zone from monsoon to continental (Fig. 1). Moreover, according to observation by Jin et al. (Jin et al. 2012) in the Dayekou Reservoir Water Park, our study site, increasing elevation leads to increases in annual total precipitation from 2600 to 3300 m (Fig. 2b), while yearly soil temperature decreased at a mean rate of 0.39 °C per 100 m along altitude gradient from 2700 to 3100 m (Fig. 2c). *P. crassifolia*, a dominant species in the study area, was the species selected for investigation. This coniferous species is tolerant to cold environments and poor soils, allowing the species to grow along an extensive elevation range (from 2600 to 3200 m AMSL) within the study area (Liu 1992).

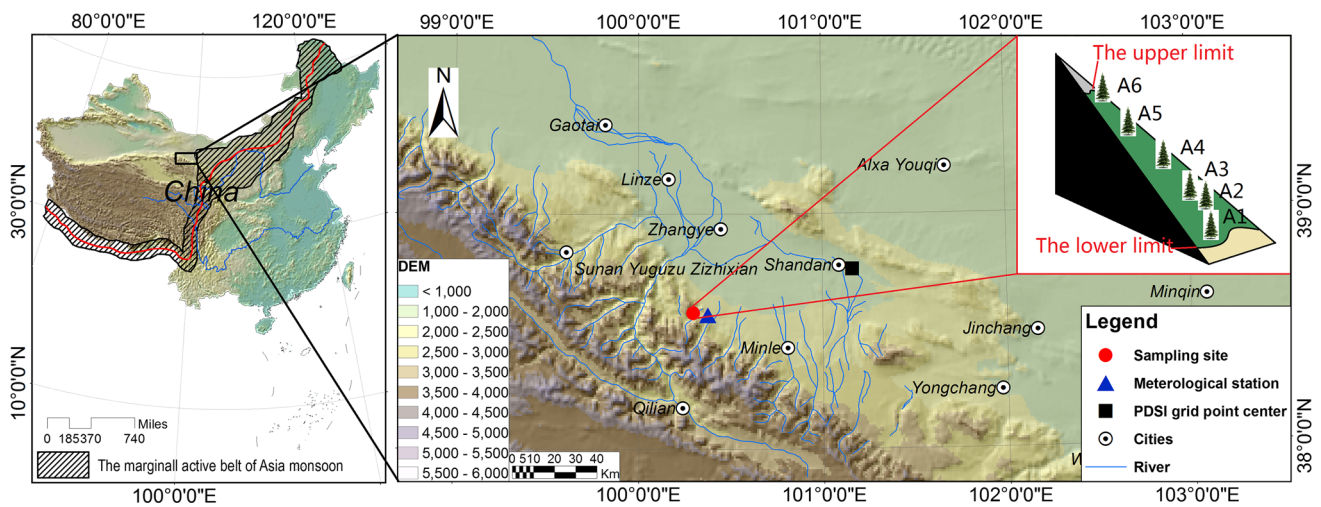


Fig. 1 Location and topography of study area and nearby meteorological stations (Zhangye Station, 43.75°N, 93.75°); the insert picture in the right panel is the abridged general view of sampling sites; the shadow area in the left panel indicates the marginal active belt of Asia monsoon

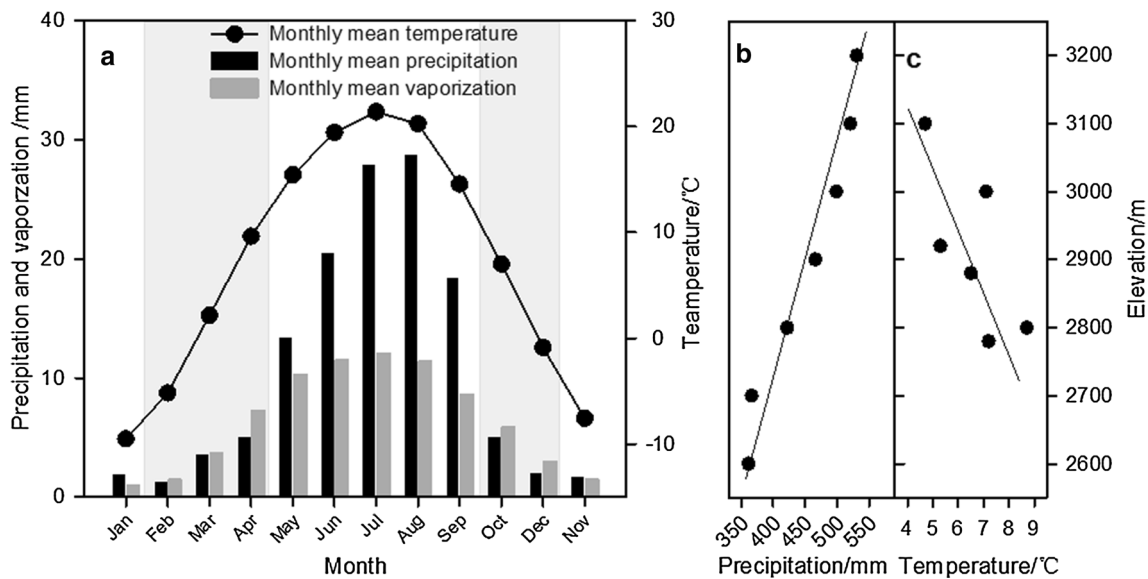


Fig. 2 Climate graph for mean monthly air temperature and mean total monthly precipitation of Zhangye station (a); observed altitudinal variabilities of precipitation (b) and temperature (c) in study area, observed altitudinal variabilities data from Jin et al. (2012)

Six closely positioned 20 m × 20 m sampling quadrats (no greater than 1 km apart) were established at six pre-selected elevations from 2600 to 3100 m AMSL along a consistent north-facing slope (Fig. 1). Features of sampling quadrats and trees were collected that include tree density, diameter at breast height, tree height, etc. Table 1 provides general information related to sampling sites. In total, 115 tree-ring cores (one to two cores per tree) were selected from *P. crassifolia* specimens using a 5.15 mm diameter increment borer at breast height (approximately 1.3 m above the surface) in July and August 2012. Most core samples had their pith intact to ensure that the actual age of the tree was ascertained correctly.

Tree-ring chronologies development

All cores were air dried and then polished using progressively finer grades of sandpaper (Fritts 2012). After cellular structure was clearly revealed, all cores were visually cross-dated based on inspection using a microscope, establishing the absolute assignment of calendar year for every growth year. All cross-dated growth rings were measured to a precision of 0.01 mm using a sliding stage micrometer (LINTAB 6; Rinntech, Heidelberg, Germany) interfaced to a computer applying time series analysis and presentation features of the dendrochronological software TASP-Win (Rinn 2003). Cross-dating was confirmed using

Table 1 Site information for six 20 m × 20 m sampling quadrats

Site code	Elevation (m)	Latitude	Longitude	Slope aspect	Density (stems/ha)	MH (m)	M-dbh (cm)
A1	2663	38°33'24"N	100°17'06"E	Northwest	1875	6.3	10.4
A2	2786	38°33'09"N	100°17'07"E	North	2600	5.2	8.6
A3	2805	38°33'02"N	100°17'25"E	Northeast	2550	5.7	8.2
A4	2940	38°32'36"N	100°17'58"E	Northwest	2625	6.2	10.7
A5	3019	38°32'30"N	100°18'05"E	North	3050	6.7	9.8
A6	3098	38°32'19"N	100°18'06"E	North	1100	7.6	14.3

MH is mean tree height, M-dbh is mean diameter at breast height, and Density is the tree density whose unit is stems per hectare

COFECHA software (Grissino-Mayer 2001; Holmes 1983).

The ring width series was standardized and auto-regressively transformed applying Program ARSTAN (Cook and Holmes 1986). Most ring width measurement series were fit with negative exponential curves to remove growth trends from the raw ring width series while retaining most low-frequency variations that may potentially be climate driven. If this curve type failed, a straight line of any slope was applied instead (Cook and Holmes 1986; Cook and Kairiukstis 1990). Robust autoregressive modeling was used to remove significantly high autocorrelation within each series (Richter et al. 1991). To reduce bias caused by endogenous stand disturbances and to enhance the common signal contained within the data, the biweight mean was used to calculate mean medium frequency and high-frequency chronologies for each study site (Cook and Holmes 1986). Three versions of tree-ring width chronologies (Standard, Residual, and Arstan) incorporating unique time series characteristics were generated by Program ARSTAN. Thereafter, the “pre-whitened” residual chronologies for which biologically related persistence was removed were used for growth–climate response analysis. Standard chronologies that retain greater low-frequency variability were used to represent long-term tree growth trends throughout the previous century (Cook and Holmes 1986). Furthermore, several descriptive statistics were calculated for chronologies. Standard deviation (SD) assessed measurement variance for the whole series; mean sensitivity (MS) quantified interannual variation in growth between two adjacent rings, and first-order autocorrelation (AC1) estimated the persistence of chronologies. Common signal strength was evaluated by the percent variance explained by the first principal component (PC1) and by the mean inter-series correlation (RBAR). The signal-to-noise ratio (SNR) served as an expression of the strength of the observed common signal between trees. The expressed population signal (EPS) was used to determine statistically reliable chronology time periods using a 30-year moving window with 15-year overlaps. The approximate threshold

for an acceptable EPS, as reported by Wigley et al. (1984), was 0.85.

