Article

Variations of Climate-Growth Response of Major Conifers at Upper Distributional Limits in Shika Snow Mountain, Northwestern Yunnan Plateau, China

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Abstract: Improved understanding of climate-growth relationships of multi-species is fundamental to understand and predict response of forest growth to future climate change. Forests are mainly composed of conifers in Northwestern Yunnan Plateau, but variations of growth response to climates among the species are not well understood. To detect growth response of multiple species to climate change, we developed residual chronologies of four major conifers, i.e. Abies georgei, Picea likiangensis, Pinus densata and Larix potaninii at upper distributional limits in Shika Snow Mountain. By using dendroclimatology method, we analyzed correlations between the residual chronologies and climate variables. The results showed that conifer radial growth was influenced by both temperature and precipitation in Shika Snow Mountain. Previous November temperature, previous July mean maximum temperature (T_{max}) and current June precipitation were the common climatic factors, which had consistent influences on radial growth of four species. Temperature in previous post growing season (September-October) and current growing season (June-August), and precipitation in previous August were the common climatic factors, which had divergent impacts on four species radial growth. Current May $T_{\rm max}$ and early growing season (April-May) precipitation showed positive and negative influences on growth of P. likiangensis, respectively. Temperature in current post growing season positively affected growth of A. georgei. According to the prediction of climate models and our understanding in growth response of four species to climate variables, we may understand growth response to climate change at species level. It is difficult to predict future forest growth in the study area, since future climate change might cause both increases or decreases for four species and indirect effects of climate change on forest should be considered.

Keywords: Hengduan Mountains; dendrochronology; climatic response; redundancy analysis

1. Introduction

Effects of global change on human living environment and earth ecosystems have caused concern. Climate change, as an important component of global change, has a great influence on the structure and function of terrestrial ecosystems, particularly for forest ecosystems [1, 2]. How forest growth will respond to climate change has become an important scientific issue [3]. Dendrocclimaology, as a traditional method of analyzing historical climatic condition, plays an important role in studying the response of tree growth to climate change [4]. Analyzing the relationship between radial growth of the main tree species and climatic variables can help to reveal key climatic factors influencing tree growth and forest growth [5-7].

The response of forest growth to future climate change can only be evaluated if species-specific responses are well understood, since forests are composed of different species and these species would show variations in response to climate due to their different physiological adaptations and growth strategies [8, 9]. Additionally, species differences in mountainous areas were suggested to be more important in adaptation to change than site differences [10-12]. The results of published studies revealed the complexity of species dependent growth response to climates and suggested that precise prediction in effects of climate change on mountainous forests

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needs a more specific understanding in relationships between climate factors and multiple species growth [7, 10].

Trees growing in the elevational limits are more sensitive to climate change, since they are under physiological stress [13-16]. Radial growth of trees at their upper distributional limits generally reflects temperature variations. Low temperature was suggested to be the limiting factor controlling tree growth [17]. However, because of the complexity of plant physiological reactions and processes, this rule is not applicable for every tree species. The response of radial growth of multiple tree species to climate change can be different in subalpine forests [18-20].

Northwestern (NW) Yunnan Plateau, located in the southeastern edge of Tibet Plateau, belongs to a sensitive region to global climate change [21]. Several tree species form the upper treeline on different snow mountains in the region, and this makes the mountains perfect sites for dendrochronological study. At present, there are several studies from this region that used tree-ring to reconstruct climate [22-27]. Additionally, tree growth response to climate change has been studied in two typical nearby sites i.e. Yulong Snow Mountain and Potatso National Park, the results showed that tree growth was affected by both temperature and precipitation [28, 29]. Previous studies have shown tree growth to be sensitive to climate variability, but sampled species were mainly limited to fir and spruce [22-24, 26] and sampled sites were concentrated on Yulong and Baima Snow Mountains [22, 26]. Shika Snow Mountain is another typical subalpine mountain in NW Yunnan Plateau, but few dendroclimatological studies have been carried out there. The increase of sampling sites and the expansion of tree species can improve the dendro dendroclimatological knowledge in the region.

The aim of this study was to elucidate the main climatic factors influencing tree growth in NW Yunnan Plateau by studying growth response of *Picea likiangensis*, *Abies georgei*, *Larix potaninii* and *Pinus densata* to climates at their upper distributional limits in Shika Snow Mountain. The selected four species were major conifers in NW Yunnan Plateau and typically formed pure forest, respectively. Based on our results and predicted climate change, we further discuss tree growth under the future climate. We hypothesized that temperature would be a limiting factor affecting the radial growth of four species due to low temperatures at the upper distributional limits, and that variation of growth response to climates depended on the respective biological characteristics of the tree species. More specifically, we studied (1) relationships between the residual chronologies of four species and climatic factors by using response function (RFA) and redundancy analysis (RDA), and (2) compared variations of growth response to climates among four species.

2. Materials and Methods

2.1 Study area

Conifer forests with different dominant canopy species are major forest types in NW Yunnan Plateau, each forest type possesses a unique assemblage of sub-canopy trees and shrubs, and vertical structure is relatively simple. Fir forests are limited to 3200-4100 m a.s.l. with *Rhododendron* species as major subcanopy trees. Spruce forests distributed from 3100 to 3800 m a.s.l. with *Quercus* species as major subcanopy trees and *Lonicera* species as major shrubs. Pine forests ranges from 2700 to 3700 m a.s.l. with *Rhododendron* species as major shrubs. Larch forests are located between 3100 and 4000 m a.s.l. with fir as subcanopy trees.

