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Original article

Age-dependent tree-ring growth responses of Schrenk spruce (*Picea schrenkiana*) to climate—A case study in the Tianshan Mountain, China

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ABSTRACT

For both its climatic and ecological importance, Schrenk spruce (*Picea schrenkiana*) is a crucial tree species living at mid-altitude on the western area of the Tianshan Mountains. It plays a key role on understanding climatic change in the Tianshan Mountains in the past 500 years. However, whether the relationship between tree growth and limiting climate factors is stable over time is still not well-known. In this study, standard and residual chronologies of four 100-year age classes (AC1 < 110a, 110a < AC2 < 210a, 210a < AC3 < 310a and AC4 > 310a) were established for detecting divergence in climate–growth relationships as well as comparing low-frequency and high-frequency variations. The results show that climate can account for a high amount of variance in tree-ring width and higher climate sensitivity was detected in younger trees. Younger trees (<210a) exhibit significantly negative growth responses to mean monthly air temperature of previous June and positive relationship with total monthly precipitation of current April and May, while mean monthly air temperature of current March may inhibit growth of older trees (>210a). Tree-ring chronology statistics and response function reveal that the age-growth patterns are non-monotonic. Our results together with previous studies demonstrate that the age effects on tree-ring growth–climate response is attributed to a combination of genetic characteristics and site microclimate, which suggests that it is necessary to consider both age-dependent and species-specific climate responses when using tree-ring measurements as a proxy for valid climate reconstructions.
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Introduction

As natural archives, tree rings are a valuable source to detect historical climate changes and provide accurate proxy data for paleo-environmental studies from local to hemispheric scales (Briffa and Cook, 1990; Schweingruber, 1996; Bradley, 1999; Carrer, 2011). Dendrochronological techniques are also commonly used to evaluate current climate–growth relationships of trees and provide vital baseline information in climate change studies (Beniston, 2002). In dendroclimatological studies, it is generally assumed that the approximate relationship between tree growth and limiting climate factors is stable over time (Fritts, 1976). However, many recent studies have reported different results challenging this assumption. Some species, such as Bristlecone pines (*Pinus aristata Engelm.*) (Fritts, 1976) and Alpine larch (*Larixlyallii Pari.*) (Colenutt and Luckman, 1995), exhibit little age effect on climate–growth relationships. Other studies suggest that there are significant difference in climate–growth relationships between old trees and young trees in certain species, such as White spruce (*Picea glauca Moench*) (Szeicz and MacDonald, 1994) and Subalpine fir (*Abies lasiocarpa*) (Ettl and Peterson, 1995). This has been explained as a decrease in the efficiency of water transport caused by increased hydraulic resistance in old trees (Ryan and Yoder, 1997; Carrer and Urbinati, 2004; Yu et al., 2008). Other studies demonstrate that in certain cases where young trees are more sensitive to climate than old trees, this is because the less well-established root systems of young trees make them more sensitive to drought (Rozas et al., 2009). Vieira et al. (2009) demonstrated that earlywood-width of young *Pinus pinaster* trees is more sensitive to the climate of the earlier growing season. Wilmking and Myers-Smith (2008) have shown that climate–growth

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correlations in a peatland-forest landscape are strongly dependent on micro-topography and vary substantially over time. Therefore, age-dependent relationships might be an essential part of dendroclimatic analysis in different regional contexts. To obtain valid historic climate records with a minimum bias caused by age effects, it was recommended to incorporate trees of all ages into the chronology (Szeicz and MacDonald, 1994; Wang et al., 2009), and to analyze in a large sample size (Esper et al., 2008).