Meteorological and climatic data

Meteorological data were obtained from Zhangye Station (100.37°E, 38.56°N, 1480 m AMSL), which was the closest meteorological station in relation to the study site (Fig. 1). Mean monthly temperature and total monthly precipitation were ascertained to detect climate response of tree-ring widths.

The Palmer Drought Severity Index (PDSI) was employed to detect whether regional moisture conditions influenced tree-ring growth. The monthly CRU sc-PDSI 3.21 dataset was obtained from the nearest grid points (scalpelling 100°–100.5°E, 38.5°–39°N) (Wells et al. 2004), derived from global coverage based on a 0.5° × 0.5° gridding system. Gridded Climate Research Unit (CRU) time series datasets produced by the Climate Research Unit at the University of East Anglia (Mitchell and Jones 2005) along with the gridded PDSI dataset (Dai et al. 2004) were employed to conduct spatial correlation analyses between tree-ring width chronologies and regional climatic factors. Yearly mean temperatures obtained from Zhangye Station, temperature reconstruction in the West China (Shi et al. 2012) and North Hemisphere temperature reconstruction (Mann et al. 2009) derived from the NOAA National Climatic Data Center were used to detect *P. crassifolia* recruitment dynamics response to temperature change.

Dendroclimatic analysis

Each tree-ring width series was compared to meteorological data obtained from Zhangye Station (1951–2012). To investigate the effects of climatic factors on tree growth, residual ring width chronologies were linked to precipitation, temperature, and PDSI records using Person correlation function and response function (Blasing et al. 1984). Correlation and response function analyses between

chronologies and climatic factors were conducted using the SPSS program and DendroClim2002 software (Biondi and Waikul 2004). These analyses were examined for a sequence of 15 months beginning in August of the previous growth year to October of the following growth year in which the ring was formed given that climate conditions in months that precede the growing season often have effects on tree growth (Wu 1990). To distinguish variation in patterns between different frequency domains, high-pass and low-pass filtering was used on raw standard tree-ring width chronologies over corresponding periods. Principal component analysis (PCA) was conducted on tree-ring width index series at six different elevations. The first (PC1) represented the common variance pattern across all elevations, and was an indicator of the optimum regional tree growth signal. Several climate variables and their correlations to PC1 were employed to allow an assessment of the common pattern of climate influence on tree growth within the study site. At the same time, to examine the integrated impact of precipitation and temperature on radial growth at these six different elevations, response surface regression analysis was conducted using Design-Expert (version 8.0.6, Stat-Ease, Inc., Minneapolis, MN, USA). Additionally, to assess whether identified tree growth–climate relationships were consistent during different decades, an 11-year moving average cross-correlation analysis was conducted between tree-ring width indices and identified influencing factors on tree growth. The coefficient of variation of moving cross-correlation series was calculated to evaluate variations in tree growth–climate relationships. Furthermore, spatial correlation analyses were conducted using the KNMI Climate Explorer (<http://climexp.knmi.nl>) to detect the response of tree-ring indices to regional climatic factors, such as May–June averaged CRU TS 3.10 precipitation (Mitchell and Jones 2005) and May–July averaged PDSI (Dai et al. 2004) datasets of all grid cells available for a user-defined region (80°E–130°E, 15°N–55°N).

Cores with piths intact were used to determine the age of sampled trees. Most core samples had their pith intact to ensure that the actual age of the tree was ascertained correctly, but some cores failed to reach the pith due to incorrect bore alignment, eccentric growth rings, or rotted tree centers. To extrapolate actual ages for missing portions of cores that failed to reach the trees' pith, the Initial Radial Growth model was adopted, which is based on the assumption that the growth of individuals of the same species from the same region must be similar (Rozas 2003). A multiple linear regression function was then applied to predict the number of rings in missing radii from the length of missing radii and the mean growing rate of rings adjacent to the pith. This was used as predictors. Additionally, Duncan (1989) geometrical model was employed to

estimate the length of the missing radii. Regression analysis of diameter at breast height (1.3 m) was then conducted and tree age was determined from 115 core samples to estimate tree age for those that were too young to be sampled in sampling quadrats (Gou et al. 2012; Rozas 2003). The linear model was chosen as the regression model and was given in the results. It should be mentioned here that larger trees probably experienced faster growth rates in the past, and only fast growing seedlings survived. Seedling growth rates were likely to be slightly overestimated, and, subsequently, ages may be slightly underestimated (Landis and Peart 2005). Furthermore, in order to explore *P. crassifolia* recruitment response to climate change in different areas of the forest, the forest itself was subdivided into three sections, including low elevations (2600–2800 m AMSL), intermediate elevations (2800–3000 m AMSL), and high elevations (greater than 3000 m AMSL). All trees in the sampling quadrat were then sorted into 20-year interval age groups. Consequently, tree number increments for different periods could be calculated to analyze *P. crassifolia* recruitment response to climate change at the lower limit (2600–2800 m AMSL), intermediate elevations (2800–3000 m AMSL) and the upper limit (greater than 3000 m AMSL) by comparing corresponding temperatures from Zhangye Station, the West China temperature reconstruction (Shi et al. 2012) and North Hemisphere temperature reconstruction (Mann et al. 2009).

Chronology variability at different elevation gradients was compared by applying the following statistical parameters: mean sensitivity (MS), standard deviation (SD), signal-to-noise ratio (SNR), mean tree-ring series inter-correlation (R_{BAR}), and the variance of the first principal component contained in each chronology (PC1). Pearson correlation coefficients between the six chronologies at different elevations over corresponding periods (1911–2012) were calculated and compared to test whether chronologies at different elevation gradients showed consistency in growth patterns. Results from spatial correlation analysis, coefficient of variation of moving correlation series, and surface analysis response were also compared between different elevations.

Results

Climatic factors driving local tree growth

When comparing tree-ring width chronologies, similar variation patterns were found in the *P. crassifolia* tree-ring width index at different elevations (Fig. 3a). Correlation analysis between chronologies also showed that correlation between tree-ring width index at different elevations was