Shika Snow Mountain, which has rich species diversity, is located in the center of Hengduan Mountains, NW Yunnan Plateau, China (Figure 1). It is characterized by a vertical zonation of forest ecosystems with little disturbance (mainly fire with low frequency and intensity). *P. likiangensis*, *P. densata*, *A. georgei* and *L. potaninii* are the main tree species in the area. *A. georgei* is a shade-tolerant and shallow-rooted species, which can adapt to cool and cold climate, distributed from 3200 m a.s.l. to 4100 m a.s.l.. *P. likiangensis* is a shade-tolerant and shallow-rooted species, distributed from 3100 m a.s.l. to 3810 m a.s.l.. *P. densata* is a *a deep rooted*, shade-intolerant species, tolerant of dry and poor soil and is distributed from 2700 m a.s.l. to 3700 m a.s.l.. *L. potaninii* is a shade-intolerant species and is tolerant to poor soil, with underdeveloped main root, distributed from 2700 m a.s.l. to 3900 m a.s.l..

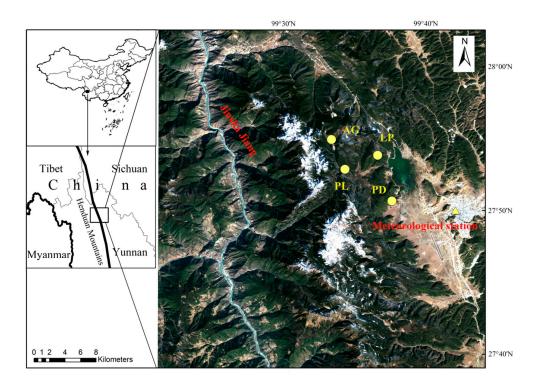


Figure 1. Location of the sampling sites and the meteorological stations nearby.

AG: Abies georgei site, LP: Larix potaninii site, PL: Picea likiangensis site, PD: Pinus densata site.

The climate in this area is strongly influenced by south Asian summer monsoon and is characterized by maximum rainfall during the summer months (June–September), whereas winter is generally dry. Shangri-La meteorological station (3276.7 m) is the station closest to the sampling sites with climate observations from 1960. According to the climatic record from Shangri-La meteorological station for the period 1960-2011, mean annual temperature is 5.9 °C, July is the hottest with average temperature of 13.6 °C and January is the coldest with average temperature of -3.0 °C. The mean annual precipitation is 634 mm. The precipitation in the summer season accounts for 73% of the annual total precipitation (Figure 2a). Temperature showed a significant increase trend (Figure 2b) while precipitation increased slightly (Figure 2c).

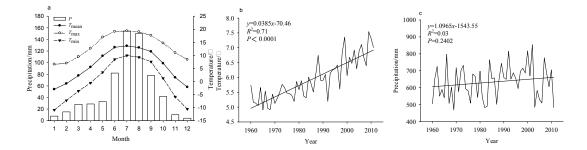


Figure 2. Climate data from the Shangri-La meteorological station (1960-2011)

 T_{max} : Monthly mean maximum temperature; T_{mean} : Monthly mean temperature; T_{min} : Monthly mean minimum temperature; P: Monthly total precipitation

2.2 Sampling and chronology development

We sampled tree ring materials from four stands at the upper distributional limits of four species at Shika Snow Mountain. In total, 162 increment cores from 83 trees were sampled at four sites, for more stand information please see Table 1. At each site, we sampled dominant trees without insect damage and fire scar at breast height (approximately 1.3 m) with an increment borer. Two (or one) cores were taken per tree from the opposite directions, which was parallel to the contour line. In order to ensure the consistency of the microclimate, the elevation variation was controlled within 10 m at each site.

 Table 1. Descriptions of the sampling sites

Tree species	Latitude	Longitude	Number of trees/cores	Elevation	Slope aspect	Slope (°)	Soil type
Picea likiangensis	27°52′52.20″N	99°34′18.48″E	14/26	3618 m	E	15	Clay
Pinus densata	27°50′39.84″N	99°37′34.72″E	34/68	3625 m	W	13	Sand
Abies georgei	27°54′56.70″N	99°33′22.32″E	19/36	4074 m	E	10	Clay
Larix potaninii	27°53′50.68″N	99°36′35.24″E	16/32	3819 m	W	15	Sand

The samples were pretreated according to the method described by Stokes and Smiley [30] after being brought back to the laboratory. The surface of a core was burnished with sandpaper until the surface was smooth enough to recognize the tree ring. The cores were placed under the microscope for dating work, and dated cores were scanned by using an EPSON scanner (Expression 11000XL) with parameter setting to image type 24- full color and resolution of 3200 dpi. The ring widths were measured on scanned images in software of CDendro and CooRecorder ver. 7.3 [31] with a resolution of 0.001 mm, and statistical tests was applied by using the software package COFECHA [32] to validate data quality. The cores with low correlation between the tree ring sequences and the main sequences were excluded, and finally 145 cores (80 trees) were kept into the main sequence (Table 2). Each series was standardized to remove the biological growth trend (age-size) as well as other low-frequency variations due to stand dynamics [33], by using a cubic smoothing spline with 67% of the

series length, linear function and exponential power function. We also used autoregressive (AR) modeling on each standardized series to remove temporal autocorrelation and enhance the common signal. The residual tree-ring series were averaged using residuals from AR modeling of the standardized measurement series, and the residual chronologies of four species (RES, Figure 3) were used to analyze the climate-growth relationships. All procedures were conducted using the program ARSTAN [34].