The Tianshan Mountains is considered to be a sensitive indicator of the potential impacts of global climate change due to their complex topography and unique natural conditions (Sang et al., 2007). There are a number of dendrochronology and dendroclimatology studies concentrated on the Tianshan Mountains with an increasing availability of extensive networks of tree-ring chronologies (Yuan and Li, 1995, 1999; Yuan et al., 2001a, 2001b, 2003; Zhu et al., 2004; Wang et al., 2005; Zhang et al., 2008, 2009). Several studies indicate that Schrenk spruce (*Picea schrenkiana*) is sensitive to climate factors and consequently is an ideal species for dendroclimatic research in the Tianshan Mountains (Yuan and Li, 1995; Zhu et al., 2004; Wang et al., 2005; Zhang et al., 2008, 2009; Chen et al., 2009). Recent studies demonstrated that tree-ring growth–climate relationships vary with age in Qilian juniper (*Sabina przewalskii Kom.*) and Dahurian larch (*Larix gmelinii*) (Yu et al., 2008; Wang et al., 2009). However, tree-ring age effects for Schrenk spruce in the Tianshan Mountains have not yet been investigated. Investigation of age-dependent climate response could be an essential part to predicting climate change accurately and to understanding the ecological characteristics of tree-ring growth in this region. The present study was conducted to investigate age differences of climate–growth responses in Schrenk spruce from the northern slopes of the Wusun Mountains in the Yili valley. The main objectives are (1) to test the consistency of climate–growth relationships over time, and (2) to detect whether age effects on climate response exist in Schrenk spruce in the Tianshan Mountains.

Materials and methods

Study area and sample sites

The Yili valley (42°14′–44°50′, 80°09′–84°56′), located in the western Tianshan Mountains in China, is an intramontane basin with the opening toward the west and surrounded by mountains on all other sides. In terms of this special topography, the westerly airflow enters directly into the valley to bring precipitation along the mountain slope, while dry and warm air flows from the Tarim Basin and Junggar Basin, whereas cold air flows from Siberia are blocked. Compared to the arid eastern Tianshan Mountain, the Yili valley is dominated with a temperate semiarid continental climate. The annual average accumulated temperature when temperature stays above 10 °C is around 3000 °C, while there are 163–211 frost-free days. The annual precipitation is 284–468 mm, with 76–82% concentrated in the spring and summer (Zhu, 1985; Zhu et al., 2004; Chen et al., 2009). In this study, we collected samples from Awuliyaqiaoke (AWL) in northern slope of the Wusun Mountains in the Yili valley (Fig. 1). The selected tree species is Schrenk spruce (*P. schrenkiana*), which is the dominant species in the Tianshan Mountains. It is an evergreen and relatively shade-tolerant tree species, which plays a role in preventing soil erosion and soil water loss, as well as in retaining ecological stability in an inland river drainage area. The samples were taken from eight sites along a consistent northwest-facing slope with a gradient of 30° and the elevations ranged from 1834 to 2750 m above sea level. A large altitude range guarantees inclusion of cores with different ages. The canopy coverage is about 30–50%. All of the trees were growing in relatively sparse or isolated conditions with minimum disturbance history at the sample sites. In total, 147 cores were extracted from 121 trees from the sample site in October 2010.

Tree-ring chronology development

All cores were mounted and polished with progressively finer sandpaper until the cellular structure could be easily distinguished (Stokes and Smiley, 1968). Tree-ring width was measured with Lintab 6.0 (Germany) with a precision of 0.01 mm. Ring-width series were cross-dated using the software COFECHA (Holmes, 1983). Nine series were excluded as the markedly deviation from the master chronology.

Cores that had pith were used to determine the trees' actual ages. For cores that were close to the pith, the respective trees' ages were estimated by adding 2–7 rings after comparison of their ring patterns with the cores that had pith (Clark and Hallgren, 2004). Six cores for which the specific age could not be estimated were excluded for chronology development. Finally, 132 cores from 111 trees were used for further study and classified as four 100-year age classes based on tree age. The 100-year interval was considered as a reasonable compromise between sufficient sample size and sufficient disaggregation of the data (Carrer and Urbinati, 2004). In order to detect the age effects on a century time scale, such as 1900–2000,1800–1900,1700–1800, we classified the age classes into AC1 (<110a, 1900–2010), AC2 (110a < AC2 < 210a, 1800–1900), AC3 (210a < AC3 < 310a, 1700–1800) and AC4 (AC4 > 310a). In each age class chronology, tree-ring cores are from different altitudes to minimize the elevation divergence on age effects and the elevation range of each age class chronology are shown in Table 1.

