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Article

Radial growth response of *Abies georgei* to climate at the upper timberlines in central Hengduan Mountains, Southwestern China

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Abstract

Climate change has a inevitable impacts on tree radial growth, particularly at mountain timeberlines. To understand climate effects on conifer radial growth in the central Hengduan Mountains and potential impacts of future climate change on conifer forest, we studied growth responses to climate variables in *Abies georgei*, the major tree species of conifer forest in Hengduan Mountains. We collected tree ring samples from four sites near the timberlines and analyzed the relationship between principle components (PC#1) of four chronologies and climatic variables by using response function analysis (RFA), redundancy analysis (RDA) and moving interval analysis (MIA). *A. georgei* growth was affected by both temperature (positive effects) and precipitation (negative effects). Specifically, the radial growth of *A. georgei* was significantly and positively correlated with current July and previous November temperature (detected by both RFA and RDA), while precipitation of current June and September inhibited tree growth (detected by RDA). More rapid warming in recent 20 years (1990-2010) clearly enhanced growth responses to July and November temperature, whereas the relationship was weaken for June and September precipitation according to MIA. Under the climate trend of the study area, if the increasing temperature could offset the negative effects of excessive precipitation, *A. georgei* radial growth would likely benefit from warming, the dynamics of conifer forest should also consider indirect impacts of climate change.

Key words: Southeastern rim of Tibetan plateau; dendrochronology; climate response; climate warming; subalpine conifer forests

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1. Introduction

Instrumental data suggest that mountain forests in high elevation area have been subject to higher rates of temperature change than the surrounding lowlands (Pepin *et al*., 2015). The global mean temperature has risen by about 0.74±0.18 ℃ over the past century and is projected to increase by 1.8~4.0 ℃ in the 21st century. During the past five decades, the area of central Hengduan Mountains has experienced a significant warming trend at a rate of

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0.3 ℃/decade (Fan *et al*., 2011). This climate change has a great influence on tree regeneration, growth and mitigating abilities in high elevation area (Pepin *et al*., 2015; Kharal *et al*., 2017), consequently affecting structure, productivity and dynamics of forests in high mountain regions (Cailleret *et al*., 2014; Yadava *et al*., 2017).

Tree radial growth is more sensitive to climate change near the species distributional boundaries (Malanson, 2001). In high mountain regions, tree radial growth at the upper timberlines is generally believed to be controlled by temperatures (Schweingruber, 1996; Bräuning, 2001; Fan *et al*., 2008), both growing season and previous winter temperatures have been found to be important factors affecting tree growth at upper distributional limits (Mayr *et al*., 2006; Elliott, 2012; Zhang *et al*., 2017). However, some studies have shown that early growing season moisture also influenced tree radial growth in high elevation forests (Leuschner, 1996; Biondi, 2001; Morales *et al*., 2004; Liang *et al*., 2014). Therefore, the mechanism of tree growth response to climate is complex at upper timberlines and needs to be better understood.

Tibetan plateau is one of the most sensitive areas to global climate change (Liu & Chen, 2000; Li *et al*., 2017) with an average elevation of more than 4000 m above sea level, many tree species have formed natural timberlines on Tibetan Plateau, and therefore the region is suitable for dendroclimatology study. The radial growth of *Betula utilis* at the upper timberlines is mainly limited by the moisture during the pre-monsoon season on Southern Tibetan Plateau (Liang *et al*., 2014), while the minimum temperature in July is the main factor affecting tree growth of *Abies georgei* at the upper timberlines on Southeastern Tibetan Plateau (Liang *et al*., 2010). Additionally, tree growth of *Juniperus tibetica* at the upper timberlines on Northeastern Tibetan Plateau is positively correlated with temperature from October to January and with the Palmer Drought Severity Index (PDSI) from September to June (Deng & Zhang, 2015). The relationships between tree growth and climate variables at the upper timberlines may vary even in the same region. Thus, dendroclimatology study of timberlines at different sites can help to reveal the main factors affecting tree growth at the distributional limit in an area.

The central Hengduan Mountains, located in Southeastern margin of Tibetan Plateau, is a climate-sensitive area and thus to be a typical place for dendroclimatology study (Fan *et al*., 2009). Up to now, several tree species in this region have been used to reconstruct the past climate variations (Fan *et al*., 2008; Guo *et al*., 2009; Li *et al*., 2012; Bi *et al*., 2015), and several studies have analyzed the tree growth response to climate change (Fan *et al*., 2009; Zhang *et al*., 2017). *A. georgei* is a typical and important component of subalpine ecoregions in the central Hengduan Mountains, as an important economic tree species, its growth has been highly focused. The previous climate-growth response studies of *A. georgei* have been concentrated in the variations of elevational trends (Fan *et al*., 2009; Liang *et al*., 2010; Panthi *et al*., 2018), while others were conducted for climate reconstruction (Li *et al*., 2012). However, most of that were carried out in a single mountain, the study of relationships between tree growth of *A. georgei* and climate variables at timberlines on regional scales was rare.

Tree ring variations often reflect the environmental change, particularly for climate conditions in the past years (Fritts, 1976). Dendroclimatology, as a traditional and valid method, has widely been used to detect the long-term growth-climate relationship and to further evaluate the impact of future climate change on tree growth and forest dynamics. In this study, we aimed at exploring key climate factors influencing radial growth of *A. georgei* at the upper timberlines in the central Hengduan Mountains. We hypothesized that *A. georgei* growth was controlled by temperature due to the cold environment at high elevations in mountain regions and *A. georgei* forests would benefit from increasing temperatures. To test the hypotheses, we studied relationships between the residual chronologies of *A. georgei* and

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climatic variables, and discussed potential effects of future climate change on *A. georgei* and related forests growth.

