

# Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains, Northwestern China

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## Abstract

Forest growth is sensitive to interannual climatic change in the **alpine treeline ecotone** (ATE). Whether the alpine treeline ecotone shares a similar pattern of forest growth with lower elevational **closed forest belt** (CFB) under changing climate remains unclear. Here, we reported an unprecedented acceleration of *Picea schrenkiana* forest growth since 1960s in the ATE of Tianshan Mountains, northwestern China by a **stand-total sampling** along **six altitudinal transects** with **three plots in each transect**: one from the **ATE between the treeline and the forest line**, and the other two from the CFB. All the sampled *P. schrenkiana* forest patches show a **higher growth speed** after 1960 and, comparatively, forest growth in the **CFB** has sped up much **slower** than that in the **ATE**. The speedup of forest growth at the ATE is mainly accounted for by climate factors, with **increasing temperature** suggested to be the **primary driver**. **Stronger water deficit** as well as **more competition** within the **CFB** might have **restricted forest growth** there more than that within the ATE, implying **biotic factors** were also significant for the accelerated forest growth in the ATE, which should be excluded from simulations and predictions of warming-induced treeline dynamics.

**Keywords:** alpine treeline, competition, interannual climate variation, tree growth, tree-ring

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## Introduction

Multiple evidences have shown that alpine treeline dynamics are sensitive to the rapid climate change (McGuire *et al.*, 2010; Liang *et al.*, 2011; Jiménez-Moreno *et al.*, 2013). Although **shifting of treeline position** has been commonly regarded as proxy of climate change, it is strongly depended on encroachment of trees into new habitats and thus might reflect climate change on a **temporal scale of multi-years** (Smith *et al.*, 2009; Borgaonkar *et al.*, 2011). Different from the shifting in treeline position, tree growth in alpine treeline ecotone (ATE) is probably more sensitive to interannual variations of climate than that in lower elevational closed forest belt (CFB), hence the interannual response of tree growth to climate variations has been becoming a new focus to understand dynamics in the ATE in response to climate change (Graybill & Funkhouser, 1999; Hughes & Funkhouser, 2003; Bunn *et al.*, 2005; Yang *et al.*, 2010).

Dozens of previous works have investigated tree growth patterns and its relationships with climatic factors in the ATE, **but come to inconsistent conclusions** (Wilmking *et al.*, 2004; Holtmeier & Broll, 2006; Salzer *et al.*, 2009; Chen *et al.*, 2011). Tree growth within the ATE has been widely regarded to be temperature-sensi-

tive (Kupfer & Cairns, 1996; Holtmeier & Broll, 2006; Briffa *et al.*, 2008; King *et al.*, 2013). Rising temperature has been reported to increase tree growth within the ATE where warmth is a prevailing limiting factor (Wilmking *et al.*, 2004; Salzer *et al.*, 2009). **However**, a growing number of studies have revealed that tree growth in high altitude could **be impaired by relatively high temperature, mostly due to heat-induced water deficit** (Salzer & Hughes, 2007; Borgaonkar *et al.*, 2011; Liang *et al.*, 2013). These results highlighted an intricate nature regarding the responses of tree growth to climate warming in the ATE, which is perhaps mediated by the diverse climate regimes and species-specific traits.

The majority of relevant works such as those mentioned above have been conducted at **individual tree level** and based on **selective samplings** (e.g. Wang *et al.*, 2005), so that their focus are on individual tree and tree growth on **forest stand level** has been relatively **less** focused on. For instance, some works preferred big trees for climate reconstruction (Littell *et al.*, 2008; Zhu *et al.*, 2011) or climatic influence on tree growth (Tene *et al.*, 2011; King *et al.*, 2013). The roles of biotic factors, for example, competition among tree individuals and age structure on tree growth at **forest stand scale** have been **paid little attention** to (Salzer *et al.*, 2009). In addition, although selective samples from trees with different diameters at breast height (d.b.h.) have been adopted in some works to estimate forest age structure

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by correlating d.b.h. with tree age (e.g. McGuire *et al.*, 2010), there could be **great biases in tree age estimation** due to biotic factors such as suppression and release of tree growth in forest with closed canopy. To distinguish the climatic effects from biotic ones, **stand-total sampling** is required (Wu *et al.*, 2013). When taking into account both biotic and abiotic factors for forest growth, there could be diversified responses of forest growth to climatic warming. We **hypothesize** that relatively lower competition within forest in the ATE might reduce water deficit and **compensate the negative effect of rising temperature**, thus enhancing tree growth in the ATE more than that in the CFB with denser canopy and more competition. **If it is the truth**, the forest growth in the ATE should be faster than in the CFB. Otherwise, the ATE and the CFB should share the same patterns of forest growth response to climate warming given temperature preliminary dominate forest growth in the ATE.