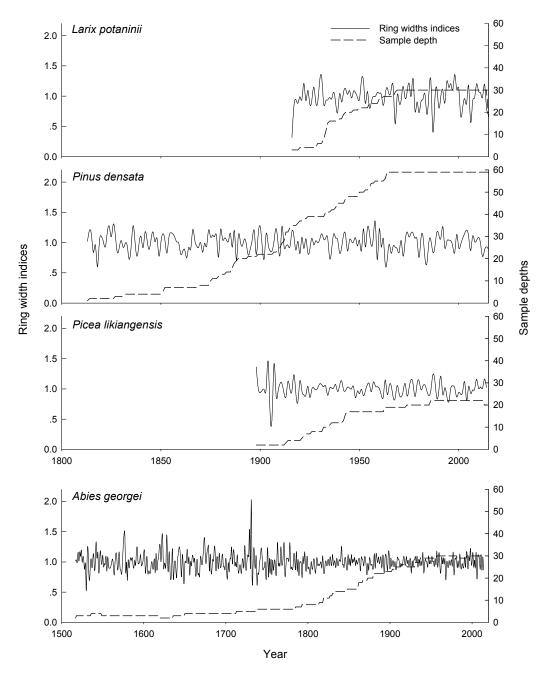


Figure 3. Residual tree-ring chronology (solid line) and sample size (dotted line)

Table 2. Statistics of residual chronologies and common interval analysis. EPS, Expressed population signal.

Chronology	P. likiangensis	A. georgei	P .densata	L. potaninii	
Chronology length	1898-2014	1517-2014	1813-2015	1916-2015	
Mean ring width (mm)	1.95	0.95	0.95	1.73	
Mean sensitivity	0.13	0.15	0.16	0.22	
1st order autocorrelation	-0.15	0.01	-0.01	0.19	
Common interval analysis (1960-2011)					
Number of trees/cores	12/22	19/34	33/59	16/30	
Variance in PC1 (%)	38.76	40.58	42.94	47.31	
Expressed population signal	0.90	0.95	0.97	0.95	
Correlation among the trees	0.33	0.37	0.41	0.43	

2.3 Climate data

We used climate data for the period 1960-2011 (common interval of four species) from Shangri-La meteorological station. For climate analyses, monthly mean temperature ($T_{\rm mean}$) and monthly total precipitation from July of previous year to October of current year, and the $T_{\rm mean}$ and total precipitation of post growing season (September–October) of previous year, early growing season (April-May), growing season (June-August) and post growing season of current year were selected. There is no heterogeneity in the climate data when tested by the Mann-Kendall method [35]. Therefore, we assume that the observed record of Shangri-La meteorological station reflects the natural climate change of the study area, and we use the meteorological data for the climate-growth relationship analysis.

2.4 Statistic analyses

We used RFA to analyze relationships between the residual chronologies of four species and climatic factors, by using software DendroClim2002 [36]. The response function is a linear multiple regression technique that uses the principal components of monthly climatic variables to estimate tree-ring growth and is usually applied in climate-growth analyses [37]. We also used a 32-year moving window with Forward evolutionary intervals to study the temporal stability of climate-growth relationships, carried out with the Evolutionary and Moving Response and Correlation module in DendroClim2002. Redundancy analysis (RDA) is also useful to analyze and verify the relationship between radial growth and climatic factors. RDA is a multivariate "direct" gradient analysis and its ordination axes are constrained to represent linear combinations of supplied environmental variables [38], and is appropriate when short environmental gradients are covered [39]. In the correlation matrix of RDA, the four residual chronologies were considered as response variables, the years were considered as samples, and climate variables were considered as explanatory variables and were transformed into ordination axes. Significant climatic variables (p<0.05) were selected after a forward selection using a Monte Carlo permutation test based on 999 random permutations. RDA was conducted by using the program CANOCO4.5 [40].

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3. Results

3.1 Characteristics of the tree-ring width chronologies

A. georgei had the longest chronology among the four species while L. potaninii chronology was the shortest, the length of chronologies of P. likiangensis and P. densata was 116 and 202 years, respectively. Two shade-intolerant species (L. potaninii and P. densata) generally had higher values in statistic indices, such as mean sensitivity (MS), the first principal component (PC1), the expressed population signal (EPS), and correlation among the trees, suggesting that these two species had higher quality in chronologies as compared to two shade-tolerant species [4, 39, 40]. EPS values of all four species were above 0.85, indicating a strong common signal among the species and suitability of constructed chronologies for dendrochronological study [41].