2. Materials and Methods

2.1. Study Area

The central Hengduan Mountains form the transitional zone between the Northwestern Yunnan, the Southern Sichuan and the Southeastern Tibet (Fig. 1). The Mountains extend roughly from north to south and separate three major Asian rivers, named as Jinsha river, Lancang river and Nujiang river, forming one of the richest biodiversity areas in the world. A distinctly altitudinal belts and vegetation types are created due to the extremely topographic gradients. The forests are dominated by *Pinus armandii* and *Pinus yunnanensis* at elevations of 1500~2800 m. From 2800 to 3500 m, *Tsuga dumosa* and *Pinus densata* are dominant species. Between 3200 and 4200 m, forests develop with *Larix potaninii*, *Picea likiangensis* and *A. georgei* as the most common species. From 4200 m to the alpine screes, vegetation is dominated by cold temperate shrubs (alpine rhododendrons) and meadows. Our study sites are located in Shika Snow Mountain (SK), Potatso National Park (PDC), Haba Snow Mountain (HB) and Yulong Snow Mountain (YL), and sampling stands are near their timberlines.

A. *georgei* is native in Southwestern Sichuan, Northwestern Yunnan and Southeastern Tibet (Zhang *et al*., 2008) and ranged from 3200 to 4100 m in this transitional area. The species is shade-tolerant and adapted to acid grey soils with humus. Typically, it forms pure forests at the upper timberlines (about 4000 m) in Hengduan Mountains, while it mixed with *Picea likiangensis* and other conifers at the lower elevation (about 3200 m) forests (Wu, 1999).

Influenced by the interaction of maritime and continental monsoon, the climate in the central Hengduan Mountains has a distinct seasonal change, with a warm and wet summer and relatively cold and dry winter. According to the instrumental data (1960~2011) in Shangri-La meteorological station (27°50′ N, 99°42′ E, 3276.7 m a.s.l.) nearby PDC and SK, the annually mean temperature is 5.9 ℃ with highest temperature (13.6 ℃) occurred in July and lowest (-3.0 ℃) in January (Fig. 2a). While the total annual precipitation is 633 mm, and amount of precipitation from June to September accounts for 73%. Lijiang meteorological station (26°52′ N, 100°13′E, 2393 m a.s.l.) is the closest one to YL and HB, climate data from 1951 to 2010 show that the annually mean temperature is 12.8 ℃ in this area, June is the warmest month with the mean temperature of 18.2 ℃ and January is the coldest month with the temperature of 6.1 ℃ (Fig. 2b). Total annual precipitation is 964.7 mm, 81% of which falls in the period of June to September.

A significant warming trend has been observed in annually mean temperature over the past six decades at both Shangri-La and Lijiang stations. More rapid warming occurred in the recent 20 years, annually mean temperature increased by 0.64 ℃ and 0.56 ℃ per decades at Shangri-La and Lijiang station since 1991, respectively (Figs. 3a, 3b). While the annually total precipitation increased slightly in both Shangri-La and Lijiang before 1991, after that there was a decreasing trend in two meteorological stations (Figs. 3c, 3d).

2.2 Tree-ring sampling and chronology development

Increment cores of *A. georgei* were collected from the timberlines at the four sites (Fig. 1). In total, 264 cores from 134 trees were sampled (Table. 1). At each site, we sampled mature and healthy living trees without insect damage at breast height (approximately 1.3 m) with an increment borer, two cores per tree were taken from opposite directions which is parallel to the contour. Moreover, in order to ensure the consistency of the climate information contained in the samples, we controlled the elevation variations in 10 m at each site.

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According to the standard dendrochronological methods (Storks and Smiley, 1996), wood surfaces of cores were smoothed with sandpaper until the tree ring boundaries were clearly visible. The cores were placed under the microscope for dating work, and dated cores were scanned by EPSON scanner (Expresstion 11000XL, Seiko Epson Corporation, Nagano country, Suwa City, Japan) with setting parameters (full image type 24-bit and a resolution of 3200 dpi). The tree ring widths were measured on the CDendro and CooRecorder ver. 7.3 programs with a resolution of 0.001 mm, all the cores were cross-dated and statistically tested by using COFFCHA program (Holmes, 1983). Cores with low correlations between the main sequences were rejected for the further analysis. In the end, 244 cores (125 trees) were used for chronology development (Table. 2).

Tree rings measurements were standardized by using ARSTAN program (Cook, 1986) to remove the biological growth trend, as well as any other low-frequency variation due to stand dynamics, while to retain the climatic signals influencing tree growth. Cores were detrended with a cubic smoothing spline with a 50% frequency-response cut-off equal to 67% the series length to retain high frequency (Cook and Peters, 1997). To reduce the influence of outliers in the computation of the mean chronologies, all detrended series were averaged on a site-by-site basis using the bi-weight robust mean. Residual chronologies (Fig. 4) were produced to remove any auto-correlation effects and enhance the common signals.

2.3 Data analysis

The monthly instrumental records of Shangri-La (1960~2011) and Lijiang (1951~2010) were obtained from the National Meteorological Information Center (NMIC), China. Monthly mean temperature and monthly total precipitation were used to study tree growth response to climate. Considering the lagged effects of the climate in the previous year on tree growth, climate data from July of prior year to October of current year between 1961 and 2010 were selected. The climate-growth relationships of four sites were analyzed by using the response function analysis (RFA) through the DENDROCLIM 2002 program (Biondi and Waikul, 2004). The response function analysis was a linear multiple regression technique which used the principle components of monthly climatic conditions to estimate the tree ring growth.