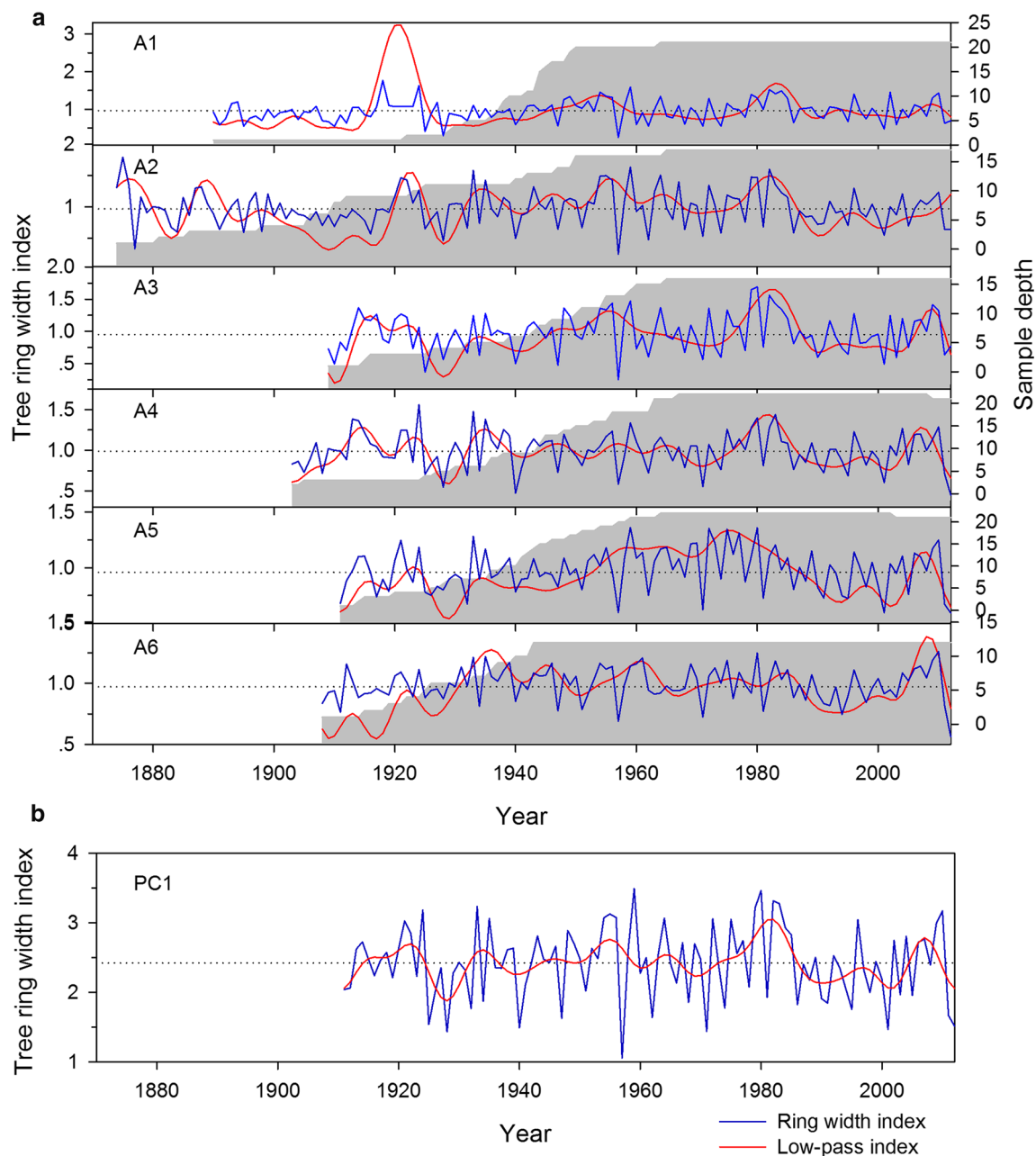


Fig. 3 Tree-ring width chronologies for Qinghai spruce from six sample sites (A1–A6) along a consistent slope (a), the blue lines indicate the residual chronologies and the red lines indicate the 8-year low-pass filtered standard chronologies at six elevations, the gray

area corresponding to the sample depth; the first principal component from the six residual chronologies (b), the red line indicates the 8-year low-pass filtered series

significant and positive ($p < 0.01$; Table 2). The six RES chronology-based PCAs for 1911–2012 demonstrated that only the first eigenvalue was greater than 1, and RES chronology-based PC1 accounted for 75.695 % of common variability extracted from the six RES chronologies (Fig. 3b). Such similar variation patterns, significant correlation between chronologies, and the high first PCA eigenvalue suggested that *P. crassifolia* radial growth at different elevations may be limited by the same climate factor.

Correlation analysis showed that *P. crassifolia* radial growth was primarily limited by drought conditions in the Qilian Mountains at all elevations. Direct evidence for this was that tree-ring width indices were positively correlated with PDSI and relative humidity during the growth season (Fig. 4). Moreover, precipitation in May was significantly and positively correlated with the *P. crassifolia* tree-ring width index at all elevations and RES chronology-based PC1, while high temperatures in June were significantly

Table 2 Correlation analysis matrix for six residual chronologies for their common period (1911–2012)

	A1	A2	A3	A4	A5	A6
A1	1					
A2	0.784**	1				
A3	0.819**	0.830**	1			
A4	0.696**	0.792**	0.807**	1		
A5	0.590**	0.754**	0.721**	0.778**	1	
A6	0.446**	0.617**	0.547**	0.679**	0.709**	1

** Correlation is significant at the 99 % level ($p < 0.01$)

and negatively correlated to *P. crassifolia* growth (Fig. 4). It is interesting to note that significant positive correlations were found between tree-ring chronologies and rainfall in August and September of the preceding growth year (Fig. 4), suggesting that precipitation had notable lag

effects on tree growth. Additionally, correlation between low-pass filtered chronologies to climate factors and correlation between high-pass filtered chronologies to climate factors showed that high-frequency signals responded better to precipitation than low-frequency signals, while low-frequency signals reflected greater information with regard to mean- and minimum temperatures than high-frequency signals (Fig. 5a, b).

Results from surface regression analysis response, which was conducted between the six RES chronologies and instrumental climate data, are provided in Fig. 6. At all six elevations, wider tree-ring widths were formed if precipitation (from the preceding August to the following May) was higher, regardless of how high or low the maximum temperature was. Results also showed that associations between tree-ring series and temperature may be stronger under higher precipitation. Overall, surface analysis response

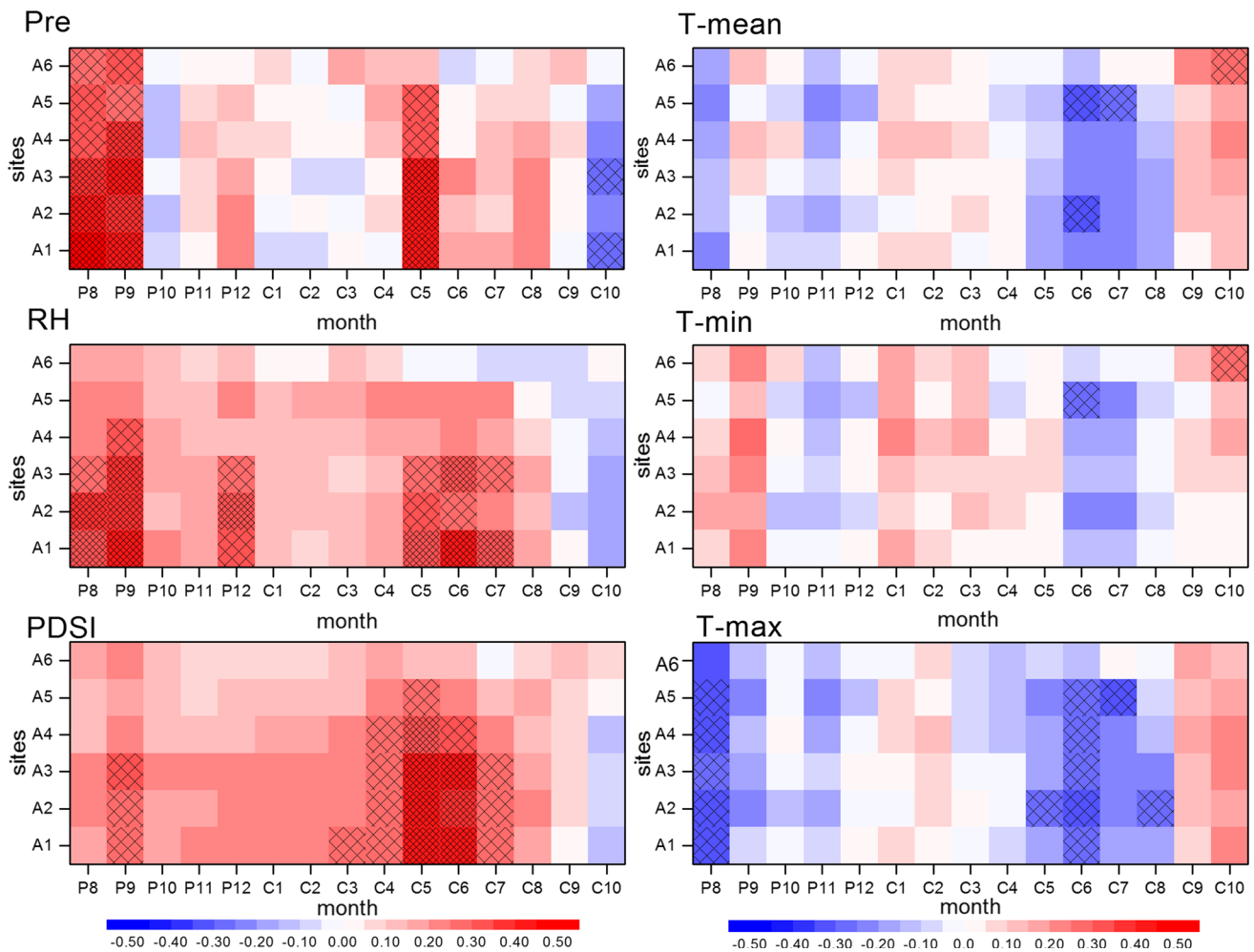


Fig. 4 Correlation analyses between the six tree-ring width chronologies and the monthly mean temperature (T-mean), minimum temperature (T-min), maximum temperature (T-max), monthly precipitation (Pre), relative humidity (RH) and PDSI; the heavier the

color, the stronger is the correlation; the red represents the positive correlation and the blue represents the negative correlation; the dense- and the sparse-grid shadow indicates the significance at 99 and 95 %, respectively