3.2 Climate-growth relationships

RFA indicated that the radial growth was mainly influenced by temperature conditions and precipitation played a minor role on the radial growth in the area (Figure 4), but the four species responded differently to climatic factors. The radial growth of P. likiangensis showed a significant and positive correlation with T_{mean} of current July. Precipitation inhibited P. likiangensis growth, by showing a negative correlation with precipitation of previous August and current early growing season (April-May) (Figure 4a). The radial growth of A. georgei was significantly and positively correlated with T_{mean} of the previous November and T_{mean} of current growing season (June-August), T_{mean} of the previous September negatively influenced its growth (Figure 4b). For P. densata, warm temperature in previous post growing season and November as well as current early growing season had a positive impact on the radial growth, hot July inhibited its growth (Figure 4c). With respect to L. potaninii, previous August precipitation was the only factor found to positively affect its radial growth (Figure 4d).

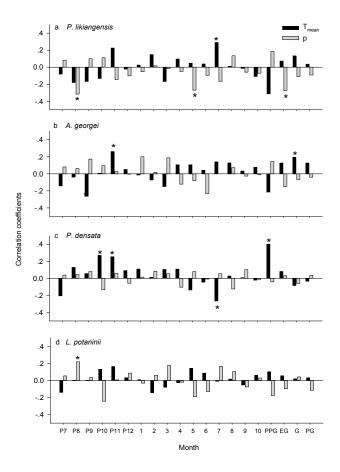


Figure 4. Correlation analyses of response function between the residual chronologies and the monthly climatic factors. *Significant at P < 0.05. PPG stands for previous post growing season, EG stands for early growing season, G stands for growing season, PG stands for post growing season.

The first two ordination axes in RDA explained 32.8% of the network's total variance (Figure 5). Axis I accounted for 21.7% and had negative loadings for all species, axis II accounted for 11.1%, which had positive loadings for residual chronologies of A. georgei and P. likiangensis, and negative loadings for residual chronologies of P. densata and L. potaninii. The previous July temperature was positively associated with the first axis, whereas T_{mean} of the previous November and precipitation of the previous August showed a negative association. The second axis was positively associated with T_{mean} of the current July and negatively with T_{mean} of the previous post growing season (September-October). The current May precipitation was associated with both axes: positive with axe I and negative with II.

RDA showed similar results as compared to RAF, presenting effects of July temperature positively affected growth of *P. likiangensis* and had negative effects on *P. densata*, of previous post growing season temperature on *P. densata* (positive) and *P. likiangensis* (negative), of previous November temperature on four species (positive), of previous August precipitation on *L. potaninii* (positive) and *P. likiangensis* (negative), of current May precipitation on *P. likiangensis* (negative). RDA also showed significant correlations between tree growth and climatic factors that response function hasn't detected. For instance, current May precipitation and

current July T_{mean} had negative and positive impacts on growth of A. georgei, respectively. Previous July temperature negatively affected radial growth of four species (Figure 5).

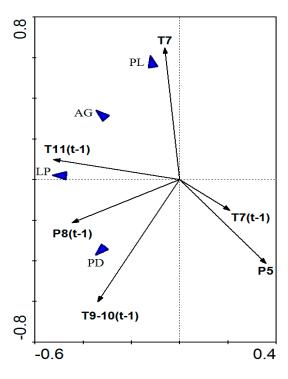


Figure 5. The redundancy analysis between two residual chronologies and the climatic factors. Only significant climate factors (P<0.05) are presented. The longer the vector of climate factor the greater the contribution. The shorter perpendicular line between chronology point and climatic vector (itself or extension line) indicates a higher correlation between them. Chronology and vectors pointing to the same direction means a positive correlation, and vice versa. P represents precipitation, T represents mean temperature, t-1 represents the previous year, the number indicates month. PL indicates residual chronology of *P. likiangensis*, AG indicates residual chronology of *A. georgei*, PD indicates residual chronology of *P. densata*, LP indicates residual chronology of *L. potaninii*.

3.3 Dynamic relationship between radial growth and climatic factors

The stability between the radial growth of P. likiangensis and climatic factors was high, by showing a significant correlation in all tested years. Radial growth of A. georgei presented a stable correlation with T_{mean} of the previous November and a partly significant correlation in tested years with T_{mean} of the previous September. The stability between the radial growth of P. densata and climatic factors was high, by showing a significant correlation in all tested years (except for T_{mean} of the previous November). More than half of tested years in current August precipitation were significantly correlated with L. potaninii growth (Table 3).

Table 3. Correlation analysis with moving intervals between the residual chronologies and the monthly climatic factors. A 32-year moving window was applied.

Tree species	Climatic factors	Significant year
P. likiangensis	$T_{\rm mean}$ of the current July	1992-2011(+)
	precipitation of the previous August	1992-2011(-)
	precipitation of the current May	1992-2011(-)
A. georgei	$T_{\rm mean}$ of the previous September	2006-2011(-)
	$T_{\rm mean}$ of the previous November	1992-2011(+)
P. densata	$T_{\rm mean}$ of the previous October	1992-2011(+)
	T _{mean} of the previous November	2011(+)
	T _{mean} of the current July	1992-2011(-)
		4007/ \ 4000 2007/ \ 2010 201/ \
L. potaninii	precipitation of the current August	1995(+), 1999-2005(+), 2010-2011(+)

⁽⁻⁾ indicates the negative correlation; (+) indicates the positive correlation.