To further explore the pattern of growth response to climate change for *A. georgei* in the central Hengduan Mountains, subsequent principal component analysis was performed for the four chronologies. The first component (PC#1) which accounts for 62.5% of the total variance over the period 1955~2015 was presented (Table. 3). Average climate data from two meteorological stations (1960-2010) were used to analyze regional tree growth response (PC#1) to climate.

In addition, to better understand the growth-climate relationships of *A. georgei*, redundancy analysis (RDA) was used to verify the results of RFA. RDA was a multivariate "direct" gradient analysis and its ordination axes were constrained to represent linear combinations of supplied environment variables (Legendre & Legendre, 1998), thus it can effectively describe the relationship between tree ring width index and climate variables (Braak, 1994) and has been widely used in dendroclimatology study (Tardif et al., 2006; Friedrichs et al., 2009; Drobyshev *et al.*, 2013). In the correlation matrix, the 4 residual chronologies were considered as response variables and the years were considered as samples, while climate variables were considered as explanatory variables. Significant (P<0.05) climate variables were selected after a forward selection using a Monte Carlo permutation test based on 499 random permutations, RDA was conducted by program CANOCO4.5 (Braak & Smilauer, 2002).

Moreover, in order to analyze the stability of the connection between tree growth (PC#1) and climate variables, moving interval analysis (MIA) was used to detect the relationship

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dynamics with a 32-year moving window on backward and forward evolutionary intervals, carried out with the Evolutionary and Moving Response and Correlation module in DendroClim2002.

3. Results

Four chronologies (Table. 2; Fig. 4) had a high mean sensitivity (MS), signal to noise ratio (SNR) and expressed population signal (EPS), which indicated that the chronologies had a high quality. Moreover, EPS values of all four chronologies were above 0.85, suggesting that the chronologies could represent the characteristics of tree-ring width in the area and could be used in dendrochronological study.

According to the results of correlation analysis (Pearson correlation) among four chronologies for the common period 1955~2015 (Table. 4), all chronologies were significantly (p<0.05 or p<0.01) and positively correlated. Distance between sampling sites or elevation affected correlation coefficients. The elevation of HB and SK were higher and had highest correlation, while distance between SK and PDC were closest and the correlation coefficient was also high. The lower correlation coefficients between YL and other three sites were due to longer distances.

The results of RFA showed that the pattern of tree growth response to climate was consistency at four sites (Fig. 5). Previous November and current July temperature positively affected tree growth, while current June precipitation had a negative impact on tree growth, although significant correlations of above relationships were detected at one or two out of four sites. Specifically, tree growth at SK and YL showed a significantly positive correlation with previous November temperature and a negative correlation with current June precipitation. While tree growth showed positive correlations with current July and previous November temperature at PDC and HB, respectively.

The RFA (Fig. 6) between PC#1 and monthly climate variables showed that the radial growth of *A. georgei* was mainly affected by temperature at the upper timberlines in the area, by showing positive effects of previous November and current July temperature on its growth.

The results of RDA further supported the results of RFA that the temperature was the important factor influencing tree growth at the upper timberlines of the studied area. Except for previous November and current July temperature influences, RDA also showed that current June and September precipitation negatively affected *A. georgei* growth.

The results of MIA (Fig. 8) showed that the relationship between tree growth (PC#1) and climate variables was not stable in recent 50 years. The positive effects of previous November and current July temperature was strengthened in recent 20 years, by showing more significant correlations than the period between 1962 and 1980. While the negative effects of current June and September was weaken, by showing no significant correlations during 1992-2010.

4. Discussion

Our study showed that both temperature and precipitation affected *A. georgei* growth in the central Hengduan Mountains, which denied the hypothesis that tree growth at the upper timberlines was only affected by temperature. However, the temperature was likely to play a more important role than the precipitation, according to more stable relationship revealed by MIA and only temperature impacts on PC#1 was detected by RFA.. Below we discuss the details of these findings and the potential effects of future climate conditions on the radial growth of *A. georgei*.

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November temperature in previous year might be the most important factor affecting *A. georgei* growth in the study area, by showing significantly positive effects on tree growth at three out of four sites and high correlation coefficients in RFA for PC#1, which supported that early winter temperature was one of the dominant climate variables at the upper timberlines (Körner, 1998). Warmer winter temperature may protect the needles from frost damage (Hawkins, 1993; Fan *et al*., 2009). Although the temperature of November was not the coldest in the area (Fig. 2), but the temperature decreased sharply from October to November and the minimum temperature was cold enough to harm needles and cause defoliate, which may reduce tree's potential for future growth by causing low photosynthetic capture and nutrients accumulation, thus restrict tree radial growth during the following year (Lazarus *et al*., 2004; Misson *et al*., 2004; Neuner, 2007). The positive effect of previous November temperature on tree growth of fir at the timberlines was also reported from previous studies in the central Hengduan Mountains (Fan *et al*., 2009; Panthi *et al*., 2018), Western Carpathian Tatra Mountain, Eastern Europe (Büntgen *et al*., 2007), and North Cascade mountains in Canada (Pederson and Pederson, 1994).