Four age-class chronologies (ACs) and individual series were standardized using the negative exponential method transformed using the program ARSTAN (Cook and Holmes, 1986). Repeated experiments showed that the growth trend of trees on drought-subjected sites is reliably estimated by the exponential curve (Fritts, 1976). The negative exponent method may remove the growth trends from raw ring-width series while retaining most low frequency variations that are potentially climate-driven (Jacoby and Cook, 1981; Cook, 1985). Next, robust autoregressive modeling was used to remove a significant high autocorrelation within each series (Richter et al., 1991). Standard chronology and residual chronology were used in the following analysis for detecting low-frequency and high frequency variations and their responses to climate among the four age classes. Several descriptive statistics were summarized to compare the two types of chronologies among different age classes over a common time period (Table 1). The quality of all chronologies was evaluated using the following statistical parameters: mean sensitivity (MS), standard deviation (SD), first principal component (PC1) and expressed population signal (EPS). Meanwhile, mean raw ring-width (MRD) was also calculated to analyze the age related differences.

Meteorological data

Meteorological data was obtained from instrument records from the nearest weather station to the sample site including mean monthly air temperature and mean total monthly precipitation. The climatic records of Zhaosu station (81°08′E, 43°09′N, 1854.6 m), which is within 100 km in the sampling areas, shows that mean annual precipitation is 508 mm (1956–2010), with 66% of the precipitation concentrated on April–July. Mean annual air temperature is 3.4 °C. The peak of mean monthly air temperature (June and July) and total monthly precipitation (May) is not synchronized (Fig. 2).

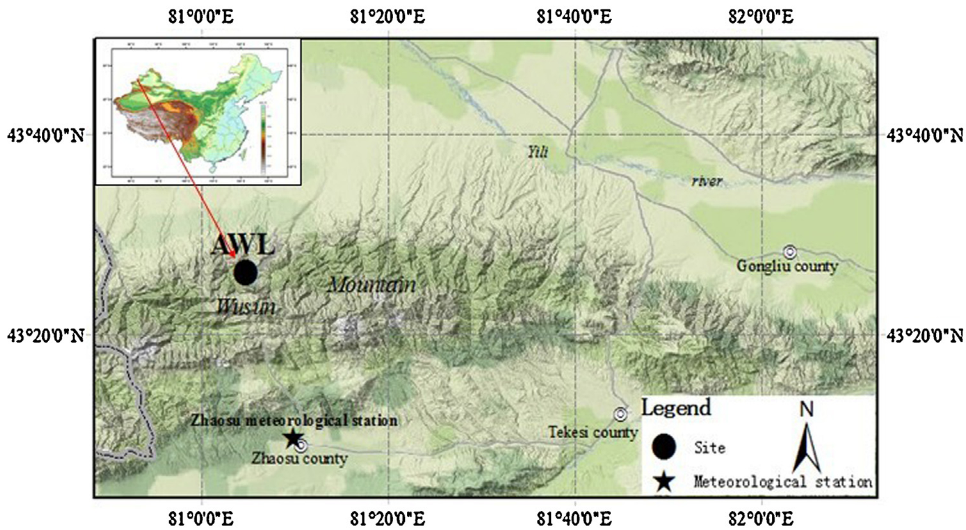

Fig. 1. Map of sampling site and meteorological station.

Table 1
Age–class tree-ring chronologies statistics.

ACs	Age	Tree/cores	MRW (mm)	EPS	Standard chronology			Residual chronology			Elevation range
					MS	SD	PC1	MS	SD	PC1	
AC1	<110a	45/52	2.14	0.940	0.142	0.160	35.8%	0.171	0.136	48.9%	1834–2642 m
AC2	110–210a	33/47	1.22	0.907	0.155	0.209	29.2%	0.162	0.134	43.3%	2150–2750 m
AC3	210–310a	15/	0.66	0.894	0.143	0.198	53.3%	0.160	0.131	57.4%	2550–2750 m
AC4	>310a	18/	0.36	0.903	0.169	0.186	32.9%	0.169	0.149	48.6%	2550–2750 m