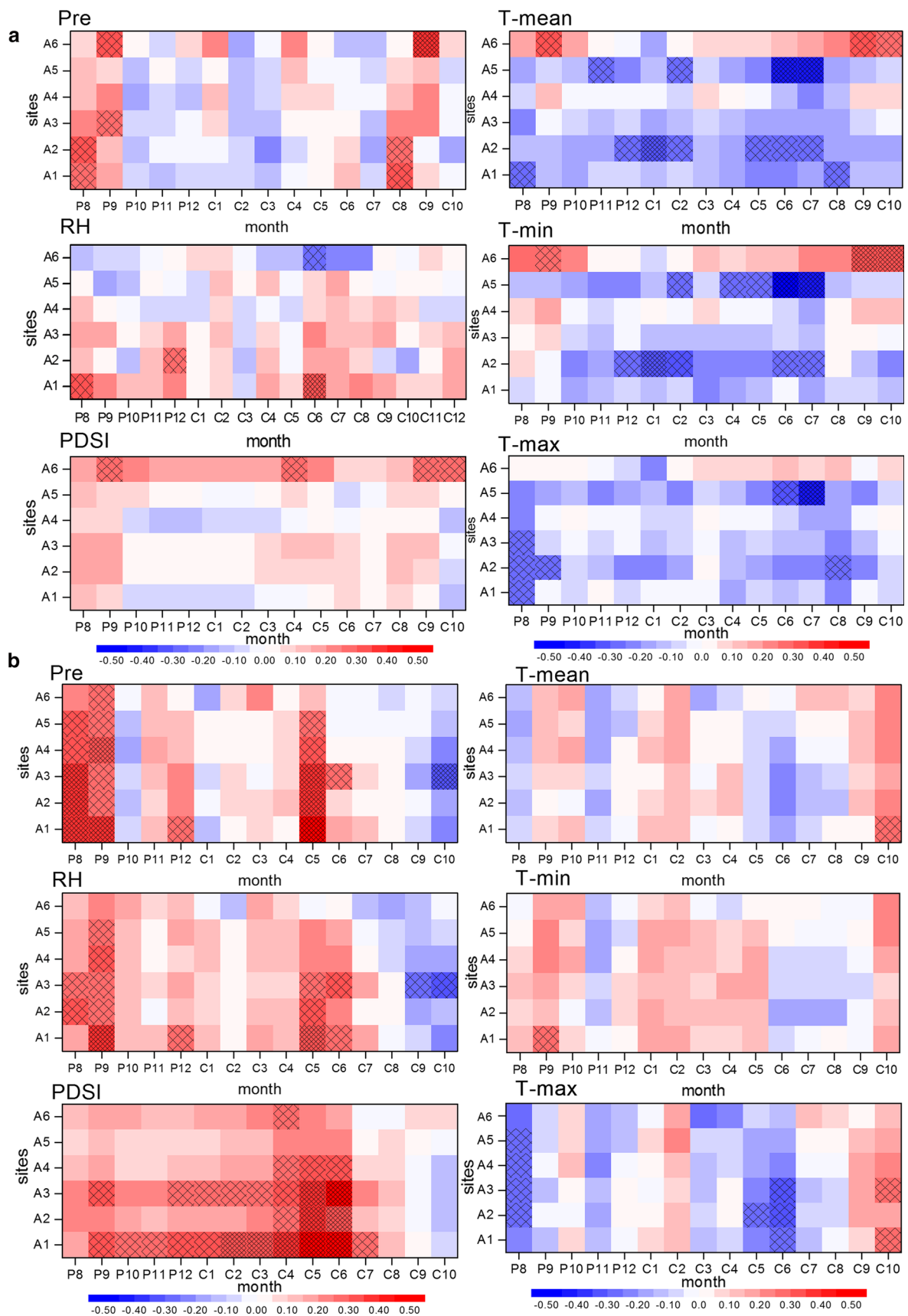


Fig. 5 Climate response of the low-pass filtered (a) and high-passed (b) chronologies to the monthly mean temperature (T-mean), minimum temperature (T-min), maximum temperature (T-max), monthly precipitation (Pre), relative humidity (RH) and PDSI; the heavier the color, the stronger is the correlation; the red represents the positive correlation and the blue represents the negative correlation; the dense- and the sparse-grid shadow indicates the significance at 99 and 95 %, respectively

provided evidence that showed that associations between *P. crassifolia* radial growth and precipitation were stronger than temperature. Nevertheless, maximum temperature still had an impact on tree growth. Therefore, drought conditions, which were determined by precipitation and temperature, are assumed to be the climate factor most responsible for the control of local tree growth patterns.

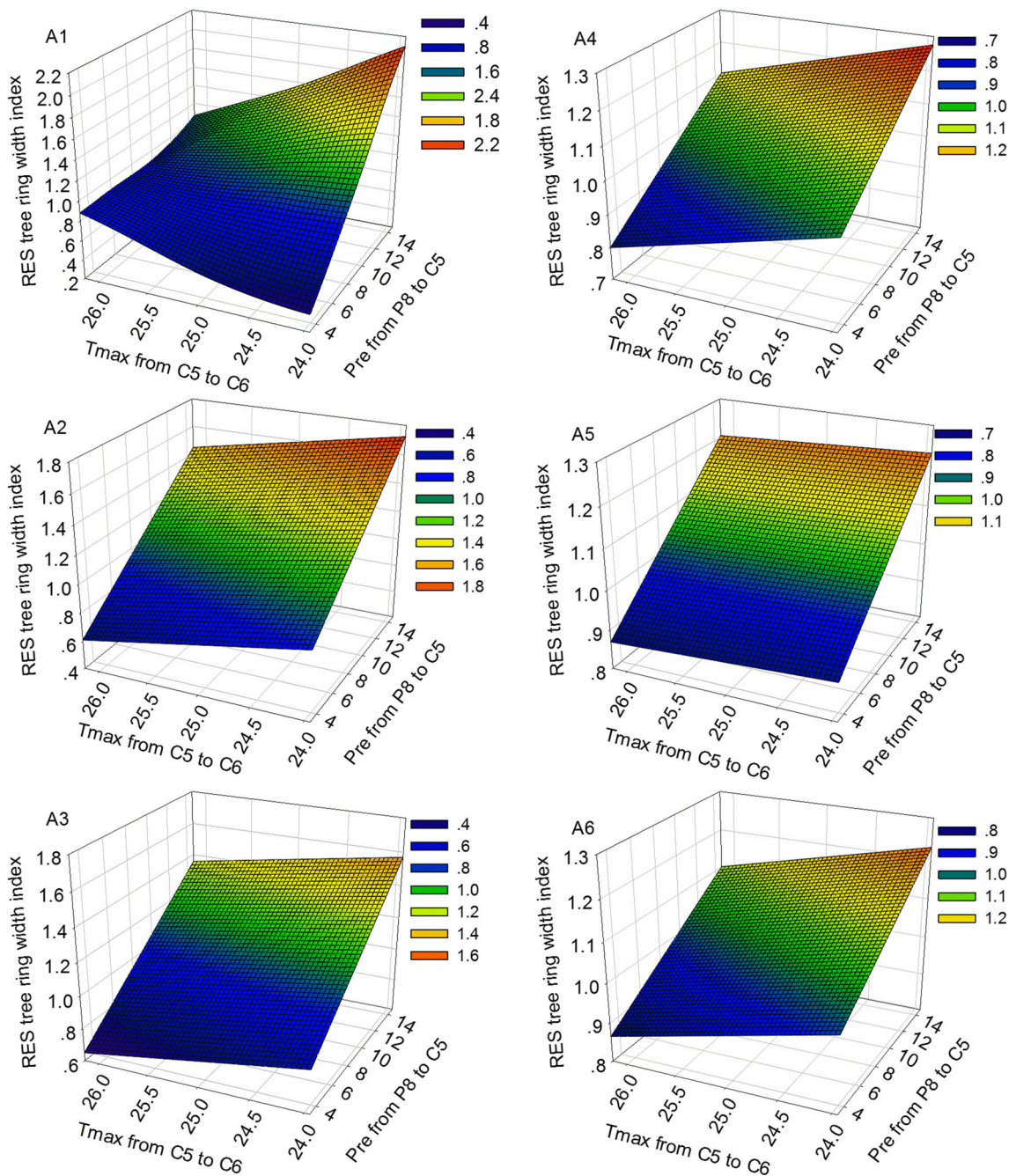


Fig. 6 Results of the response surface analysis, the X, Y and Z axes denote accumulating precipitation from previous August to current May, current May–June maximum temperature and residual tree-ring width index, respectively

In the present study, *P. crassifolia* recruitment response to climate change was explored for different sections of the forest. First, it was determined that tree recruitment in different sections exhibited identical characteristics of variance (Fig. 7). The establishment of all three sections of the forest began in the late nineteenth century. Between the early to late twentieth century, *P. crassifolia* recruitment acceleration increased. However, between the 1950s to the 1990s, *P. crassifolia* recruitment decreased to a relatively low level. Furthermore, *P. crassifolia* recruitment rates for all three sections coincided well with the temperature changes (local observed temperature as well as reconstructions in larger spatial scales), which may indicate that the forest recruitment rate and tree density of the *P. crassifolia* forest were significantly influenced by temperature (Fig. 7). However, similar patterns were not found between the tree recruitment rate and precipitation at all elevations.