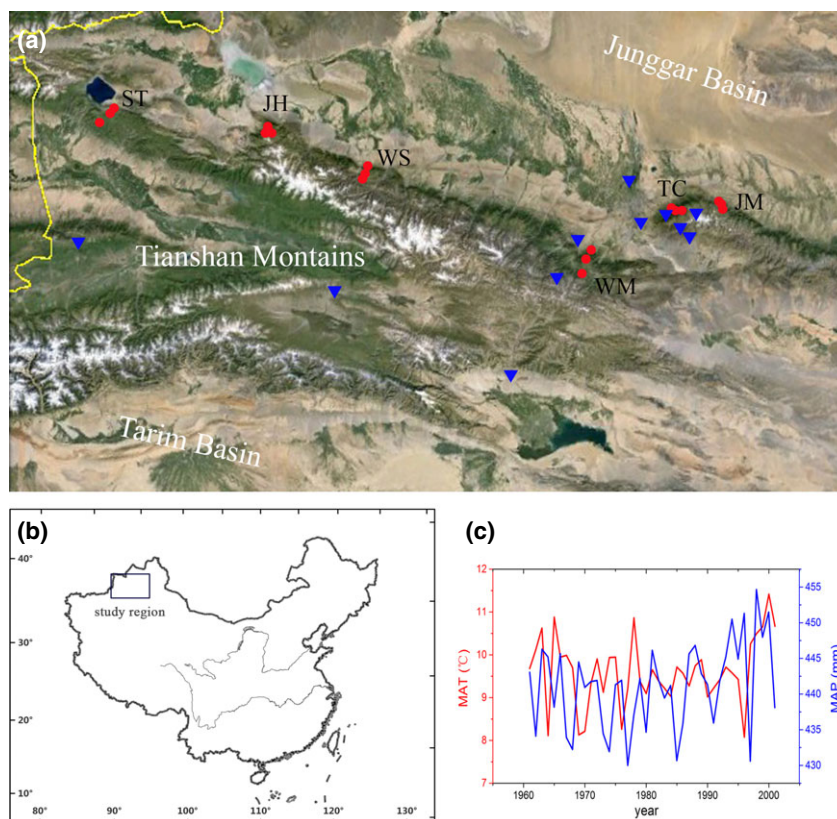
In this study, we investigated the treeline dynamics in the Tianshan Mountains in northwest China based on a stand-total sampling strategy along an

elevational gradient with meteorological observations at different elevations, to better understand the ATE dynamics in response to climate change as well as biotic factors within forest. Stand-total sampling was adopted to core *P. schrenkiana* in the Tianshan Mountains along six elevation transect from the ATE down to the CFB. We focus our work on **tree growth at forest stand scale**, particularly the following questions: (i) What are the patterns of tree growth at forest stand level; (ii) How climate factors influence forest growth; and (iii) How biotic factors influence forest growth?

## Material and methods

### Study area and sampling sites

The Tianshan Mountains in Central Asia extend across Kyrgyzstan, Kazakhstan, and China (Xinjiang Autonomous Region). *P. schrenkiana* forest is the most dominant and widespread forest type on its northern slopes in China (Li *et al.*, 2005). It dominates elevations of about 1400–2700 m a.s.l. in



**Fig. 1** Geographical features of the study area at regional and local scales. (a) Satellite image of the study area showing the location of sampling sites (red dots) and meteorological stations (blue triangles); (b) Map of China showing location of the study area; (c) Mean annual temperature and annual precipitation of the study area averaged from observation data of all the selected meteorological stations. Red line is MAT and blue line is MAP.

the study area mostly because of temperature limit at its upper boundary and precipitation limit at its lower boundary (Wang *et al.*, 2005). Mean annual temperature is about  $-1.2^{\circ}\text{C}$  in the ATE and about  $2.2^{\circ}\text{C}$  in the CFB, while mean annual precipitation is about 550 mm in the ATE and 350 mm in the CFB. Soil thickness, nutrition, and slope angle here were relatively homogeneous in the whole forest zone (Zhang *et al.*, 2010).

In 2011, six altitudinal transects are chosen in this region with three plots in each transect: one at the ATE (between the treeline and the forest line), the second roughly at the middle, and the third near the low boundary of the forest belt. All 18 plots are located on the north mountain slope with similar slope of around  $25\text{--}35^{\circ}$ . They were carefully chosen to avoid disturbance such as forest fire, logging, or grazing at six transects from east to west: Jimusar (JM), Tianchi (TC), Wulumuqi (Urumuq) River (WM), Wusu (WS), Jinghe (JH), and Santai (ST) (Fig. 1). Each of the six transects is about 100–200 km aside from each other and the total distance from the east to the west is about 550 km in straight line.

#### Tree-ring sampling and laboratory treatment

Each plot is  $25\text{ m} \times 25\text{ m}$  in size. In each plot, we measured the height and d.b.h. of each tree. For those too small to measure d.b.h., diameter at base (about 5 cm from ground) was measured instead. Two cores, one parallel to slope and another parallel to contour, were taken for all trees with d.b.h. > 5 cm and height  $\geq 2\text{ m}$ . Cores were carefully collected to ensure that each core reached pith of the tree. For other small trees, seedlings, and saplings, tree age was estimated by counting number of branches (Liang *et al.*, 2011). Canopy

cover of each plot was also visually estimated during field work (Table 1).

Cores were dried, mounted in wooden stripes, sanded with coarse-to-fine sandpapers and measured using TSAPwin system. Quality of all measurement series were then checked using COFECHA software (Holmes, 1983). Series that were not correlated with the entire dataset were discarded. A total of 1256 cores from 659 trees are available after crossdating (Table 1).