Dendroclimatic analysis

Tree-ring statistics above may indirectly estimate the influence of climate, while a specific assessment of species growth patterns can be achieved by calculating specific climate–growth relationship parameters (Carrer and Urbinati, 2004; Yu et al., 2008; Wang et al., 2009). The relationship between climate and tree-ring widths, for the period 1956–2010, was investigated by bootstrapped response function analyses using the program PRECON (Briffa and Cook, 1990; Serre-Bachet and Tessier, 1990; Guiot and Goeury, 1996; Fritts, 1998, 1999). Since temperature and precipitation in months that precede the growing season often influence tree growth (Fritts, 1976; Yadav and Singh, 2002), temperature and precipitation beginning in May of the previous growth year until September of the current growth year were used for analysis.

To determine climate influence within different ACs more efficiently, an ANOVA *F*-test was used. In the ANOVA *F*-test, the response parameter r/s (the partial regression coefficients divided by their standard deviations) values were chosen. The r/s values were selected from the response function results from one type of tree-ring chronology, in which the results had a relatively clear climate–growth trend. To analyze climatic variables, r/s values were chosen that reached a significant level for at least one age class. ANOVA analysis was also used to test whether the trees belonging to dfferent sampling sites have different climate–growth response patterns.

We also analyzed the relationship between ages and response function parameters of individual trees (r/s and R^2 (coefficient of determination)) which concisely displayed evident climate variability retained in their tree-ring widths. Simultaneously, linear regressions were performed to fit the variation trend with increasing age.

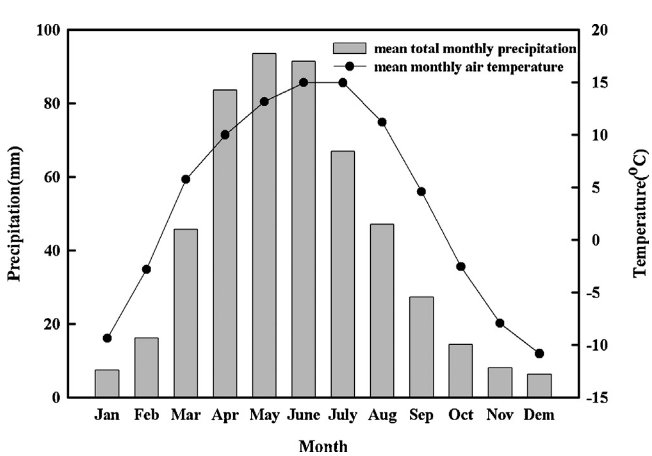

Fig. 2. Climate graph for mean monthly air temperature (°C) and mean total monthly precipitation (mm) of Zhaosu station.

Results

The statistics of tree-ring width chronology

Chronology statistics are summarized in Table 1. The mean raw width (MRW) shows a biological-geometrical trend decreasing with age, which is in agreement with other studies. Values of mean sensitivities (MS) are higher and homogeneous in residual chronologies, which indicate the considerable common high-frequency variation response. Standard deviations (SDs) increase at the beginning then decrease with the increasing age in standard chronologies. However, SDs displays highly homogeneous values in the four age classes in residual chronologies. The EPS values