July was another important factor that positively affected *A. georgei* growth in the central Hengduan Mountains. The higher temperature in current July could promote photosynthesis, thereby increasing the formation of carbohydrates (Salzer *et al*., 2009). Our results supported the traditional opinion that the summer temperature was the main factor influencing tree growth at the timberlines due to the cold environment. The positive effects of July temperature on tree growth was found by previous studies carried out in the Southern Tibetan Plateau (Liang *et al*., 2009; Lyu *et al*., 2017), Mount Norikura in central Japan (Takahashi *et al*., 2005), Mount Alps in Switzerland (Meyer and Braker, 2001), and Mount Rockies in Canada (Luckman *et al*., 2005).

The negative correlations between June precipitation and tree growth may reflect the indirect effects of temperature on radial growth. June was the transitional month for the abrupt precipitation fluctuations, although maritime monsoon from Indian ocean brought sufficient precipitation in this month, it also increased cloud cover and the frequency of foggy conditions combined with comparatively lower solar radiation and temperature, which may reduce photosynthetic activity (lacking the nutrients) and consequently negatively affected tree growth (Panthi *et al*., 2018), . The negative influence of June precipitation on *A. georgei* growth was also reported in previous studies in Shika and Baima Snow Mountain of the study area (Zhang *et al*., 2017; Panthi *et al*., 2018).

Although September was the late growth stage and cambial growth was slowly, climatic variations still had influences on tree growth. We speculated that excessive precipitation would cause the decrease of the oxygen content of the soil and the increase of carbon dioxide concentration, thus reduced the oxidation reduction potential in the soil and decreased the accumulation of nutrients by limiting the activity of the roots (Bazzoffi & Nieddu, 2011). Moreover, excessive moisture in soil might increase anaerobic respiration in the roots, which may decrease the net accumulation of nutrients, and thus inhibit the radial growth.

The RFA and RDA both indicated that previous November and current July temperature was the main factor affecting tree growth, which further proved that RDA could effectively quantify the relationship between tree-ring width index and climatic variables. But there was a difference, RDA also indicated that June and September precipitation also had influence on tree growth, which was not found in RFA for PC#1. The reason for this difference might be related to the statistical theory of the two methods. It was more comprehensively and accurately to reveal the key climatic factors affecting tree growth by using two methods together, which has been proved in previous studies (Fan *et al*., 2009; Zhang *et al*., 2017).

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The stability between tree growth and climate variables has been highly focused in tree-ring research (Jump *et al.*, 2007), which could provide an important reference for more accurately climate reconstruction. The promotion effects of previous November and July temperature on tree growth became more significant in recent 20 years because of the rapid increase in temperature since 1990s. In contrast, the negative effects of June and September precipitation on tree growth were not detected in recent 20 years, probably due to the decline trend in precipitation since 1990s. Stronger temperature and weaker precipitation influences on tree growth with the warming trend has also been reported in previous dendroclimatology study in the central Hengduan Mountains (Panthi *et al.*, 2018). Our study suggested that growth-climate relationship might vary even in a small time scale, therefore stability analyses of such relationships could help us better understand dynamics of climate conditions and promote climate reconstruction accuracy.

According to the regional climate model system (PRECIS), the seasonal (spring, summer, autumn, and winter) mean temperature in Southwestern China would increase 2.6 ℃, 3.1 ℃, 2.7 ℃, and 3.1 ℃, respectively, while the total precipitation would increase 8%, 7%, 6%, and 8%, respectively (Xu *et al.*,. 2006). Combined with the climate-growth relationships of *A. georgei*, the impact of future climate change on tree growth might be complex. If the increasing temperature could offset the negative effects of excessive precipitation, the radial growth of *A. georgei* would likely benefit from the future warming trend at the upper timberlines. Furthermore, indirect impacts of climate change on tree growth should be considered, such as the frequency and intensity of extreme climate events, e.g. fire, pest, drought, and wind disturbances. All these changes may lead to changes in tree growth rate and their relative abundances, and which in turn eventually affect the structure, diversity, and position of the fir forest in the central Hengduan Mountains.

5. Conclusions

Tree cores of *A. georgei* were taken from four typical sites near upper timberlines in the central Hengduan Mountains, both temperature (positive effects of previous November and current July) and precipitation (negative effects of current June and September) influenced its radial growth, but temperature seemed to be play a more important role. Combined with the pattern of growth-climate relationships and the prediction of future climate change, if the increasing temperature could offset the negative effects of excessive precipitation, the radial growth of *A. georgei* at the upper timberlines would likely benefit from the future warming.

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Table 1. Sampling sites information.

Site	Longitude	Latitude	Elevation (m)	No. (tree/radii)	Aspect	Slope (°)
SK	99.56	27.92	4074	35/70	W	10
PDC	100.01	27.79	3954	29/58	SW	15
HB	100.10	27.35	4105	38/76	W	16
YL	100.21	27.10	4014	27/54	NW	13

SK: Shika Snow Mountain, PDC: Potatso National Park, HB: Haba Snow Mountain, YL: Yulong Snow Mountain. The same below.

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Table 2. Statistics of tree-ring width residual chronologies.

Chronology	SK	PDC	HB	YL
Trees/Cores	35/68	27/52	37/73	26/51
Time span	1707~2016	1761~2016	1733~2016	1750~2017
AGR	1.087	0.819	0.995	0.906
MS	0.14	0.16	0.11	0.22
EPS>0.85 since	1768	1807	1796	1913
Common interval analysis (1961~2010)				
Trees/cores	31/62	24/48	30/59	16/32
PC1	31.35	34.28	39.60	34.42
SNR	25.29	22.63	35.73	14.88
EPS	0.96	0.96	0.97	0.94

AGR, average annual growth rate (mm); MS, mean sensitivity; SNR, signal to noise ratio; EPS, expressed population signal; PC1, variance in first eigenvector.