4 Discussion

Our study found out that both temperature and precipitation affected conifer growth in Shika Snow Mountain which rejected the first hypothesis that low temperature would be the only key factor influencing radial growth, suggesting the complexity of tree growth response to climate change in the area. Species presented common response (but with consistency or inverse effects) and species-specific response to climate change which supported the second hypothesis that growth sensitivity to climates was variable among species, indicating the importance of understanding species-dependant response to climates for evaluating impacts of climate change on forest growth. Although the analyzed climate period was short, the relationship between climate variables and radial growth was stable, pointing out the reliability of our results. The study also proved that RFA and RDA were complemented for each other to analyze relationships between climate change and tree radial growth.

4.1 Consistent effects of common climatic factors among species

Both response RFA and RDA results showed that previous November temperature positively affected four species growth, suggesting its dominant role in controlling tree radial growth in Shika Snow Mountain. Severe cold combined with dry condition in November may lead to deep soil frost which can damage roots [43, 44], particularly for *A. georgei*, *L. potaninii* and *P. likiangensis* which are shallow-roots species, and consequently resulting in low assimilation of nutrient in the following year. On the other hand, a warm temperature in previous November may allow optimal growth condition of below ground to stimulate radial growth of the next year. Positive influences of previous November temperatures on radial growth of different conifers have also been found at nearby sites (Baima Snow Mountain and Bitahai Nature Reserve) and subalpine mountain in North America for *Picea brachytyla*, *Abies lasiocarpa*, *Picea engelmannii* and *Larix lyallii* [22, 45].

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Current May precipitation was found to negatively affect radial growth of *A. georgei* and *P. likiangensis*. Raining is typically accompanied with low temperature and cloudy condition, which can reduce photosynthesis rate and photosynthetic capture, and slow soil thawing which can weaken root activity and may trigger onset of photosynthesis [46, 47]. In addition, more precipitation during early growing season can create water logged conditions associated with a decrease in soil oxygen content and an increase in carbon dioxide concentration, resulting in anaerobic respiration of the root, excessive consumption of photosynthates, and consequently inhibiting tree radial growth [48]. Negative influences of current early growing season precipitation on radial growth have also been found for *Picea brachytyla* in Potatso National Park (20 km away from our site) [29].

In addition, previous July temperature had negative impacts on growth of all four species. It is likely that previous hot summer could enhance stand evapotranspiration and thereby cause water deficits [49]. This water-stress effect was also indicated by a positive effect of previous August precipitation on radial growth of *A. georgei*, *L. potaninii* and *P. densata*. Previous summer moisture condition could affect the size of buds within leaf area for photosynthetic efficiency of the current year, and thereby suitable previous summer condition allowed optional growth of the following year [50]. Previous summer water-stress effect on tree radial growth was also reported for *P. likiangensis* in Small Zhongdian (100 km away from our site) [51] and other subalpine conifers [22, 24].

4.2 Divergent effects of common climatic factors among species

Temperatures of previous post growing season (September–October) was found to be a critical climatic factor influencing tree growth in the area, showing positive effects on *P. densata* and negative effects on *P. likiangensis*, respectively. This may reflect differences of physiology responses at daytime and nighttime to between two species. High daily temperature can raise photosynthesis rate and therefore produce more carbohydrates for radial growth [50], but increases in nighttime temperature could enhance tree respiration, thus leading to the consumption of the carbohydrates that were reserved for the following year's growth [49].

Our results also revealed that current summer moisture condition was important for tree growth in the area. Temperature of current growing season (June-August), especially for July temperature, showed positive effects on growth of *A. georgei* and *P. likiangensis* and negative effects on *P. densata*. This moisture stress effect was also confirmed by positive influences of current August precipitation on radial growth of *A. georgei* and *P. likiangensis*. The inverse growth response was mainly due to the habitat difference. High temperature during the growing season can improve the photosynthesis rate and increase the pool of stored carbohydrates for tree growth [53], however, higher temperature could cause higher stand respiration and evaporation, consequently resulting in water deficits which may inhibit radial growth [54]. *P. likiangensis* and *A. georgei* are the shade-tolerant species, growing in the shaded and half shaded slopes with less radiation and evaporation, and therefore higher amounts of moisture are available for tree growth. The positive influence of current July temperature on radial growth of *P. likiangensis* and *A. georgei* was also reported in Southeastern Tibetan Plateau (the same region of our study area) [33, 55]. In contrast, *P. densata* is a shade-intolerant species, typically distributed in sunny and half sunny slopes with strong solar radiation and high evaporation, thus high summer temperature could cause soil moisture stress and growth was limited.

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4.3 Prediction of future climate change on tree radial growth

Global warming has become an indisputable fact since the 20th century. The global mean temperature rose 0.72 [0.49 to 0.89] °C from 1901 to 2012, and the warming of the second half of the 20th century is more obvious with the increase of 0.12 [0.08 to 0.14] °C per decade from 1951 to 2012 [57]. Relative to temperature, the precipitation since 1901 is only slightly increased [58]. In Southwest China, compared with the data in 1961-1990, the mean temperature in spring, summer, autumn and winter will relatively increase 2.6 °C, 3.1 °C, 2.7 °C and 3.1 °C in 2071-2100, and precipitation in spring, summer, autumn and winter will relatively increase 8%, 7%, 6% and 8% (under Special Report on Emissions Scenarios (SRES) B2 scenario) [59].