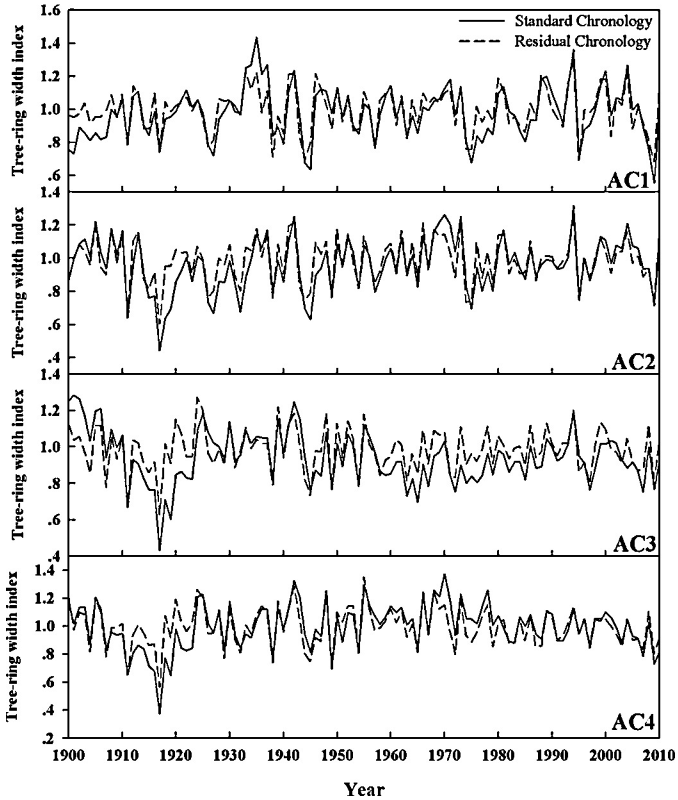

Fig. 3. Standard and residual tree-ring width chronologies for Schrenk Spruce are shown in the upper panel from four age classes.

were all above 0.85, which indicates that the age class chronology is reliable for further analysis. High PC1 values indicate that residual chronology may contain considerable short term variation compared to standard chronology. In general, values from standard chronology contain variability among different age classes, while values from residual chronology exhibit higher consistency in the four age classes.

Standard chronologies correlation analysis between age classes over the time period (1900–2010) suggested that there are different physiological processes between young and old trees (Table 2). A high correlation between AC1 and AC2, AC3 and AC4 was observed, but for AC1 and AC3, AC1 and AC4 it is lower (Table 2). However, the residual chronologies correlation analysis has a higher correlation coefficient compared to that for the standard chronology, which indicates considerable common responses in high frequency information in the four age classes. Tree-ring width index from the two types of chronologies indicate a similar growth pattern among age classes in the common period (Fig. 3). Growth variability is highly consistent among AC1 and AC2, as well as AC3 and AC4. For example, during 1900–1910 and 1930–1940, young trees (AC1 and AC2) exhibit a persistent increase in radial width, while older trees maintained constant growth or showed a decline.

Tree ring growth–climate relationship

Response function (RF) analysis reflects (Table 3) that climate accounts for a high amount of variance (up to 50%) in tree-ring width. Compared with ACs of standard chronology, residual chronologies have higher values for variance explanation especially in AC1. Mean V-climates (percentage of the variance in the tree-ring width explained by climatic factors) attain 0.4838 and 0.4910 respectively for the ACs contained in the two types of chronology, while the values of mean V-growth (percentage of the variance in the tree-ring width explained by previous year's growth) are only 0.0264 and 0.0154 respectively, which indicate a very small contribution to the variance in radial growth.

The parameters V-climate, V-growth and R^2 were compared for different age-class chronologies among standard and residual chronology (Table 3). For standard chronology, the variance explained by the climate decreases substantially from AC1 to AC4 in a twofold pattern. The V-climate value increases for trees younger than 200 years and decreases or is constant in older trees (from 0.5801 to 0.3649). V-growth is much higher in AC1 and R^2 values change greatly for all ACs. For residual chronology, V-climate values indicate that AC1 contains more climate-driven information. The variance explained by prior radial growth is relatively low as indicated by using autoregressive modeling. The R^2 indicates a clear distinction between younger trees (AC1 and AC2) and old trees (AC3 and AC4). RF parameters remain higher than the standard chronology in AC1 and AC2, but in AC3 and AC4 the RF values does not reach a significant level for the same climate variables.