#### Development of BAI chronology

In standardized dendroclimatology works, after tree rings were measured and crossdated, ring width series from each tree was detrended, standardized, and a ring width index (RWI) chronology was built to estimate year-to-year tree growth variability. As we focused on tree growth speed and trend rather than interannual ring width variability in our study, we chose basal area increment (BAI) to estimate tree growth. BAI was calculated based on measured ring widths as the following equation:

$$\text{BAI} = \pi(r_t^2 - r_{t-1}^2)$$

where  $r_t$  is the radial radius at year  $t$  and  $r_{t-1}$  is the radial radius at year  $t-1$  (Monserud & Sterba, 1996).  $\text{BAI}_t$  is the estimated basal area increment for year  $t$ . It is widely proven that BAI can estimate real tree growth trends and meanwhile avoid detrending and standardizing in RWI (Salzer *et al.*, 2009). BAI chronology for each plot was made separately and presented as supplementary material (Figure S1). Then BAI of all trees within the six ATEs were averaged as ATE BAI sequence, and similarly BAI of all trees at the CFB were also averaged as CFB BAI sequence.

**Table 1** Details about the 18 plots and statistics of chronologies. Seedlings and saplings are included in average tree age and age range

Sites	Altitude (m a.s.l.)	No. of cores (Trees)	Average tree age (Age range)	EPS	Mean Sensitivity (M.S.)	Canopy cover
JM3	2468	42 (21)	129 (1–278)	0.922	0.478	45%
JM2	2005	38 (20)	96 (6–280)	0.974	0.471	65%
JM1	1886	127 (64)	71 (6–101)	0.965	0.549	80%
TC3	2700	62 (31)	142 (1–293)	0.996	0.391	40%
TC2	2340	39 (20)	143 (3–161)	0.977	0.327	60%
TC1	1740	134 (77)	60 (4–190)	0.997	0.352	80%
WM3	2566	36 (18)	87 (1–216)	0.933	0.314	40%
WM2	2100	40 (20)	121 (1–207)	0.981	0.362	65%
WM1	1819	124(62)	58 (1–82)	0.99	0.568	75%
ST3	2454	59 (30)	119 (1–247)	0.907	0.42	35%
ST2	2100	36 (20)	69 (1–135)	0.976	0.338	45%
ST1	2000	80 (45)	68 (5–83)	0.984	0.421	70%
WS3	2590	71 (36)	128 (2–228)	0.954	0.39	20%
WS2	2135	90 (45)	189 (5–251)	0.996	0.377	50%
WS1	1836	98 (50)	65 (7–158)	0.96	0.482	60%
JH3	2600	60 (38)	99 (1–182)	0.987	0.331	15%
JH2	2200	37 (20)	131 (5–146)	0.941	0.501	75%
JH1	1770	83 (42)	76 (6–153)	0.935	0.438	65%

### Quantification of forest stand features

We used **density of big trees** (d.b.h >5 cm, height >2 m) to estimate within-community competition, because competitions among big trees were predominated for forest community in this region (Li *et al.*, 2005). **Numbers of big trees were counted within each plot where tree rings were cored.** In JH and WS where stand conditions were relatively homogeneous, we expanded the plot size to count numbers of big trees. **For each of the six transects, average big tree density of the ATE plots and average density of big tree for the two CFB plots at each transect were calculated, respectively.**

We get **tree age** by counting number of the rings of two cores from each tree. This estimation is reliable because we have carefully ensured that each core contains rings from bark to pith. After that, trees were categorized to different age groups by every 30 years. Because determining actual tree ages requires destructive sampling (Niklasson, 2002), we defined the number of rings at 1.3 m height (breast height) as tree age. In our study, due to steep mountain slope and dense stretching branches for some trees, sometimes we had to sample two cores from different position of the trunk, which makes the number of rings of two cores from one tree different. In this case, we took the older age from the two cores as tree age. In subalpine spruce forests, the usual time needed to reach a height of 1.3 m is believed to be at least 20 years (Szewczyk *et al.*, 2011). However, spruce seedlings may survive under shade for many decades, and we had no data that would have allowed us to make reliable assumptions about the accurate year of germination of each tree. As using cores at **1.3 m** to estimate tree age is widely used (Briffa *et al.*, 1998; Wilmking *et al.*, 2004; Fraver *et al.*, 2011; Kunstler *et al.*, 2011), we used it to estimate tree age to make comparison with other studies.

We also define **juvenile trees and grown-up ones** to avoid the effect of fast growth from juveniles. No previous result indicates the accurate age dividing juvenile and mature trees for *P. schrenkiana*, but many studies have used **60 years** as partition between juvenile and grown-up trees for *P. schrenkiana* (e.g. Li *et al.*, 2010). In our study, we also use 60 years as division between juvenile and mature trees.

### Interpolation of climatic data and CO<sub>2</sub> concentration

**Daily data** from 11 **meteorological stations** in this region were derived and used to calculate temperature and precipitation at different elevational belts (Table 2). Nine of all the 11 stations began their record around 1960, with six of them ended in 2001, while the other five extended to the sampling year 2011. For each station, mean monthly temperature and monthly precipitation were calculated from daily data. For those stations began after 1960 or ended before 2011, average monthly temperature and monthly precipitation during their missing years were linearly interpolated from the two stations above and below its elevation.