Based on understanding of growth response of four species to climates (see above) and the prediction of future temperature and precipitation, our study may allow us to assess potential changes in tree and forest growth in this area. We focus more on temperature influences on tree growth than precipitation since predictions of temperature from different models might be very similar while precipitation would be different. In general, November temperature, summer moisture condition, autumn temperature and June precipitation mainly influenced the radial growth of four species. All four species might benefit from warming in November to enhance their radial growth. The effects of summer moisture condition on tree growth were difficult to predict, since both temperature and precipitation were forecasted to increase. Nevertheless, the increase in summer temperature may put more evaporative stress on two shade-intolerant species due to their higher stand evaporation rate and requirement for water in physiology. If water compensation is insufficient, warming summer in coming decades may limit radial growth of four species, particularly for P. densata and L. potaninii. Warming autumn will probably promote growth of two shade-intolerant conifers and inhibit growth of two shade-tolerant conifers. Radial growth of four species might be decreasing due to increases in future June precipitation. In accordance with above description, we may predict how species respond in the context of future climate change, but it is difficult to predict the pattern of forest growth since future climate change might cause both increases or decreases for those species (the main component of forest). In addition, the future forest growth would be strongly modified by indirect influences of climate change such as extreme climate events, fire and wind disturbances, and insects outbreak. Therefore, prediction in forest growth is complex and needs comprehensive consideration.

5 Conclusions

In this paper, we compared the growth response of four species to temperatures and precipitation at upper distributional limits in Shika Snow Mountain. We found that temperature from September to November in the previous year, current summer moisture condition, and current May precipitation were important factors affecting the radial growth of dominant conifers in the study area. The growth sensitivity to climates was variable among species, this was mainly due to their different physiological adaptations, growth strategies, and site conditions.

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References

- 1. Boisvenue, C.; Running, S.W. Impacts of climate change on natural forest productivity: Evidence since the middle of the 20th century. *Global Change Biology* **2006**, *12*, 862-882.
- Van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C.; Daniels, L.D.; Franklin, J.F.; Fulé, P.Z.; Harmon, M.K.; Larson, A.J.; Smith, J.M.; Taylor, A.H.; Veblen, T.T. Widespread increase of tree mortality rates in the western United States. *Science* 2009, 323, 521-524.
- 3. Tao, J.; Chen, Y.F., He, D.K., Ding, C.Z. Relationships between Climate and growth of *Gymnocypris selincuoensis* in the Tibetan Plateau. *Ecology and Evolution* **2015**, *5*, 1693-1701.
- 4. Fritts, H.C. Tree Rings and Climate; Academic Press: New York, 1976.
- 5. Zhang, Q.B.; Cheng, G.D.; Yao, T.D.; Kang, X.C.; Huang, J.G. A 2,326-year tree-ring record of climate variability on the northeastern Qinghai-Tibetan Plateau. *Geophysical Research Letters* **2003**, *30*, HLS 2-1.
- 6. Shao, X.; Xu, Y.; Yin, Z.Y.; Liang, E.; Zhu, H.; Wang, S. Climatic implications of a 3585-year tree-ring width chronology from the northeastern Qinghai-Tibetan Plateau. *Quaternary Science Reviews* **2010**, *29*, 2111-2122.
- 7. Liang, E.Y.; Shao, X.M.; Eckstein, D.; Huang, L.; Liu, X.H. Topography- and Species- dependent growth responses of *Sabina przewalskii* and *Picea crassifolia* to climate on the northeast Tibetan Plateau. *Forest Ecology and Management* **2006**, *236*, 268-277.
- 8. Cook, E.R.; Glitzenstein, J.S.; Krusic, P.J.; Harcombe, P.A. Identifying functional groups of trees in west Gulf Coast forests (USA): a tree-ring approach. *Ecological Applications* **2001**, *11*, 883-903.
- Friedrichs, D.A.; Trouet, V.; Büntgen, U.; Frank, D.C.; Esper, J.; Neuwirth, B.; Löffler, J. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees* 2009, 23, 729-739.
- Yu, D.P.; Wang, Q.W.; Wang, Y.; Zhou, W.M.; Ding, H.; Fang, X.M.; Jiang, S.W.; Dai, L.M. Climatic effects on radial growth of major tree species on Changbai Mountain. *Annals of Forest Science* 2011, 68, 921-933.
- 11. Frits, H.C.; Smith D.G.; Cardis J.W.; Budelsky C.A. Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology* **1965**, *46*: 393-401.