The RF analysis shows that the influence of climate on tree-ring growth is mainly concentrated in later winter and early spring (Fig. 4). The climate variables which produce significant impact on tree growth are consistent among the two types of chronologies. The tree-ring growth index from the standard chronology has a significant positive correlation with the mean monthly air temperature of the previous August (r/s = 2.1, AC1) and November (r/s = 2.3, AC1), and with total monthly precipitation of the previous June (r/s = 2.5, AC2) and current April (r/s = 2.2, AC2). It is negatively correlated with the mean monthly air temperature of the previous June (r/s = −2.3, AC2) and December (r/s = −2.5, AC4). Yet for residual chronology, there is a significant negative relationship with the mean monthly air temperature of the previous June (r/s = −2.3, AC1) and current March (r/s = −2.5, AC4), and with total monthly precipitation of the current August (r/s = −2.4, AC2), and a positive correlation with total monthly precipitation of the previous August (r/s = 2.3, AC1), current April (r/s = 2.5, AC1) and May (r/s = 2.1, AC2). The above higher response r/s values from the residual chronology indicate that the four high-frequency age-class chronologies contain considerable common climate responses. Both the standard chronology and residual chronology revealed that AC1 and AC2 are the highest climate sensitive age classes. The response results demonstrated that total monthly precipitation of the current year months (March, April and May) prior to the growing season has significant positive impacts on radial growth. From the RF analysis, we can conclude that radial growth is intensively influenced by both moisture conditions and lower temperatures before the growing season in this region. Comparing the chronology statistics and response function analysis in the two types of chronology, the results indicate that the standard chronology has a clear climate-driven trend resulting from increasing tree age, while the residual chronology shows considerable and homogeneous high-frequency variations in climate among the four age classes. Therefore, the standard chronology analysis results were continually used to detect the stability of long term climate variation with increasing age in the following analysis.

ANOVA analysis

The results of an ANOVA *F*-test (Table 4) show that there are significant differences between the non-adjacent age classes, in line with the above correction matrix analysis (Table 2). Three variables (mean monthly air temperature of the previous December, monthly precipitation of the current April and R^2) show very significant differences ($P < 0.005$) among the ACs, with the highest *F* value for the R^2. These significant differences between older and young trees

Table 2
Correlation matrix between the standard and residual ring-width chronologies for the four age classes, 1900–2010.

ACs	Standard chronology			Residual chronology		
	AC1	AC2	AC3	AC1	AC2	AC3
AC2	0.652**			0.829**		
AC3	0.251**	0.503**		0.534**	0.717**	
AC4	0.252**	0.540**	0.622**	0.458**	0.689**	0.863**

** Correlation is significant at the 0.01 level.

Table 3
Growth–climate relationships.

ACs	AGE	Standard chronology			Residual chronology		
		V-climate	V-growth	RSQ	V-climate	V-growth	RSQ
AC1	<110a	0.5474	0.0619	0.7383	0.6072	0.0001	0.7218
AC2	110–210a	0.5801	0.0119	0.6816	0.5572	0.0264	0.7010
AC3	210–310a	0.3649	0.0252	0.5637	0.3842	0.0179	0.5509
AC4	>310a	0.4428	0.0066	0.6111	0.4155	0.0172	0.6024
Mean		0.4838	0.0264	0.6487	0.4910	0.0154	0.6440

RSQ is coefficient of determination.