**Monthly temperature and precipitation** of each sample site were **linearly interpolated** from the **two stations above and below its elevation.** By doing so, we can directly use meteorological data at different altitudes, which avoid altitudinal bias using large scale pixel data as commonly adopted in previous studies (e.g. Toledo *et al.*, 2011). Based on the interpolated monthly climate data, **seasonal (spring: April–May, summer: June–August, autumn: September–October, and winter: November–March) mean temperature and summed precipitation were calculated.** Seasons in our study region are divided based on the phenology of *P. schrenkiana* here (Li *et al.*, 2005). Analyses were conducted for a 19-month temporal window, from **April in the calendar year prior to the growing season to October of the current year.** This window was chosen because all of the chronologies had highly significant first-order autocorrelation, but only about 30% of them had significant second-order or higher autocorrelation. That means tree growth here was highly affected by climate conditions of the growing year and the year prior to growing year, but more prior years were not relevant, so that a within 2 year 19-month window was appropriate to analyze forest growth with climate factors. Winter of growing year was excluded because by then trees had already stopped growing.

We extracted the global **annual CO<sub>2</sub> concentration** from internet to represent the regional dynamics of annual CO<sub>2</sub> concentration (Ballantyne *et al.*, 2012). As we focus on interannual variations of CO<sub>2</sub> concentration on forest growth and the altitudinal difference between the ATE and the CFB is limited,

**Table 2** General information of meteorological stations for climatic interpolation in this study

Stations	Beginning Year	End Year	Longitude (°E)	Latitude (°N)	Altitude (m a.s.l.)
Baluntai	1957	2001	86.2	42.4	1753
Bayinbuluke	1957	2001	84.1	43.0	2458
Caijiahu	1958	2001	87.5	44.2	441
Daxigou	1957	2011	86.8	43.1	3539
Houxia	1982	2001	88.2	43.7	2350
Kongbingdou	1982	2001	88.3	43.6	3805
Tianchi	1958	2011	88.1	43.9	1935
Wulumuqi	1951	2011	87.6	43.8	917
Xiaoquzi	1961	2011	87.1	43.6	2121
Zhaosu	1954	2011	81.1	43.1	1851
Zongkong	1982	2001	88.3	43.8	3408

the annual CO<sub>2</sub> concentration has not interpolated for each plot.

### Tree growth–climate relationships

Tree growth–climate relationships were analyzed for the period 1960–2011. Pearson correlation analysis was performed between BAI and seasonal climate for individual plot and presented in supplementary material (Figure S2, Figure S3). It was further performed for all plots at the ATE and those at the CFB, respectively. BAI of 1 year was correlated with seasonal temperature and precipitation, respectively, from previous spring till this autumn **to identify which climate factor at which season exerted the most influence on tree growth**. After that, we made piecewise linear regression for BAI, seasonal temperature, and precipitation sequences for each site and for all sites together. Then we subtracted regression results from measured data for BAI, seasonal temperature, and precipitation sequences to get their residual chronologies to detrend those sequences and get their interannual fluctuation. Then the residual BAI of 1 year was correlated with residual seasonal temperature and precipitation, respectively, from previous spring till this autumn.

Besides, we divided trees into different **30-year age groups** and try to find out **if age group affected the climatic response of forest growth**.

## Results

### Patterns of forest growth along time

For each plot, its own annual BAI and cumulated sample size are shown in Figure S1. The years when **sub-**

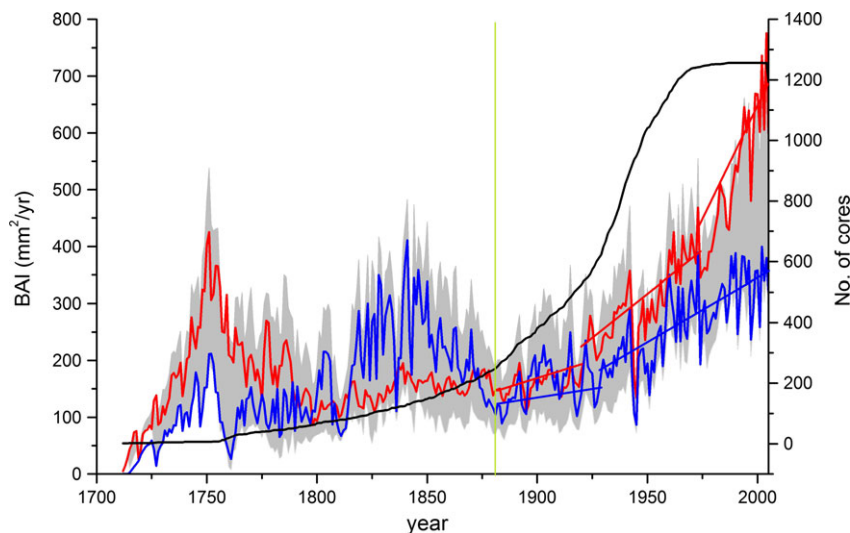
**sample signal strength (SSS) reached 85% differ across plots, but all of them are earlier than 1960**. Therefore, the BAI data are statistically reliable for the period from 1960 to 2011 that we focus on in this study (Figure S1).

Our regional BAI sequence lasted from AD 1711 to 2005. The year when subsample signal strength (SSS) reached 85% was 1882, so only data after 1882 were statistically reliable for further analysis. In our study region, average forest growth speed was the highest after 1960 ( $933 \text{ mm}^2 \text{ yr}^{-1}$ ,  $n = 330$ ) during the last three centuries at the ATE. For forests at the CFB, growth speed was also the highest after 1960 ( $516 \text{ mm}^2 \text{ yr}^{-1}$ ,  $n = 926$ ) (Fig. 2).