- Takahashi, K.; Azuma, H.; Yasue, K. Effects of climate on the radial growth of tree species in the upper and lower distribution limits of an altitudinal ecotone on Mount Norikura, central Japan. *Ecological Research* 2003, 18: 549-558.
- Zhang, Y.; Bergeron, Y.; Gao, L.S.; Zhao, X.H.; Wang, X.M.; Drobyshev, I. Tree growth and regeneration dynamics at a mountain ecotone on Changbai Mountain, northeastern China: which factors control species distributions?. Écoscience 2014, 21, 387-404.
- 14. Zhang, Y.; Bergeron, Y.; Zhao, X.H.; Drobyshev, I. Stand history is more important than climate in controlling red maple (*Acer rubrum* L.) growth at its northern distribution limit in western Quebec, Canada. *Journal of Plant Ecology* **2015**, *8*, 368-379.
- 15. Smith, W.K.; Germino, M.J.; Johnson, D.M.; Reinhardt, K. The altitude of alpine treeline: A bellwether of climate change effects. *The botanical Review* **2009**, *75*, 163-190.
- Payette, S.; Delwalde, A.; Morneau, C.; Lavole, C. Patterns of tree stem decline along a snow-drift gradient at treeline: a case study using stem analysis. *Canadian Journal of Botany* 1996, 74, 1671-1683.
- 17. Zhang, W.T.; Jiang, Y.; Dong, M.Y.; Kang, M.Y.; Yang, H.C. Relationship between the radial growth of *picea meyeri* and climate along elevations of the Luyashan Mountain in North-Central China. *Forest Ecology and Management* **2012**, *265*, 142-149.
- 18. Leal, S.; Melvin, T.; Grabner, M.; Wimmer, R.; Briffa, K. Tree-ring growth variability in the Austrian Alps: The influence of site, altitude, tree species and climate. *Boreas* **2007**, *36*, 426-440.
- 19. Liang, E.; Wang, Y.; Xu, Y.; Liu, B.; Shao, X. Growth variation in *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. *Trees* **2010**, *24*, 363-373.
- 20. Shi, J.F.; Li, J.B.; Cook, E.R.; Zhang, X.Y.; Lu, H.Y. Growth response of *Pinus tabulaeformis* to climate along an elevation gradient in the eastern Qinling Mountains, central China. *Climate Research* **2012**, *53*, 157-167.
- 21. Liu, X.D.; Chen, B.D. Climatic warming in the Tibetan Plateau during recent decades. *International Journal of Climatology* **2000**, *20*, 1729-1742.
- Fan, Z.X.; Bräuning, A.; Cao, K.F. Annual temperature reconstruction in the central Hengduan Mountains, China, as deduced from tree rings. *Dendrochronologia* 2008, 26, 97-107.
- 23. Fan, Z.X.; Bräuning, A.; Cao, K.F. Tree-ring based drought reconstruction in the central Hengduan Mountains region (China) since A.D. 1655. *International Journal of Climatology* **2008**, 28, 1879-1887.

- 24. Fan, Z.X.; Bräuning, A.; Yang, B.; Cao, K.F. Tree ring density-based summer temperature reconstruction for the central Hengduan Mountains in southern China. *Global and Planetary Change* **2009**, *65*, 1-11.
- Bi, Y.F., Xu, J.C., Gebrekirstos, A.; Guo, L.; Zhao, M.X.; Liang, E.Y.; Yang, X.F. Assessing drought variability since 1650 AD from tree-rings on the Jade Dragon Snow Mountain, southwest China. *International Journal of Climatology* 2015, 35, 4057-4065.
- 26. Guo, G.A.; Li, Z.S.; Zhang, Q.B.; Ma, K.P.; Mu, C. L. Dendroclimatological studies of *Picea likiangensis* and *Tsuga dumosa* in Lijiang, China. *IAWA Journal* **2009**, *30*, 435-441.
- Li, Z.S.; Zhang, Q.B.; Ma, K.P. Tree-ring reconstruction of summer temperature for A.D. 1475-2003 in the central Hengduan Mountains, Northwestern Yunnan, China. *Climate Change* 2002, 110, 455-467.
- 28. Zhang, W.G.; Xiao, D.R.; Tian, K.; Chen, G.L.; He, R.H.; Zhang, Y. Response of radial growth of three conifer species to climate at their respective upper distributional limits on Yulong Snow Mountain. *Acta Ecologica Sinica* **2017**, *37*, 3796-3804. (In Chinese).
- 29. Yu, J.L.; Zhang, W.G.; Tian, K.; Song, W.H.; Li, Q.P.; Yang, R.; Zhang, Y. Response of radial growth of three conifer trees to climate change at their upper distribution limits in Potatso National Park, Shangri-La, southwestern China. *Journal of Beijing Forestry University* 2017, 39, 43-51. (In Chinese)
- 30. Stokes, M.A.; Smiley, T.L. *An Introduction to Tree-Ring Dating*; University of Chicago Press: Chicago, 1968.
- 31. Larsson, L. A. CDendro v. 7.3. Cybis Elektronik & Data AB; Sweden, Saltsjöbaden, 2010.
- 32. Holmes, R.L. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* **1983**, 43, 69-75.
- 33. Liang, E.Y.; Shao, X.M.; Xu, Y. Tree-ring evidence of recent abnormal warming on the southeast Tibetan Plateau. *Theoretical and Applied Climatology* **2009**, *98*, 9-18.
- 34. Cook, E.R.; Holmes, R.L. *Users Manual for Program ARSTAN*; Tucson: Laboratory of Tree-ring Research, University of Arizona, 1986.
- 35. Kendall, M.G.; Gibbons, J.D. *Rank Correlation Methods*; 5th ed. London, Edward Arnold, 1990.
- 36. Biondi, F.; Waikul, K. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences* **2004**, *30*, 303-311.
- 37. Fritts, H.C.; Blasing, T.J.; Hayden, B.P.; Kutzbach J.E. Multivariate techniques for specifying tree-growth and climate relationships ad for reconstructing anomalies in paleoclimate, *Journal of Applied Meteorology and Climatology* **1971**, *10*, 845-864.
- 38. Legendre, P., Legendre, L. Numerical Ecology. Elsevier Scientific; New York, 1998.