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Table 3. Eigenvalues of principal component analysis of the four residual chronologies for the common period 1955~2015.

Component	Eigenvalue	Variance	Cumulative variance (%)
1	2.501	62.529	62.529
2	0.799	19.966	82.495
3	0.413	10.329	92.824
4	0.287	7.176	100

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Table 4. Person correlation coefficients between tree ring width residual chronologies of four sites for the common period 1955~2015.

	SK	PDC	HB
PDC	0.637**	-	-
HB	0.704**	0.586**	-
YL	0.331**	0.265*	0.387**

Significance level: *$p<0.05$, **$p<0.01$.

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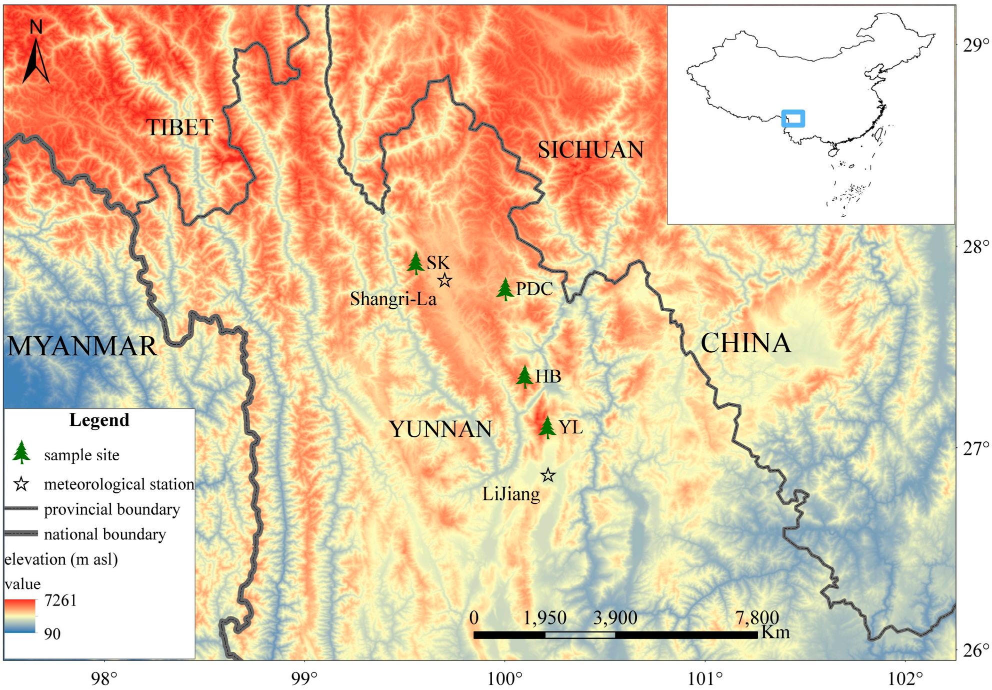

Fig. 1 The location of sampling sites and meteorological stations.

SK: Shika Snow Mountain, PDC: Potatso National Park, HB: Haba Snow Mountain, YL: Yulong Snow Mountain, the same below.

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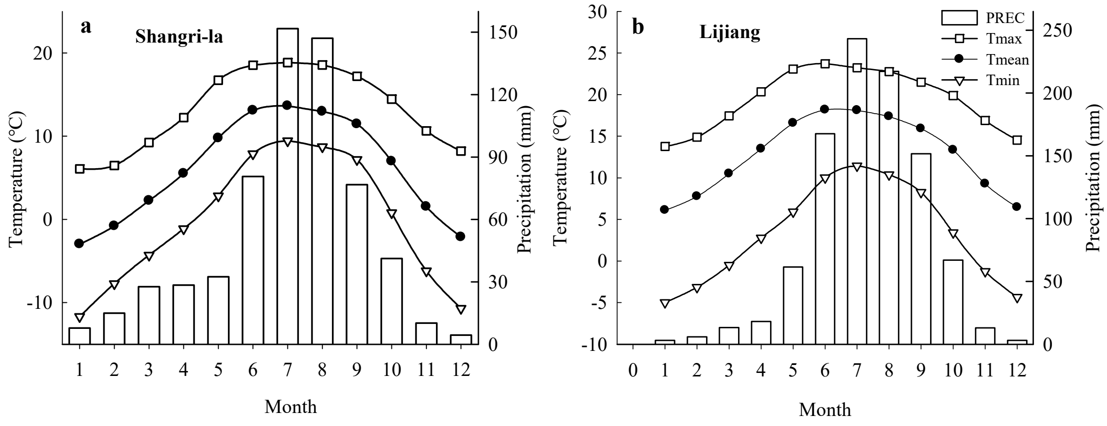
471 

472 Fig. 2 Climate diagrams for the Shangri-La (1960~2011) and Lijiang (1951~2010) meteorological stations.

473 PREC, monthly total precipitation; Tmin, monthly mean minimum temperature; Tmean, monthly mean
474 temperature; Tmax, monthly mean maximum temperature.