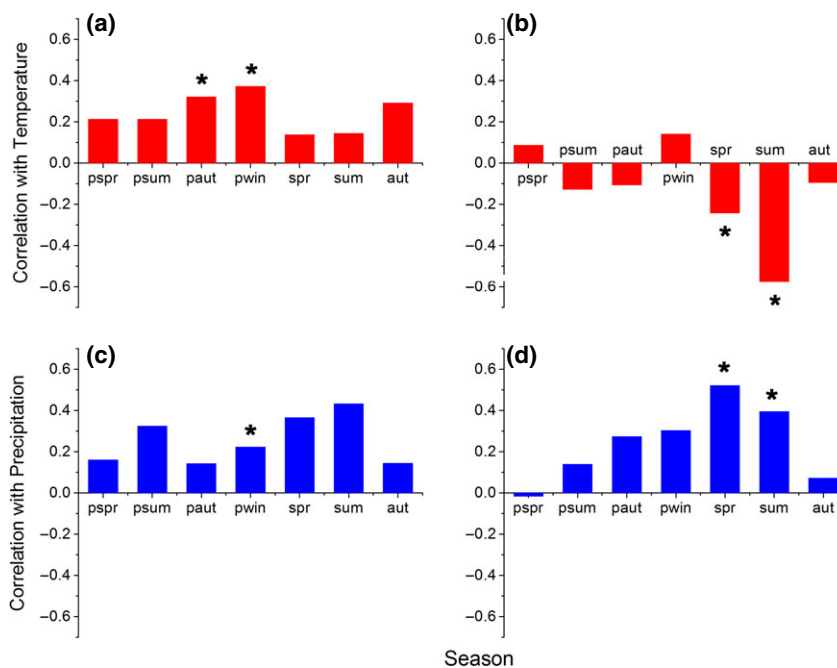
After 1960, when forest began to accelerate growth, forests in the ATE appeared an accelerating growth speed, whereas those in the CFB grow at a relatively lower speed. The forest growth speed acceleration in the ATE is about 2 times of that in the CFB (Fig. 2).

### Relationships between forest growth and climate/CO<sub>2</sub> concentration

For the six plots at ATE, plot ST3 show different BAI–temperature and BAI–precipitation correlations from the others, and the other five plots show similar correlation results ( $P < 0.01$ ). However, neither significant ( $P < 0.05$ ) BAI–temperature nor BAI–precipitation correlations were found in the plot ST3 (Figure S2; Figure S3), which means it does not change the relationship between BAI and climate factors when taking plots



**Fig. 2** BAI chronologies of sites in the alpine tree line ecotone (ATE) and the lower elevational closed forest belt (CFB). Red curve is BAI of ATE sites and red straight lines show piecewise linear regression results of BAI for the ATE sites after 1882. Blue curve is BAI of CFB sites and blue straight lines show piecewise regression results for BAI of the CFB sites after 1882. Gray area is variation in all BAI (average BAI  $\pm$  standard variation). Black curve shows cumulated number of cores. Green line separates the years with a threshold of subsample signal strength (SSS) value of 85%. Black curve shows cumulated number of cores.



**Fig. 3** Correlation between BAI chronology and (a) seasonal temperature within the alpine treeline ecotone (ATE); (b) seasonal temperature within the lower elevational closed forest belt (CFB); (c) seasonal precipitation within the ATE; (d) seasonal precipitation within the CFB. Star indicates significant correlation ( $P < 0.05$ ). The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).

at the ATE as a whole. For the 12 plots at the CFB, JM2, and WS2 have similar pattern and the other 10 sites are similar in BAI–temperature correlations ( $P < 0.01$ ). For BAI–precipitation correlation, ST2, JH1, and WS1 show different pattern from the other nine plots. Most sites show statistically similar correlation pattern, so it is reliable to consider the region as a whole (Figure S2; Figure S3).

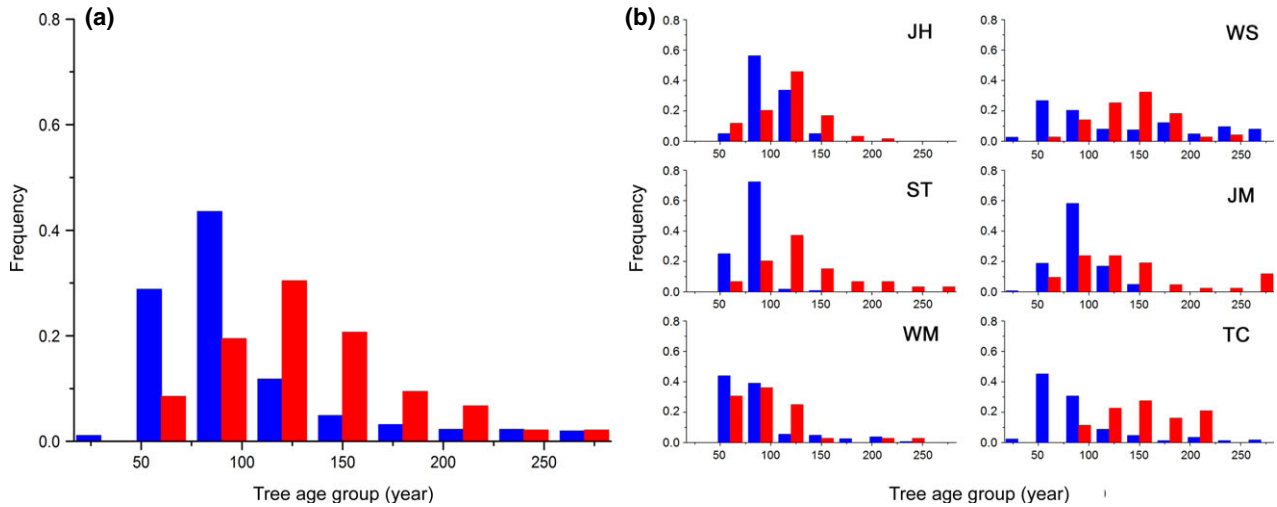
In our study region, there is a striking change in the pattern of correlation between seasonal climate and BAI chronologies between the forest at the ATE and that at the CFB (Fig. 3). The chronologies at the ATE showed strong positive correlations with temperature and markedly weakened, mostly positive, correlation with precipitation (Fig. 3a, c). Significant ( $P < 0.05$ ) positive correlation was found in previous autumn and winter for temperature, and in previous winter for precipitation for the ATE. Meanwhile, the CFB chronologies showed a strong positive correlation with precipitation, but a negative association with temperature (Fig. 3b, d). Significant negative correlation was found in present spring and summer for temperature ( $P < 0.05$ ), and significant positive correlation was found in present spring and summer for precipitation for the CFB ( $P < 0.05$ ). The relationships between residual BAI chronologies and climate factors show similar patterns (Figure S4).