Elevation-dependent variability of *P. crassifolia* growth and the growth–climate response

First, ring width pattern similarity between chronologies decreased with distance, showing a decreasing tendency in correlation coefficients between chronologies with increasing perpendicular distance (Table 2). This may indicate that altitude was a significant factor influencing tree growth and climate–growth response. Furthermore,

MS and SD values in chronologies decreased significantly at higher elevations (Table 3), indicating that tree growth response to climate may weaken at higher elevations.

At higher elevations, climate–growth correlations decreased considerably (Fig. 4). Correlations between tree growth and precipitation in May as well as rainfall in August and September of the preceding growth year varied from significantly positive to weakly positive. Furthermore, at lower elevations (A1–A5), significant negative correlations were found between tree-ring width and the maximum temperature in June. In contrast, near the upper tree-line (A6), relationships between tree-ring width and temperature were much weaker (Fig. 4). A linear decrease in correlation coefficient values of ring widths and PDSI between March and July was also found from the lower to upper limit. Additionally, at lower elevations, radial growth responded to drought conditions (PDSI) far longer than at higher elevations (Fig. 4). Results from spatial correlation analyses also showed that spatial correlation fields of tree-ring width indices to regional climatic factors (May–June precipitation and May–July PDSI) significantly decreased at higher elevations. Especially near the upper tree-line (A6), spatial correlation field area was too small to be observed (Fig. 8).

Moreover, even though variance patterns in moving correlations between *P. crassifolia* radial growth and identified influencing factors were similar at all elevations,

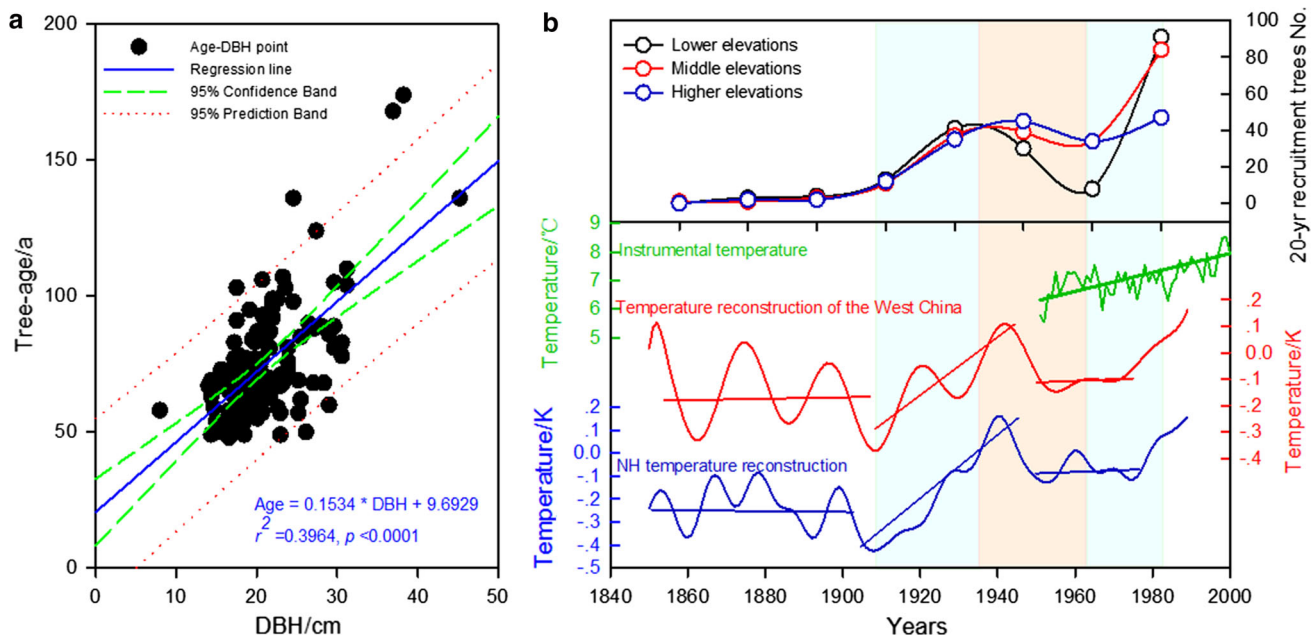


Fig. 7 The regression equation obtained for the diameter–age relationship of *P. crassifolia*, r^2 and p values (a); twenty-year change of increment of the number of trees in 800 m² of *P. crassifolia* e at low elevations (2600–2800 m a.s.l.), middle elevations (2800–3000 m a.s.l.) and high elevations (higher than 3000 m a.s.l.), and their

comparisons with temperature change (local observed 20 years-averaged temperature, temperature reconstruction in the West China and 20 years-averaged North Hemisphere temperature reconstruction) (b); temperature reconstructions data from the NOAA

Table 3 Basic statistic of residual chronologies for Qinghai spruce at six elevations in the mid-Qilian Mountains

Chronology	Chronology length (years)	Mean ring width Indices (mm)	SD	MS	PC1 (%)	SNR	EPS	RBAR	ac1
A1	123	0.960	0.281	0.339	71.0	44.536	0.978	0.690	0.402
A2	139	0.985	0.284	0.339	68.3	30.117	0.968	0.653	0.447
A3	104	0.979	0.293	0.359	76.9	45.305	0.978	0.751	0.464
A4	110	0.997	0.222	0.269	61.2	24.529	0.961	0.577	0.352
A5	102	0.98	0.186	0.230	65.6	36.216	0.973	0.633	0.517
A6	105	0.991	0.133	0.152	52.9	11.08	0.917	0.480	0.635

SD is chronology common interval standard deviation, MS is mean sensitivity, PC1 is the variance in the first eigenvalue contained in each chronology, SNR is signal-to-noise ratio, EPS is the express population signal, RBAR is mean tree-ring series inter-correlation, ac1 is the first-order tree-ring series auto-correlation coefficient

variation in ratio analysis showed that the coefficient of variation (CV) of the moving correlation series was highest near the upper tree-line, suggesting that stability was lowest near the upper limit (Fig. 9). Additionally, surface analysis response showed that when water was in sufficient supply, the limitation of higher temperatures on radial growth at the lower limit was greater than that at higher elevations. The limitation of higher temperatures on radial growth at A5 appeared weakest (Fig. 6).

In spite of the fact that the *P. crassifolia* recruitment rate coincided well with the temperature changes for all three sections, response sensitivity of *P. crassifolia* recruitment to temperature changes at low elevations (2600–2800 m AMSL), mid-elevations (2800–3000 m AMSL), and high elevations (greater than 3000 m AMSL) differed from one another. Figure 7 shows the amplitude of *P. crassifolia* recruitment rate variation, which may have resulted from lower temperature changes at high elevations compared to mid-elevations. Moreover, amplitude at mid-elevations was weaker than at lower elevations. This phenomenon was particularly evident between 1930–1950, 1970–1990, and 1990–2010. The decrease in amplitude of variation of tree number increments may indicate that the response of *P. crassifolia* tree density and the forest recruitment rate to climate change weakened at higher elevations (Fig. 7).

Discussion

Identical factors limiting *P. crassifolia* growth at different elevations

Picea crassifolia growth rates at different elevations were limited by identical factors. Tree-ring growth was primarily limited by drought conditions, which was determined by precipitation and temperature along the entire elevation in the Qilian Mountains. This was in agreement with conclusions reported by Gou et al. (2005) that stated that

springtime precipitation was the most significant limiting factor on *P. crassifolia* growth rates. Results from the present study together with previously published results demonstrated that, in springtime and summer, precipitation was the primary means of water supply for *P. crassifolia* growth, which makes precipitation a leading limiting factor on *P. crassifolia* growth rates (Gou et al. 2005; Wang et al. 2001). This also fits with characteristics of *P. crassifolia* phenology. Because the species is not particularly drought-tolerant and favors moist conditions on shady or semi-shady slopes, it is sensitive to soil drought (Liu 1992). Furthermore, negative effects of high temperatures on tree growth may result from the fact that high temperatures in June can aggravate plant transpiration, leading plants to close part of their stomata to reduce water loss during transpiration. This would affect the ability of leaves to absorb CO₂ for photosynthesis, and subsequently inhibit tree growth (Cao and Song 1998; Downton et al. 1988; Wu 1990). Moreover, high temperatures had negative effects on key enzymes related to plant photosynthesis, reducing the overall photosynthetic rate, which would also inhibit tree growth (Kobza and Edwards 1987; Weis 1988). Additionally, results showed that temperature exhibited no obvious limitations on tree growth at higher altitudes, which differed from previous views that tree growth at high elevations was controlled by temperature (Kienast et al. 1987; Wu 1990; Zhang and Wilmking 2010).