- ter Braak, C.J.F.; Smilauer, P. CANOCO reference manual and user's guide to Canoco for Windows-software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY, 1998.
- ter Braak, C.J.F.; Smilauer, P. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination. Version 4.5. Microcomputer Power, Ithaca, New York, 2002.
- 41. Wigley, T.M.L.; Briffa, K.R., Jones, P.D. On the average value of correlated time series with application in dendroclimatology and hydrometeorology. *Journal of Applied Meteorology and Climatology* **1984**, *23*, 201-213.
- 42. Briffa, K.R. Interpreting high-resolution proxy climate data—the example of dendroclimatology. In: von Storch, H., Navarra, A. (Eds.), Analysis of Climate Variability: Applications of Statistical Techniques. Springer, Berlin, pp. 1995, 77-94.
- 43. Vogt, K.A.; Edmonds, R.L.; Grier, C.C.; Piper, S.R. Seasonal changes in mycorrhizal and fibrous-textured root biomass in 23- and 180-year-old Pacific silver fir stands in western Washington. *Canadian Journal of Forest Research* **1980**, *10*, 523-529.
- 44. Neuner, G. Frost resistance at the upper timberline. In: Wieser, G.; Tausz, M. (Eds.), Trees at their upper limit—treelife limitation at the alpine timberline. Springer, Dordrecht, The Netherlands, pp **2007**, 171-180.
- 45. Peterson, D.W.; Peterson, D.L. Effects of climate on the radial growth of subalpine conifers in the North Cascade Mountains. *Canadian Journal of Forest Research* **1994**, *24*, 1921-1932.
- Fan, Z.X.; Bräuning, A.; Cao, K.F.; Zhu, S.D. Growth-climate responses of high-elevation conifers in the central Hengduan Mountains, southwestern China. Forest Ecology and Management 2009, 258, 306-313.
- 47. Goodine, G.K.; Lavigne, M.B.; Krasowski, M.J. Springtime resumption of photosynthesis in balsam fir (*Abies balsamea*). *Tree Physiology* **2008**, *28*, 1069-1076.
- 48. Gao L.S.; Wang, X.M.; Zhao, X.H. Response of *Pinus koraiensis* and *Picea jezoensis* var. *komarovii* to climate in the transition zone of Changbai Mountain, China. *Chinese Journal of Plant Ecology* **2011**, *35*, 27-34. (In Chinese)
- Huang, J.G.; Tardif, J.; Bergeron, Y.; Denneler, B.; Berninger, F.; Girardin, M.P. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change biology* 2010, 16, 711-731.
- Dang, Q.L.; Margolis, H.A.; Collatz, G.J. Parameterization and testing of a coupled photosynthesis-stomatal conductance model for boreal trees. *Tree Physiology* 1998, 18, 141-153.
- 51. Zhao, Z.J.; Tan, L.Y.; Kang, D.W.; Liu, Q.J.; Li, J.Q. Response of *Picea likiangensis* radial growth to climate change in the Small Zhongdian area of Yunnan Province, Southwest China. *Chinese Journal of Applied Ecology* **2012**, *23*, 603-609. (In Chinese)

- 52. Dang, H.S.; Zhang, Y.J.; Zhang, K.R.; Jiang M.X.; Zhang, Q.F. Climate-growth relationships of subalpine fir (*Abies fragesii*) across the altitudinal range in the Shennongjia Mountains, central China. *Climatic Change* **2013**, *117*, 903-917.
- Wang, X.; Zhao, X.; Gao, L. Climatic response of *Betula ermanii* along an altitudinal gradient in the northern slope of Changbai Mountain, China. *Dendrobiology* 2013, 70, 99-107.
- 54. Shi, X.H.; Qin, N.S.; Zhu, H.F.; Shao, X.M.; Wang, Q.C.; Zhu, X.D. May–June mean maximum temperature change during 1360–2005 as reconstructed by tree rings of Sabina Tibetica in Zaduo, Qinghai Province. *Chinese science bulletin* **2010**, *26*, 3023-3029.
- 55. Liang, E.Y.; Shao, X.M.; Qin, N.S. Tree-ring based summer temperature reconstruction for the source region of the Yangtze River on the Tibetan Plateau. *Global and Planetary Change* **2008**, *61*:313-320.
- Takahashi, K.; Okuhara, I.; Tokumitsu, Y.; Yasue. K. Responses to climate by tree-ring widths and maximum latewood densities of two *Abies* species at upper and lower altitudinal distribution limits in central Japan. *Trees* 2011, 25, 745-753.
- 57. IPCC, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, 2013; Cambridge University Press; UK and New York, USA, 2013.
- 58. IPCC, Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007; Cambridge University Press; London, UK, 2007.
- 59. Xu, Y.L.; Huang X.Y.; Zhang, Y.; Lin, W.T.; Lin, E.D. Statistical analyses of climate change scenarios over China in the 21st century. *Advances in Climate Change Research* **2005**, *2*, 50-53.