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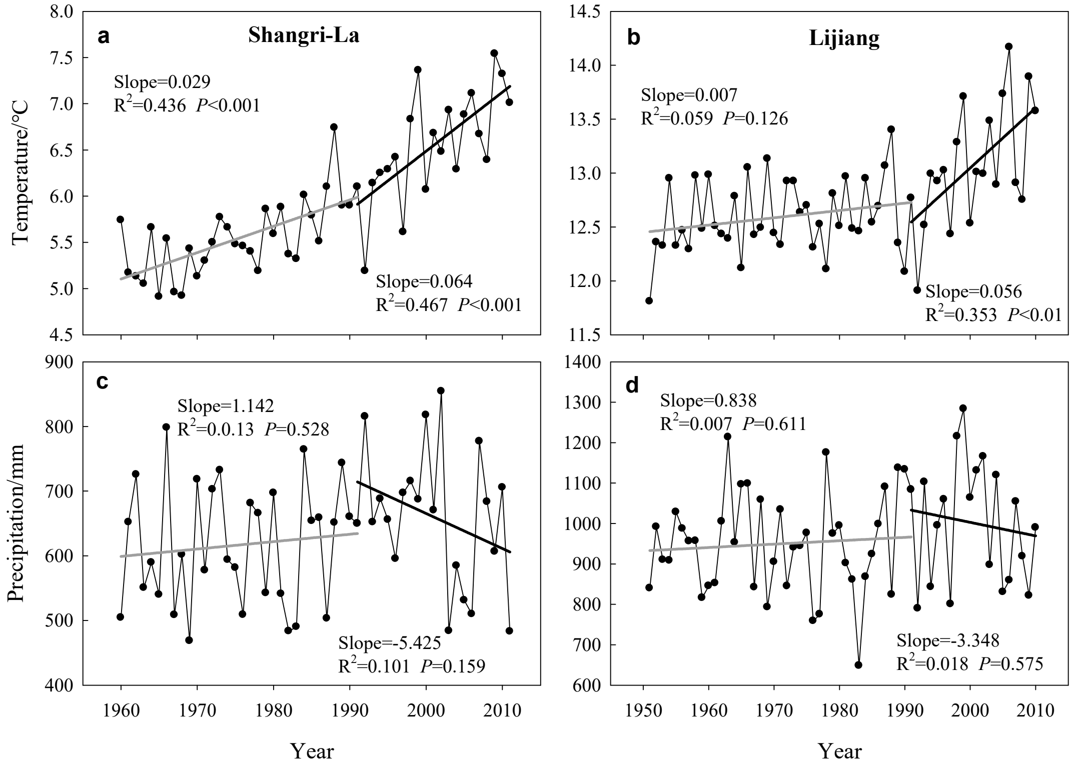

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476 Fig. 3 Annually climate trends in Shangri-La (1960~2011) and Lijiang (1951~2010).

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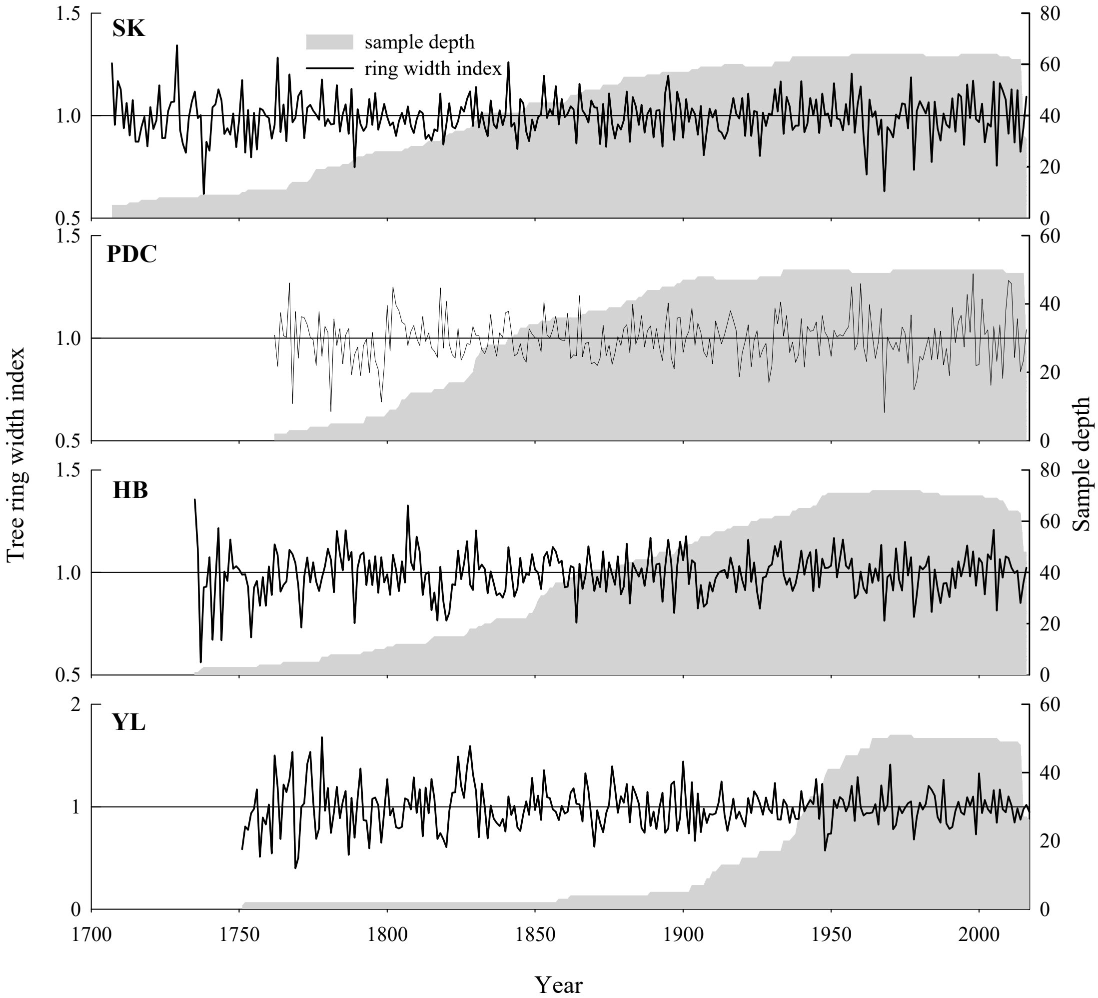

477

478 Fig.4 Residual tree ring width chronologies of *Abies georgei* at four sites with annual variation in ring
479 width index (black line), and sample depth (gray shading).