Furthermore, long-term studies on the relationship between changes in tree population and climate showed that similar variation patterns existed in tree recruitment dynamics and temperature, indicating that *P. crassifolia* forest recruitment rate was primarily influenced by temperature. This result was consistent for all three sections of the *P. crassifolia* forest investigated in this study. This conclusion was also in agreement with a report by Fang et al. (2009) which stated that the number of surviving trees at tree-lines in the Anyemaqen Mountains in the north-eastern Tibetan Plateau region coincided well with the

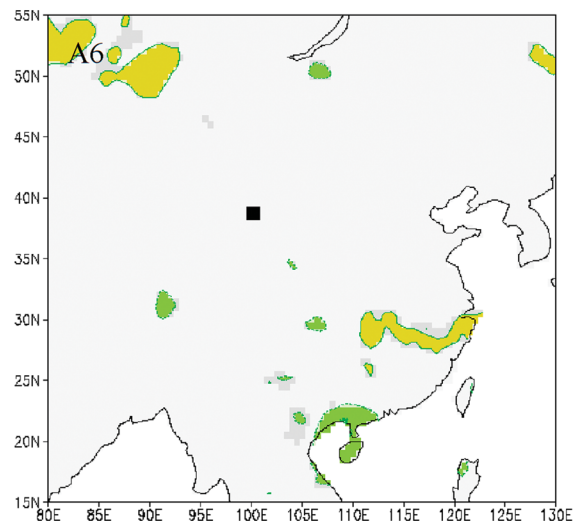
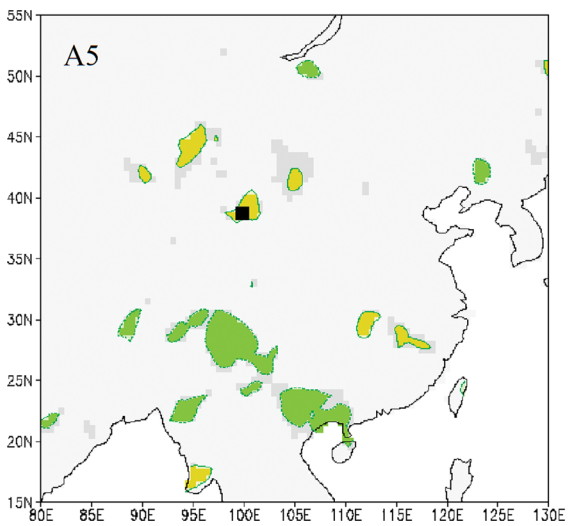
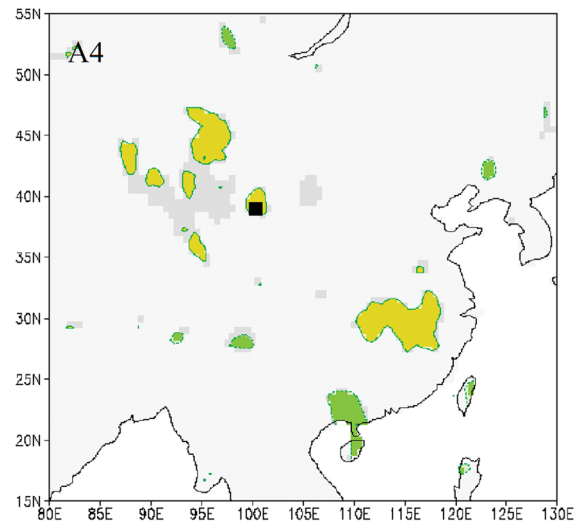
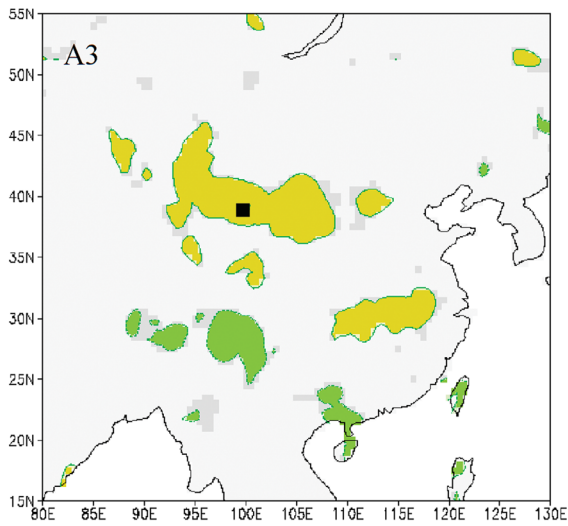
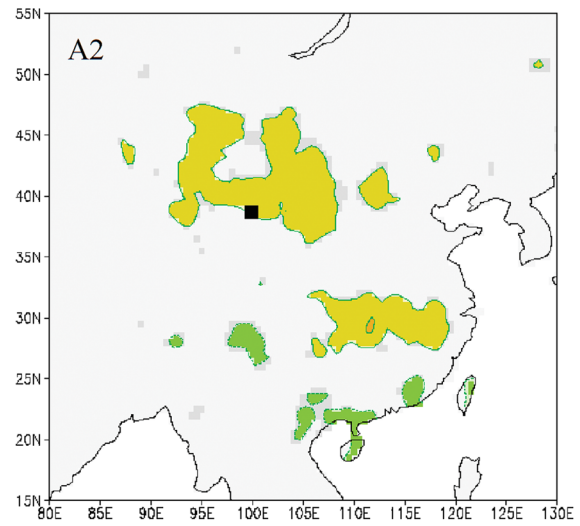
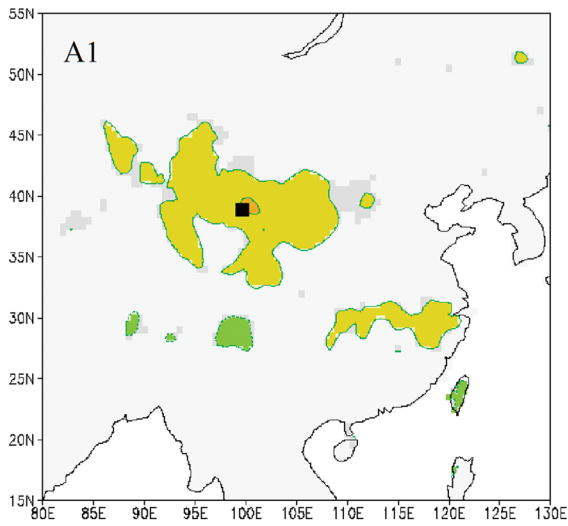


Fig. 8 Spatial correlation pattern between tree-ring width indices and May–June averaged CRU TS 3.10 precipitation dataset during 1911–2009, $p < 10\%$, black dots indicate the location of the study site

accelerated global warming. This conclusion may provide greater insight into forest dynamics in the northeastern Tibetan Plateau region and forest management practices under a background of global warming.