At site level, most of the plots share similar patterns of correlation with climatic factors for the ATE and CFB separately (Figure S2; Figure S3).

The BAI chronologies show nonsignificant ( $P > 0.05$ ) relationship with corresponding annual  $\text{CO}_2$  concentra-

**Table 3** Density of big tree at the six transects. For each pairs, -l means the average results of the two CFB plots and -h means results of ATE plot. For example, JH-l means the average results of CFB plots at JH transect, and JH-h means results of ATE plot of this transect. The same is for the other five transects

Sites	Area ( $\text{m}^2$ )	No. of big trees	Density of big trees ( $/\text{m}^2$ )
JH-l	2415	572	0.088
JH-h	7500	104	0.009
WS-l	1000	526	0.287
WS-h	5000	164	0.022
ST-l	1250	116	0.092
ST-h	625	59	0.094
JM-l	1250	165	0.132
JM-h	625	42	0.067
TC-l	1250	173	0.138
TC-h	625	62	0.099
WM-l	1250	164	0.131
WM-h	625	36	0.058

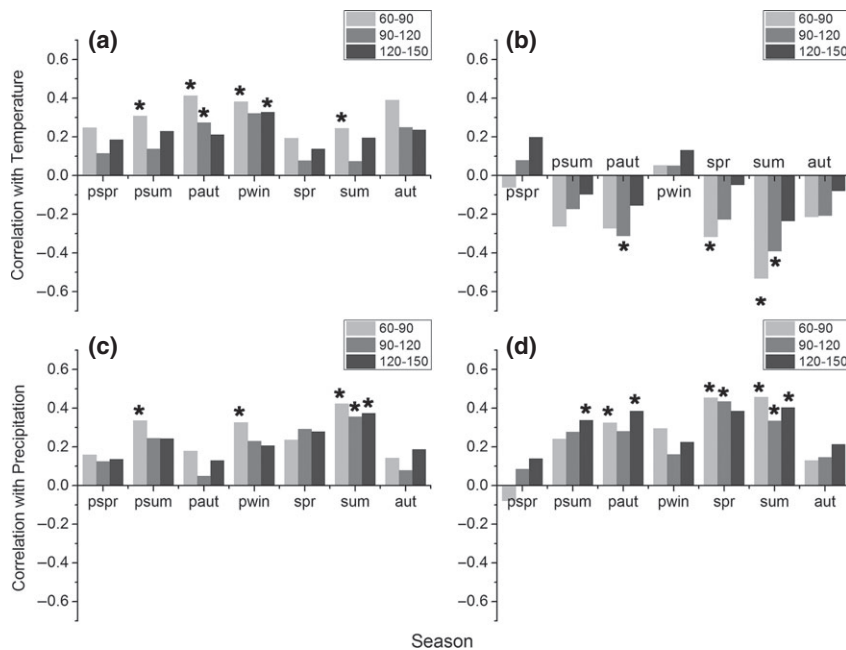


**Fig. 4** Frequency distribution of age structure for sampled trees in all of the study transects (a) and within each of the six transects (b). Age distributions for trees from the alpine treeline ecotone (ATE) and the lower elevational closed forest belt (CFB) are indicated by red and blue bars, respectively. Age groups are divided every 30 years.

tion. Similar is the relationship between residual BAI chronologies and residual annual CO<sub>2</sub> concentration, indicating that CO<sub>2</sub> does not play a major role in inter-annual variations in forest growth.

*Relationship between tree growth and forest stand factors*

One of the six gradient pairs (ATE vs. CFB) have similar big tree density (ST pair, treeline 0.092 trees m<sup>-2</sup> vs. nontreeline 0.094 trees m<sup>-2</sup>), the other five pairs



**Fig. 5** Correlations between BAI for the major three age groups (60–90 years, 90–120 years, and 120–150 years) and climatic factors, (a) seasonal temperature in the alpine treeline ecotone (ATE); (b) seasonal temperature in the lower elevational closed forest belt (CFB); (c) seasonal precipitation in the ATE; (d) seasonal precipitation in the CFB. Star indicates significant correlation ( $P < 0.05$ ). The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).

showed that trees in the CFB were significantly denser than trees in the ATE ( $P < 0.05$ ), which means trees within the CFB were facing more competition than those within the ATE (Table 3).