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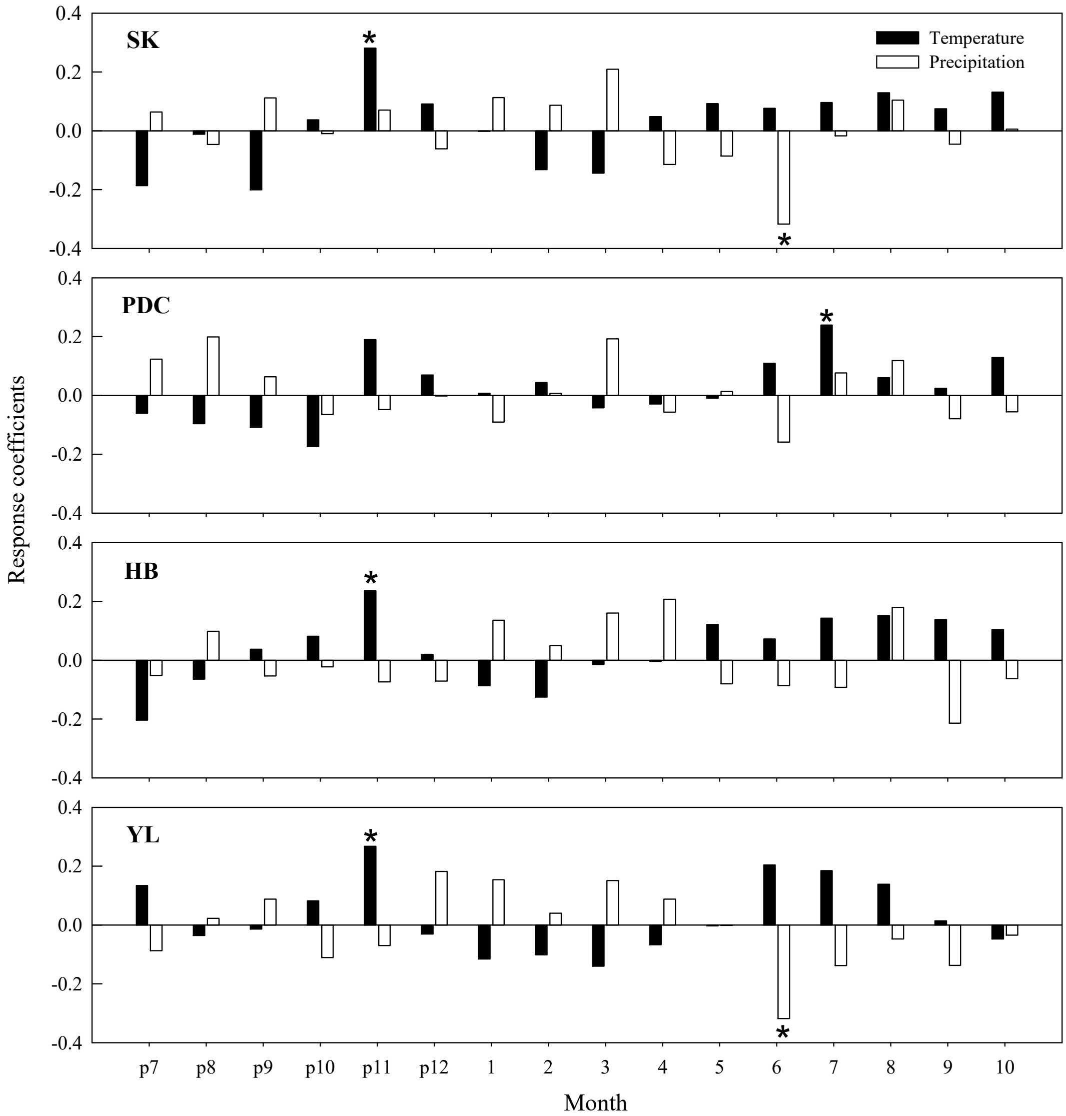

480

481 Fig. 5 Correlation coefficients from response function analysis between the residual chronologies and
482 the monthly climate variables at four sites over the period 1961-2010. *indicates the 95% confidence level.
483 p, previous year, the same below.