Weaker *P. crassifolia* climate–growth response at higher elevations

Picea crassifolia growth response to climate decreased with increasing altitude. This conclusion was supported by a significant decrease in MS and SD, a decrease in climate–growth correlation coefficients, a reduction in spatial correlation fields between tree-ring width indices and regional climatic factors, and a weakened response of *P. crassifolia*

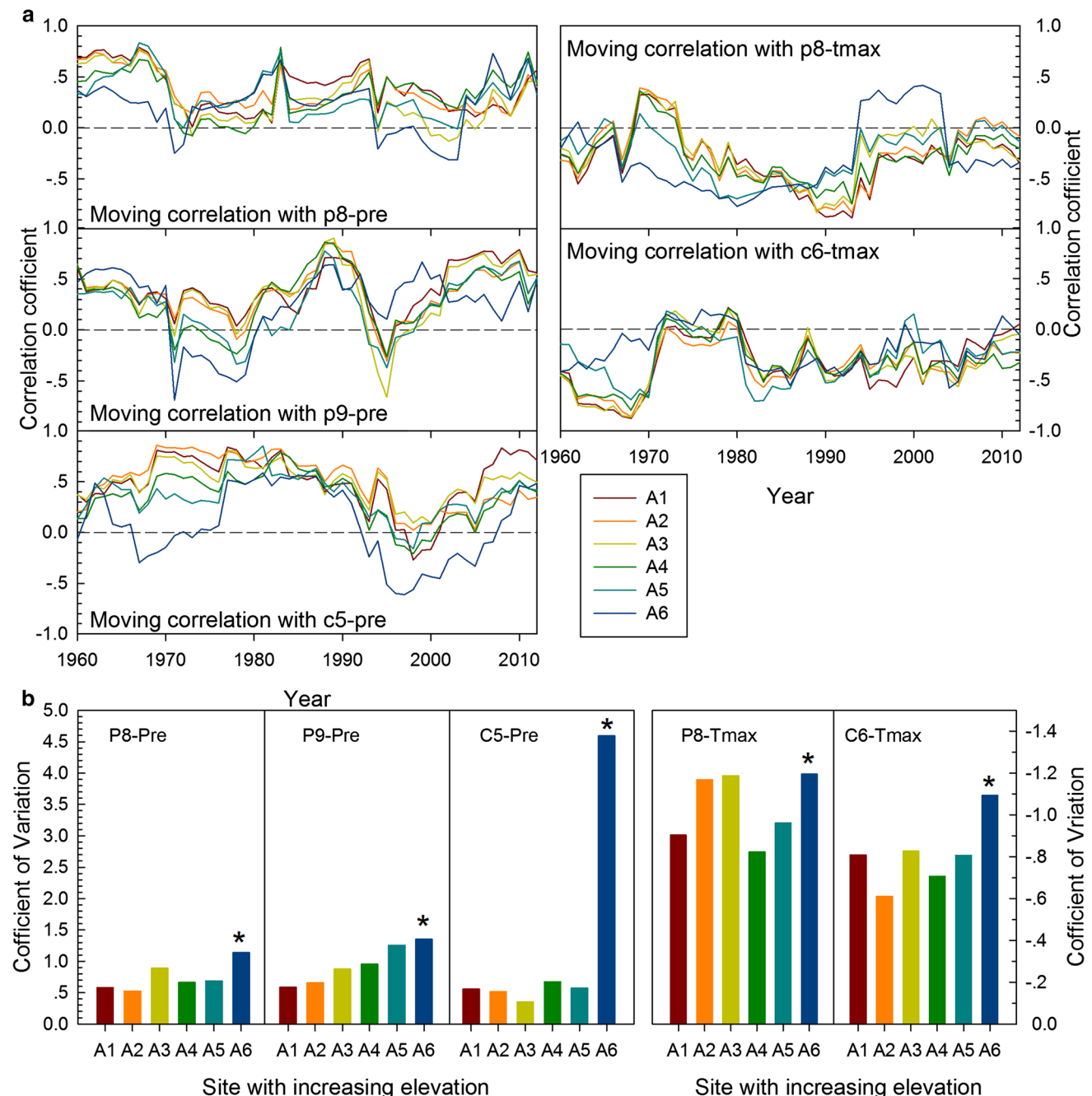


Fig. 9 Elven-year moving average cross-correlation analysis of chronologies with identified influencing climate factors (a); and the coefficient of variation (CV) of these moving cross-correlation series (b), the *indicates the highest values of CV

recruitment to temperature changes at higher elevations. This stands in agreement with earlier conclusions drawn by previous research in the study area, although effects of landform variance and tree-age diversity received insufficient attention in these studies (Gou et al. 2005; Peng et al. 2008). This result, however, was not in agreement with results from Gao et al. (2013) and Yang et al. (2013) who stated that altitude in itself is not an influencing factor on climate–growth associations in the Qilian Mountains. Differences between these conclusions may result from differences in study areas and tree species investigated. Furthermore, differences in topography (Bunn et al. 2005; Leonelli et al. 2009; Liang et al. 2006) and tree age (Camarero and Gutiérrez 2004; Linán et al. 2012; Wu et al. 2013) may have also had effects on conclusions.

Decreases in *P. crassifolia* sensitivity to climate were probably due to altitudinal variations of climatic factors and the plant species self-regulations. For one thing, by observations in previous studies, it has been well established that increasing elevation leads to increases in precipitation and decreases in temperature (Jin et al. 2012; Tang 1985). Sufficient rainfall at high elevations may provide enough water supply for *P. crassifolia* growth, which may lead the limiting effect of precipitation become weaker than those at lower elevations. Additionally, the lower the temperature at high elevations is, the weaker its negative effects on tree photosynthesis and its aggravation of plant transpiration become. For another, Qiang et al. (2003) measured leaf morphology and indicated that stomata density and characteristics, needle length and dry weight, as well as needle stable carbon isotope composition ($\delta^{13}\text{C}$) decreased dramatically above 3000 m AMSL, which indicated that the species could alter (lower) its metabolic rate at higher altitudes. A lower metabolism allowed the species to avoid effects of the severe environmental conditions inherent to higher elevations. Moreover, according to the study by Wu et al. (2010), the leaf lifespan of *P. crassifolia* increased greatly along altitude gradient from 2700 to 3300 m, and the maximum lifespan was observed at the upper tree-line. All these morphological and physiological variations of *P. crassifolia* at higher elevations, as suggested to above, can be seen as self-regulations to environmental change, which is believed to be a plant strategy to minimize the effects of alpine environments. Therefore, trees growing at higher elevations showed a lower sensitivity to climate.

Conclusions

By analyzing the tree growth–climate response of *P. crassifolia* at different elevations along a consistent slope in the Qilian Mountains, this study concluded that: (1) Growth–climate responses of *P. crassifolia* at different

elevations were limited by identical factors. *P. crassifolia* tree-ring growth was primarily limited by drought conditions, which are determined by precipitation and temperature in the Qilian Mountains along the entire elevation gradient. Moreover, *P. crassifolia* densities and forest recruitment rates at different elevations were all primarily influenced by temperature. (2) The climate–growth response of *P. crassifolia* at higher elevations was weaker than at lower altitudes. Chronologies related to mean sensitivity (MS), standard deviation (SD), and correlations between tree-ring-climate (both the correlation between tree-ring width indices and climate factors and spatial correlation fields between tree-ring width indices and regional climate factors) significantly decreased at higher elevations, supporting this conclusion. The response of forest recruitment to temperature changes decreased with increasing elevation, confirming results.

The study of elevation-dependent variation is fundamental to tree-ring research. This study on the elevation-dependent response of *P. crassifolia* to climate in the mid-Qilian Mountains region could provide insight into forest dynamics and offer clues for further studies on climate change using tree-ring data in arid and semi-arid regions in northwestern China.

Acknowledgments We are grateful to the editors and reviewers for valuable comments and suggestions that substantially improved the manuscript. This work was supported by the National Key Technology R&D Program of China [No. 2014BAC05B02], Key Research Program of the Chinese Academy of Sciences [No. KZZD-EW-04-05], the National Natural Science Foundation of China [Nos. 31200299, and 41501049], and the Light of West China Program of Chinese Academy of Sciences. We should express our appreciation to Dr. Tai Xisheng and Dr. Kong Dongsheng for their help in field works. We also thank Dr. Richard Michalet for his advices on this work and Dr. Brain Doonan for his work on language editing.

Compliance with ethical standards

Conflict of interest The authors have declared that no conflict of interest exists.