ATE and CFB have different age structures (Fig. 4). The average age is higher in the ATE than in the CFB. Peak frequency of trees from CFB aged from 60 to 120 years, and that of ATE trees aged from 90 to 150 years (Fig. 4a).

For those tree groups (aged from 60 to 150 years) in which most trees are found, their growth response to temperature and precipitation were similar (Fig. 5), which is confirmed by ANOVA result ( $P < 0.01$ ). The ATE chronologies showed strong positive association with temperature and markedly weaker, mostly positive, correlation with precipitation, while the CFB chronologies showed a stronger positive correlation with precipitation, but a negative correlation with temperature. This result is similar with response of all age groups as a whole to climate (Fig. 3). The relationships between residual BAI chronologies and climate factors for the three age groups do not change the above patterns (Figure S5).

## Discussion

### *Faster speedup of treeline forest growth*

We found tree growth has been accelerating in the ATE since 1960s, with rate higher than in the CFB (Fig. 2). Despite altitude variations of treeline position at different sites, patchy forest in the ATE show an accelerating growth speed, whereas other plots in the CFB show a relatively slower growth speed, regardless of their absolute altitude.

This fast growth could not be the result of juvenile growth. Young trees typically grow wider rings than old trees, and the rings are the largest in the first few decades of a tree's life and become narrower as the tree ages (Fritts, 1976; Speer *et al.*, 2010). In our study area, after 1882, from which year tree-ring data are statistically reliable, over 93% trees were older than 60 years, which has been widely used as partition between juvenile and grown-up trees for *P. schrenkiana* (e.g. Li *et al.*, 2010). That means juvenile trees account only a small portion during our study period. So the majority of these rings are not from the juvenile period of the trees' lives. Besides, the pattern of accelerating forest growth speed were, categorically, not a result of statistical techniques commonly applied to tree-ring data and designed to remove effects associated with the age or size of the tree. We use simple, nonstandardized raw ring width data to calculate BAI to estimate the newly added ring area as the indicator of growth speed, which is a highly conservative approach that retains

the original data and eliminates any data-transformation biases (Salzer *et al.*, 2009).

### *The role of climate change on recent speedup of forest growth*

In our study region, there was a marked transition in the nature of the climate associations of forest growth speed. The positive correlations with temperature in the ATE supported that increases in temperature played a major role in the modern growth surge and the weaker correlation with precipitation suggested that precipitation might have less contributed to the recent growth trend (Fig. 3). The relationship between the BAI at the ATE and temperature at corresponding elevation from 1960 was relatively strong, but for these sites no such strong relationship with precipitation emerged. The nature of the transition in the properties of the BAI and their associations with climate factors near treeline was suggestive of a threshold in environmental control of tree growth as seen near treeline in the high mountains, where the climatic response of trees includes a temperature threshold component (e.g. Salzer *et al.*, 2009). Direct observations of xylogenesis (wood formation) coupled with soil, air, and stem temperatures provide strong corroboration for temperature-limited growth in alpine and boreal conifers (Rossi *et al.*, 2008). The upper treeline was suggested to be created by the temperature limitation of trees' ability to form new tissue (sink inhibition) rather than by a shortage of photosynthesis (source limitation) (Körner, 1998). This global model of treeline suggests a narrow range of growing season temperatures of treelines at different elevations around the globe and supported a common minimum temperature limit on tree growth. The reported general critical value of mean daily temperature for the onset of wood formation is 8–9 °C, and tree growth at the ATE requires that temperatures at critical times of year consistently equal to or exceed this general minimum temperature for wood formation (Körner & Paulsen, 2004). Even with sufficient moisture to support growth, tissue formation (ring growth) could not occur if the threshold temperature was not met for a sufficiently long period. For *P. schrenkiana*, no precise temperature threshold for wood formation onset has been reported. Our climate data show that there are 3 months with mean monthly temperature exceeding 8 °C, which ensure the existence and growth of the forest here. In our study area, temperature has been obviously rising within the recent century, especially after the 1960s (Fig. 1c; Wang *et al.*, 2005; Yuan & Wei, 2006). ATE benefit from it because growing season has become longer: temperature rising over growth threshold earlier in spring and falling below it later in



autumn. With relatively lower evapotranspiration comparing to the CFB, ATE showed a higher speedup of growth speed than the CFB.

For the CFB, where evapotranspiration was higher, rising temperature enhanced soil water loss thus made forests growth suffering from this temperature-induced drought. Forest here has been suffering from relatively high evapotranspiration (Yuan & Wei, 2006). With rising temperature from the 1960s, forest growth in the CFB might have been impaired by the temperature-induced water deficit, as tested by previous works (Wu *et al.*, 2013). Therefore, its speedup is much weaker than that of ATE, although CFB have been growing faster.

**Site-level difference in responses to climate factors further confirmed the role of moisture in regulating speedup of forest growth rate.** Tianshan Mountains in China has a slightly decreasing mean annual precipitation from west to east (Yuan *et al.*, 2008), which means western transects (ST, WS, and JS) suffer from water deficit less than eastern ones (WM, TC, and JM). With similar rising temperature, forest growth may response differently due to their current different precipitation restrictions. **This may help to explain why plots in the western part of Tianshan Mountains and those in the eastern parts do not show the same BAI-climate correlation pattern.** Such difference is most obvious between the ST transect plots, which are at the westernmost of the study region and thus with least water deficit, and the others.