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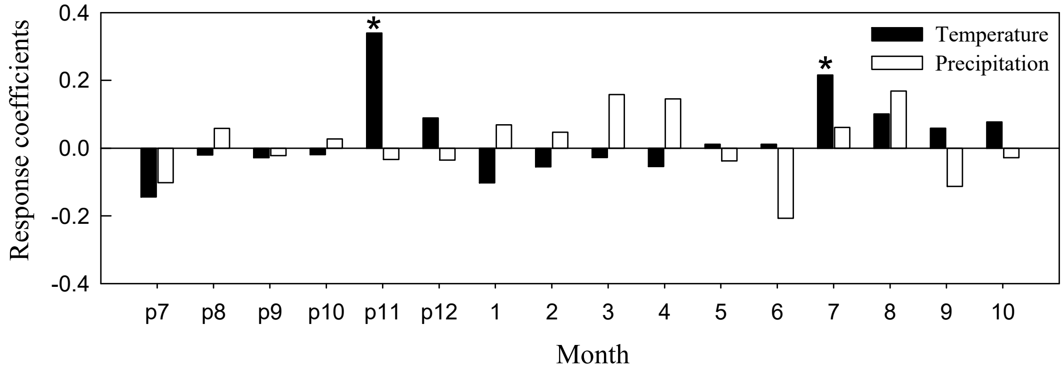

Fig. 6 Response function analysis between the PC#1 of four chronologies and climate variables for the common period 1961-2010.

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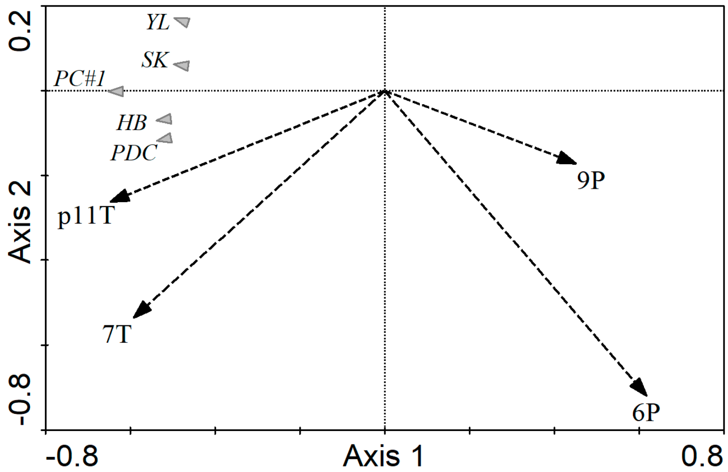

Fig. 7 The redundancy analysis between five chronologies and the climate variables for the common period (1961~2010).

Only significant (*P*<0.05) climate variables were presented. The longer vector of the climate factor (dotted line) indicated the greater contribution. The shorter perpendicular line between the chronology (triangle) and the climate vector (itself, or the extension line) indicated a higher correlation between them. Chronology (gray triangle) and climate vectors pointing the same direction represented a positive correlation, and in opposite directions indicated a negative correlation. PC#1, the first component of four residual chronologies. p11t, November temperature of previous year, 7t,July temperature in current year, 6P, June precipitation, 9P, September precipitation. The same below.

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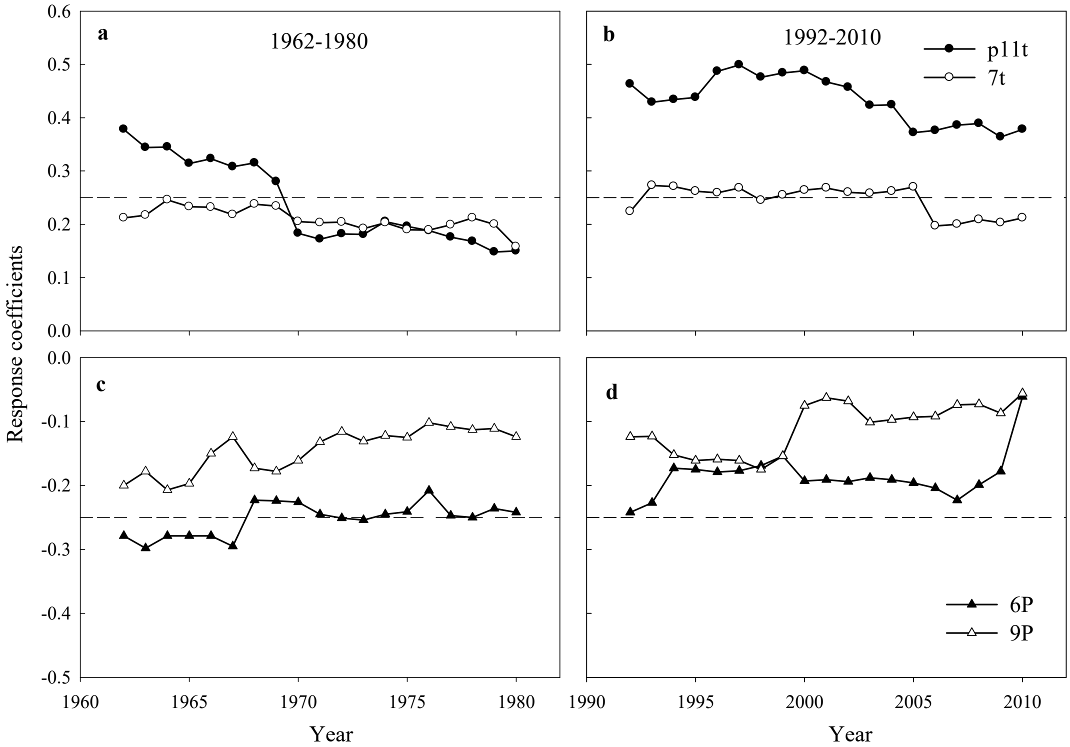

Fig. 8 Moving interval analysis between PC#1 of four chronologies and climate variables, A window with 32-year backward (1962-1980) and forward (1992-2010) evolutionary intervals. Dashed line indicates the 95% confidence level. A significantly positive relationship happened when dotted lines were above significant level, while dotted lines below the significant level indicated a significantly negative relationship.