References

- Biondi F, Waikul K (2004) DendroClim2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput Geosci* 30:303–311
- Blasing T, Solomon A, Duvick D (1984) Response functions revisited. *Tree-Ring Bull* 44:1–15
- Briffa K, Cook E (1990) Methods of response function analysis. In: Cook ER, Kairiukstis L (eds) *Methods of dendrochronology*. Kluwer, Dordrecht, pp 165–178
- Brookhouse MT, Bi HQ (2009) Elevation-dependent climate sensitivity in *Eucalyptus pauciflora* Sieb. ex Spreng. *Trees* 23:1309–1320
- Bunn AG, Waggoner LA, Graumlich LJ (2005) Topographic mediation of growth in high elevation foxtail pine (*Pinus*

- balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA. *Glob Ecol Biogeogr* 14:103–114
- Camarero JJ, Gutiérrez E (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Clim Change* 63:181–200
- Cao YZ, Song ZW (1998) *Plant physiology*. The University of Lanzhou Press, Lanzhou
- Carrer M, Urbinati C (2004) Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85:730–740
- Cook ER, Holmes RL (1986) Users manual for program ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson
- Cook ER, Kairiukstis LA (1990) *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic, Boston
- Dai AG, Trenberth KE, Qian TT (2004) A global dataset of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *J Hydrometeorol* 5(6):1117–1130
- Downton W, Loveys B, Grant W (1988) Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. *New Phytol* 108:263–266
- Duncan R (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*) New Zealand. *Nat Sci* 16(3):1–37
- Fang KY, Gou XH, Chen FH, Peng JF, D'Arrigo R, Wright W, Li MH (2009) Response of regional tree-line forests to climate change: evidence from the northeastern Tibetan Plateau. *Trees* 23:1321–1329
- Fritts H (2012) *Tree rings and climate*. Elsevier, Amsterdam
- Gao LL, Gou XH, Deng Y, Liu WH, Yang MX, Zhao ZQ (2013) Climate-growth analysis of Qilian juniper across an altitudinal gradient in the central Qilian Mountains, northwest China. *Trees* 27:379–388
- Gou XH, Chen FH, Yang MX, Li J, Peng JF, Jin L (2005) Climatic response of thick leaf spruce (*Picea crassifolia*) tree-ring width at different elevations over Qilian Mountains, northwestern China. *J Arid Environ* 61(4):513–524
- Gou XH, Zhang F, Deng Y, Ettl GJ, Yang MX, Gao LL, Fang KY (2012) Patterns and dynamics of tree-line response to climate change in the eastern Qilian Mountains, northwestern China. *Dendrochronologia* 30:121–126
- Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res* 57(2):205–221
- He MH, Yang B, Bräuning A (2013) Tree growth-climate relationships of *Juniperus tibetica* along an altitudinal gradient on the southern Tibetan Plateau. *Trees* 27:429–439
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:69–78
- Jin M, Che ZX, Jing WM, Zhao WJ, Ma Y, Liu SR (2012) Spatiotemporal changes of precipitation and temperature at water resources conservation forests area in Qilian Mountains, China. *J Desert Res* 32(4):1071–1076
- Kang XC, Cheng GD, Chen FH, Gou XH (2003) A record of drought and flood series by tree-ring data in the middle section of Qilian Mountain Since 904 A. D. *J Glaciol Geocryol* 25:517–525
- Kienast F, Schweingruber FH, Bräker OU, Schär E (1987) Tree-ring studies on conifers along ecological gradients and the potential of single-year analyses. *Can J For Res* 17:683–696
- Kobza J, Edwards GE (1987) Influences of leaf temperature on photosynthetic carbon metabolism in wheat. *Plant Physiol* 83:69–74
- Landis RM, Peart DR (2005) Early performance predicts canopy attainment across life histories in subalpine forest trees. *Ecology* 86:63–72
- Leonelli G, Pelfini M, Battipaglia G, Cherubini P (2009) Site-aspect influence on climate sensitivity over time of a high-altitude *Pinus cembra* tree-ring network. *Clim Change* 96:185–201
- Li XX, Liu XD, Zhao WJ (2012) Population structure and spatial distribution pattern of *Picea crassifolia* in dayekou basin of Qilian Mountains. *Arid Land Geogr* 35(6):960–967
- Liang EY, Shao XM, Eckstein D, Huang L, Liu XH (2006) Topography-and species-dependent growth responses of *Sabina przewalskii* and *Picea crassifolia* to climate on the northeast Tibetan Plateau. *For Ecol Manag* 236:268–277
- Liang EY, Wang YF, Xu Y, Liu B, Shao XM (2010) Growth variation in *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. *Trees* 24:363–373
- Linán ID, Gutiérrez E, Heinrich I, Andreu-Hayles L, Muntán E, Campelo F, Helle G (2012) Age effects and climate response in trees: a multi-proxy tree-ring test in old-growth life stages European. *J For Res* 131:933–944
- Liu XC (1992) *Qinghai spruce*. The University of Lanzhou Press, Lanzhou
- Liu XH, Shao XM, Liang EY, Chen T, Qin DH, An WL, Xu GB, Sun WZ, Wang Y (2009) Climatic significance of tree-ring delta O-18 in the Qilian Mountains, northwestern China and its relationship to atmospheric circulation patterns. *Chem Geol* 268(1–2):147–154
- Mäkinen H, Nöjd P, Kahle H, Neumann U, Tveite B, Mielikäinen K, Röhle H, Spiecker H (2002) Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. *For Ecol Manag* 171:243–259
- Mann ME, Zhang Z, Rutherford S, Bradley RS, Hughes MK, Shindell D, Ammann C, Faluvegi G, Ni F (2009) Global signatures and dynamical origins of the Little Ice Age and Medieval. *Clim Anom Sci* 326:1256–1260
- Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int J Climatol* 25:693–712
- Norton D (1985) A dendrochronological study of *Nothofagus solandri* tree growth along an elevational gradient, South Island, New Zealand. *Berichte, Eidgenössische Anstalt für das Forstliche Versuchswesen, Switzerland* 270:159–171
- Peng JF, Gou XH, Chen FH, Liu PX, Zhang Y, Fang KY (2007) Characteristics of ring-width chronologies of *Picea crassifolia* and their responses to climate at different elevations in the Anyemaqen Mountains. *Acta Ecol Sin* 27:3268–3276
- Peng JF, Gou XH, Chen FH, Li JB, Liu PX, Zhang Y (2008) Altitudinal variability of climate-tree growth relationships along a consistent slope of Anyemaqen Mountains, northeastern Tibetan Plateau. *Dendrochronologia* 26:87–96
- Qiang WY, Wang XL, Chen T, Feng HY, An LZ, He YQ, Wang G (2003) Variations of stomatal density and carbon isotope values of *Picea crassifolia* at different altitudes in the Qilian Mountains. *Trees* 17:258–262
- Richter K, Eckstein D, Holmes R (1991) The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. *Tree-Ring Bull* 51:1–13
- Rinn F (2003) TSAP-Win: time series analysis and presentation for dendrochronology and related applications Version 0.55 User reference. Heidelberg, Germany
- Rozas V (2003) Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. *Plant Ecol* 167:193–212
- Shi F, Yang B, von Gunten L (2012) Preliminary multiproxy surface air temperature field reconstruction for China over the past millennium. *Sci China Earth Sci* 55(12):2058–2067
- Tang MC (1985) The distribution of precipitation in Mountain Qilian (nanshan). *Acta Geogr Sin* 4:002

- Wang YJ, Chen FH, Gou XH, Du S (2001) Study on response relationship between tree-ring and climate factors and climate reconstruction in middle region of Qilianshan Mountains. *J Desert Res* 21:135–140
- Wang T, Ren HB, Ma KP (2005) Climatic signals in tree ring of *Picea schrenkiana* along an altitudinal gradient in the central Tianshan Mountains, northwestern China. *Trees* 19:736–742
- Weis E (1988) Plants and high temperature stress. *Plants Temp* 42:329–346
- Wells N, Goddard S, Hayes MJ (2004) A self-calibrating Palmer Drought Severity Index. *J Clim* 17:2335–2351
- Wigley TM, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J Climate Appl Meteorol* 23:201–213
- Wilmking M, Juday GP (2005) Longitudinal variation of radial growth at Alaska's northern treeline—recent changes and possible scenarios for the 21st century. *Glob Planet Change* 47:282–300
- Wu XD (1990) Tree ring and climatic change. Meteorology Press, Beijing
- Wu Q, Hu QW, Zheng L, Zhang F, Song MH, Liu XD (2010) Variations of leaf lifespan and leaf mass per area of *Picea crassifolia* along altitude gradient. *Acta Bot Boreal Occident Sci* 30(8):1689–1694
- Wu GJ, Xu GB, Chen T, Liu XH, Zhang Y, An WL, Wang WZ, Fang ZA, Yu SL (2013) Age-dependent tree-ring growth responses of Schrenk spruce (*Picea schrenkiana*) to climate—a case study in the Tianshan Mountain, China. *Dendrochronologia* 31:318–326
- Yang YK, Liu Y, Cai QF, Ma HZ, Ma LM, Guo JW (2005) Precipitation reconstruction from tree ring width over the central Qilian Mountains for the last 248 years. *Mar Geol Quat Geol* 25:113–118
- Yang B, He MH, Melvin TM, Zhao Y, Briffa KR (2013) Climate control on tree growth at the upper and lower treelines: a case study in the Qilian Mountains, Tibetan Plateau. *PloS One* 8(7):e69065
- Zhang LJ, Jiang ZR (2006) Fractal properties of spatial pattern of *Picea crassifolia* population at different altitudes. *J N W For Univ* 21:64–66
- Zhang YX, Wilmking M (2010) Divergent growth responses and increasing temperature limitation of Qinghai spruce growth along an elevation gradient at the northeast Tibet Plateau. *For Ecol Manag* 260:1076–1082