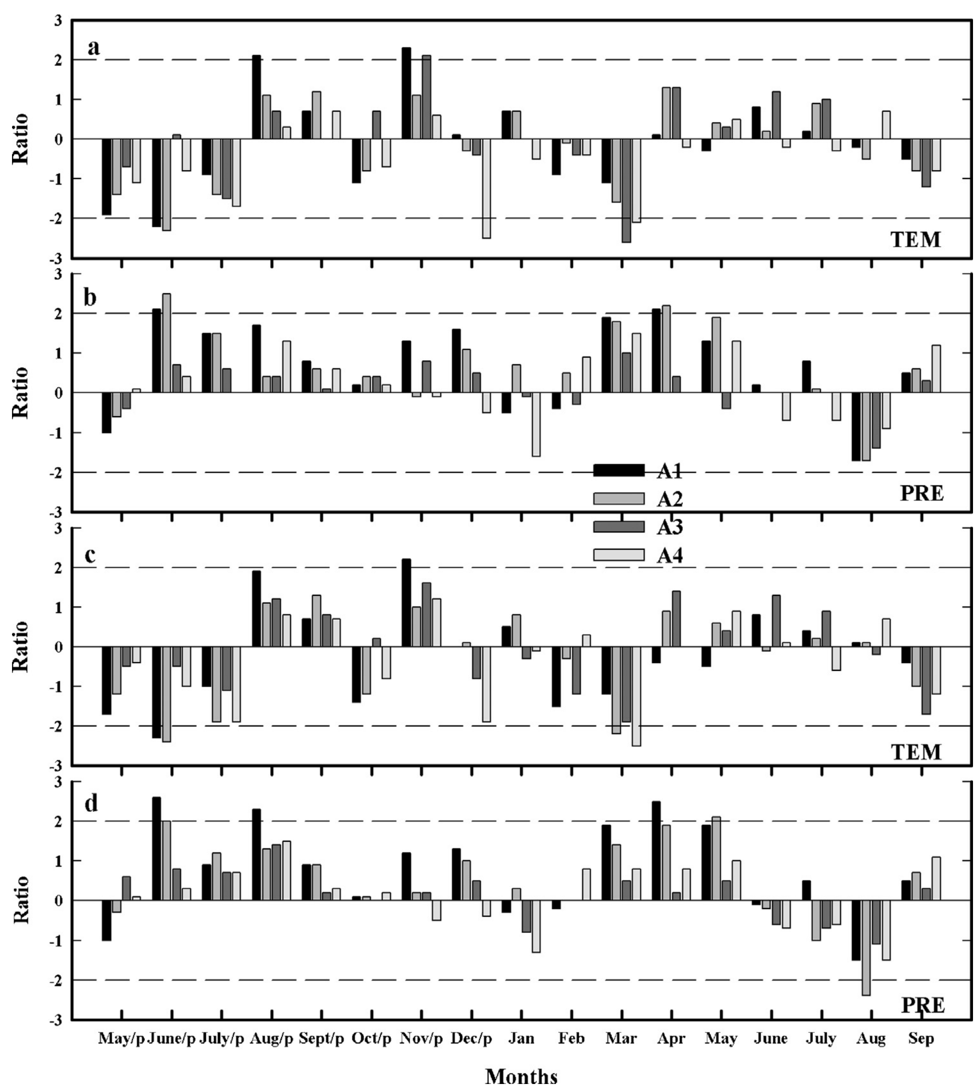

Fig. 4. Age–class response functions for standard chronology in a and b; age–class response functions for residual chronology in c and d (ratio, the partial regression coefficients divided by their standard deviations obtained after the 1000 bootstrap replications).

Table 4
Results of ANOVA analysis for the selected climatic variables.

Variable	F	1 vs. 2	1 vs. 3	1 vs. 4	2 vs. 3	2 vs. 4	3 vs. 4
Tem-June/p	1.504	0.187	0.529	0.408	0.129	0.077	0.905
Tem-August/p	0.107	0.761	0.610	0.987	0.769	0.812	0.659
Tem-November/p	2.601	0.104	0.148	0.282	0.012*	0.892	0.041*
Tem-December/p	4.645***	0.792	0.678	0.000***	0.820	0.001***	0.016*
Tem-March	4.043**	0.279	0.008**	0.007**	0.06	0.059	0.922
Pre-June/p	3.564*	0.009**	0.860	0.400	0.105	0.007**	0.420
Pre-April	5.368***	0.186	0.029*	0.023*	0.003***	0.002***	0.960
R^2	6.522***	0.000***	0.554	0.211	0.019*	0.055	0.628

Age classes are coded from 1 (youngest) to 4 (oldest). The degrees of freedom of the among-groups and within-groups comparisons are 3, 129.
* P, 0.05.
** P, 0.01.
*** P, 0.005.

indicate that the climate–growth relationship may have divergence among different age classes in the crucial growth periods especially before the growing season. In terms of R^2, significant difference was found between the two younger age classes. It may also be concluded that the lag climate effects show little significant difference between all age classes. The results of ANOVA analysis for different sites showed that the climate–growth response parameter *r*/*s* for the same climatic variable among all sites did not have significant differences ($P > 0.05$).

The ANOVA-*F* test indicates that the current year climate variables significantly influenced the tree-ring radial growth–climate relationship. In terms of different age classes, trees displayed inconsistent responses to climate variables.