#### *The role of biotic factors on tree growth*

It was clearly shown that forests within the ATE are much less dense than those within CFB, which might help to explain the ATE tree growth rate. Plant interactions can regulate plant communities, and this role can be altered by abiotic stress (Littell *et al.*, 2008; Kunstler *et al.*, 2011). With increasing climate stress, the role of competition decreased (Pedersen, 1998). In our study region, the patchy forests within the ATE suffered from less competition than the CFB. Moreover, forests in the ATE were confined by low temperature, i.e. climate stress here was harsher than that in the CFB, so that competition played an even weaker role. This further helped to explain different growth rate within the ATE and the CFB.

Effect of different age structures between the ATE and the CFB on the forest response to climate factors was not evident in our study, as indicated by the similar responses of different age groups to climatic factors (Fig. 5). Age structure as an important biotic factor has widely been reported to adapt tree radial growth response to climate factors (Carrer & Urbinati, 2004;

Copenheaver *et al.*, 2011; Zuidema *et al.*, 2011), so that different forests with their own age structure may response differently to similar regional climate change (Villalba & Veblen, 1997; Hogg *et al.*, 2008; Allen *et al.*, 2010). It was suggested that age-dependent response to climate may be related to variations in the timing of secondary growth because old trees are capable of responding to warmer spring conditions earlier in the growing season than young trees (McMillan & Goulden, 2008; Rossi *et al.*, 2008). But it was also suggested that the young trees started the cambial cell division earlier than the old trees so that the young trees have a longer growing season (Li *et al.*, 2014). Another potential age-dependent difference might be root structure: old trees often have more extensive rooting systems in the deeper mineral soil layers than young trees (Devine & Harrington, 2005; Børja *et al.*, 2008). **In our study area, however, soil on the steep mountain slope is relatively thin (Zhang *et al.*, 2010), which limit root distribution divergence that may happen between different age groups.** This may help to explain why major age groups (60–150 years), where the majority of trees are within, show similar growth response to climatic factors (Fig. 5). So, in all, the role of forest age structure is not evident in our study area.

#### *The role of other lesser factors on tree growth*

It has widely reported that rising CO<sub>2</sub> may enhance tree growth (e.g. Hattenschwiler *et al.*, 1997; Girardin *et al.*, 2011), but in our study area, no such significant enhancement was found. Disturbance also constrains tree growth, but in our study, it might not be an important factor. In our study area, the disturbance history in forest zone was not clear. But, as we have carefully chosen plots without logging or grazing trace, their influence has been excluded. Meanwhile, forest belt in the Tianshan mountains is ~1000 m wide, disturbance such as forest fire influence should be similar among those forests, so that it may not contribute to different growth speed between ATE forests and forests in the CFB.

In summary, our study has revealed by stand-total sampling that in the Tianshan Mountains of China, *P. schrenkiana* forest showed accelerating forest growth speed after 1960 ever since 1711 in the ATE, while forest growth speed in the CFB was relatively lower than that in the ATE. Climatic factors such as temperature and precipitation were primary determinants, while biotic factors such as competition within forest and different forest age structure played a secondary role. For climate factors, increasing temperature has enhanced forest growth at the ATE where precipitation is sufficient, but forest growth might suffer from water deficit caused by increasing temperature in the CFB. For biotic

factors, competition between trees restricted forest growth more severely in the CFB than in the ATE, where forest was denser than in the ATE. Effect of different age structures on the forest response to climate factors were not evident in our study. Our study has found out that alpine tree growth is primarily controlled by rising temperature, so that alpine tree growth could serve as a good indicator of climatic warming. Considering that alpine treeline movement is less sensitive than tree growth at annual scale, we suggest more work on tree growth near the alpine treeline in the future.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** BAI chronologies and cumulated sample size for each plot. In each panel, black line is its BAI chronology and blue line is cumulated sample size.

**Figure S2.** Correlation between BAI chronology and seasonal mean temperature for each plot. The six panels at the left column represent the alpine treeline ecotone (ATE) plots, while the other 12 small panels represent plots from the lower elevational closed forest belt (CFB). Stars indicate correlation that is significant ( $P < 0.05$ ). The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).

**Figure S3.** Correlation between BAI chronology and seasonal precipitation for every site. The six panels at the left column are plots from alpine treeline ecotone (ATE) sites, and the other 12 small panels are plots from the lower elevational closed forest belt (CFB). Stars indicate correlation that is significant ( $P < 0.05$ ). The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).

**Figure S4.** Correlation between residuals of BAI chronology and (a) seasonal temperature in the alpine treeline ecotone (ATE); (b) seasonal temperature in the lower elevational closed forest belt (CFB); (c) seasonal precipitation in the ATE; (d) seasonal precipitation in the CFB. Star indicates significant ( $P < 0.05$ ) correlation. The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).

**Figure S5.** Correlations between residuals of BAI for the major three age groups (60–90 years, 90–120 years, and 120–150 years) and climatic factors. (a) seasonal temperature in the alpine treeline ecotone (ATE); (b) seasonal temperature in the lower elevational closed forest belt (CFB); (c) seasonal precipitation in the ATE; (d) seasonal precipitation in the CFB. Star indicates significant correlation ( $P < 0.05$ ). The seasons are previous spring (pspr), previous summer (psum), previous autumn (paut), previous winter (pwin), current year spring (spr), current year summer (sum), and current year autumn (aut).