Age effect analysis for individual tree

The results of scatter plots (Fig. 5) of tree age versus response function parameters show that the overall trends are of significant negative linear relation ($P < 0.05$), especially for monthly precipitation of the current April, mean monthly air temperature of the previous December and current March. But the relationships for other climate variables display either positive, very weak, or even nonexistent. An implication is that climate–growth relationships may be intensified in crucial growth periods. In terms of individual trees, the results of scatter plots of tree age versus R^2 vary little since negative and positive growth trends are evident among the individual trees (Carrer, 2011).

Scatter plot and linear regressions (Fig. 5) may not contain enough explanation of climate variance. However, they simply indicate that there is a significant negative growth trend among four age classes in certain months.

Discussion and conclusion

In this study, we demonstrated that the growth responses of Schrenk spruce to climate are related to tree age, as well as different growth patterns exist in this species. Younger trees are sensitive to climate change influences and favorable climate conditions may facilitate their radial growth, while older trees may be insensitive to climate change as the adjustments of growth strategies under stressed climate conditions. This is not in line with other studies on tree-ring age effects in other species, which found greater climatic sensitivity in older trees as a decrease in the efficiency of water transport caused by increased hydraulic resistance (Szeicz and MacDonald, 1994; Ettl and Peterson, 1995; Ryan et al., 1997; Carrer and Urbinati, 2004). In addition, the RMW values decreased with age (Table 1), which can be explained by the amount of new wood added each year being constant while the circumference increases (Nash et al., 1975; Yu et al., 2008). This long-term growth pattern related to the advancing tree age is typical in all trees (Fritts, 1976).

Schrenk spruce displays a sensitivity reduction to total precipitation in spring when they are older than 200 years (Fig. 4). It may be the decline of growth rate which leads to a reduction of resources and water need for trees (Carrer and Urbinati, 2004; Rozas et al., 2008). In addition, cambium division and postcambial growth are closely connected so that delays in cell growth pronouncedly lead to a response sensitivity reduction for older trees (Tuominen et al., 1997; Uggla et al., 1998; Rossi et al., 2008). Some research has demonstrated that the greatest change affecting the water status of a tree as it grows larger in semiarid regions is the development of a more efficient root system that may provide the access to water in deep soil layers (Fritts, 1976; Kozlowski and Pallardy, 1997). Young trees (<210a) with less efficient root systems are less able to tap the available water and become water-limited, while older trees with extensive root systems may tap deeper water sources, allowing them to have higher rates of transpiration and photosynthesis (Bond, 2000). However, a distinct area limitation existing in climate–growth relationships have been detected. For example, climate sensitivity has no large discrepancies among age classes in moist areas (Linderholm and Linderholm, 2004), while there is a decline in water using efficiency with increasing ages in water-limited areas (Yu et al., 2008). Interestingly, earlywood and latewood displayed opposite responses to the same climatic factors in the distinctive Mediterranean climate (Vieira et al., 2009). Therefore, we proposed that climate–growth relationships are site-specific, and should be taken into account in future dendroclimatological studies (Wang et al., 2009). Other investigations have also pointed out that site differences might modify the manner of age-dependent responses (Fritts, 1976; Szeicz and MacDonald, 1994).

Compared with responses to precipitation, the influence of temperature on climate–growth relationships was complicated. Among four age classes, the oldest age classes showed a significantly negative relationship with the temperature before the growing season, while younger age classes have a significantly negative relationship with the temperature in previous growing season. These different response functions are related to different physiological processes connected to tree age. Young trees at early stages of growth often operate "overspending" strategies to ensure the growth potential necessary for tree establishment (Carrer and Urbinati, 2004). The over-spending capacity may be decided by the prior year's growth and nutrition, while a reduction in photosynthesis and growth would be expected due to high temperature alone (Meinzer et al., 2011). As a consequence, growth of young trees exhibits a significantly negative relationship with the temperature in previous growing season which may ensure that enough nutrition serves for rapid tree growth in the current year. However, the oldest trees with a relatively lower growth rate were

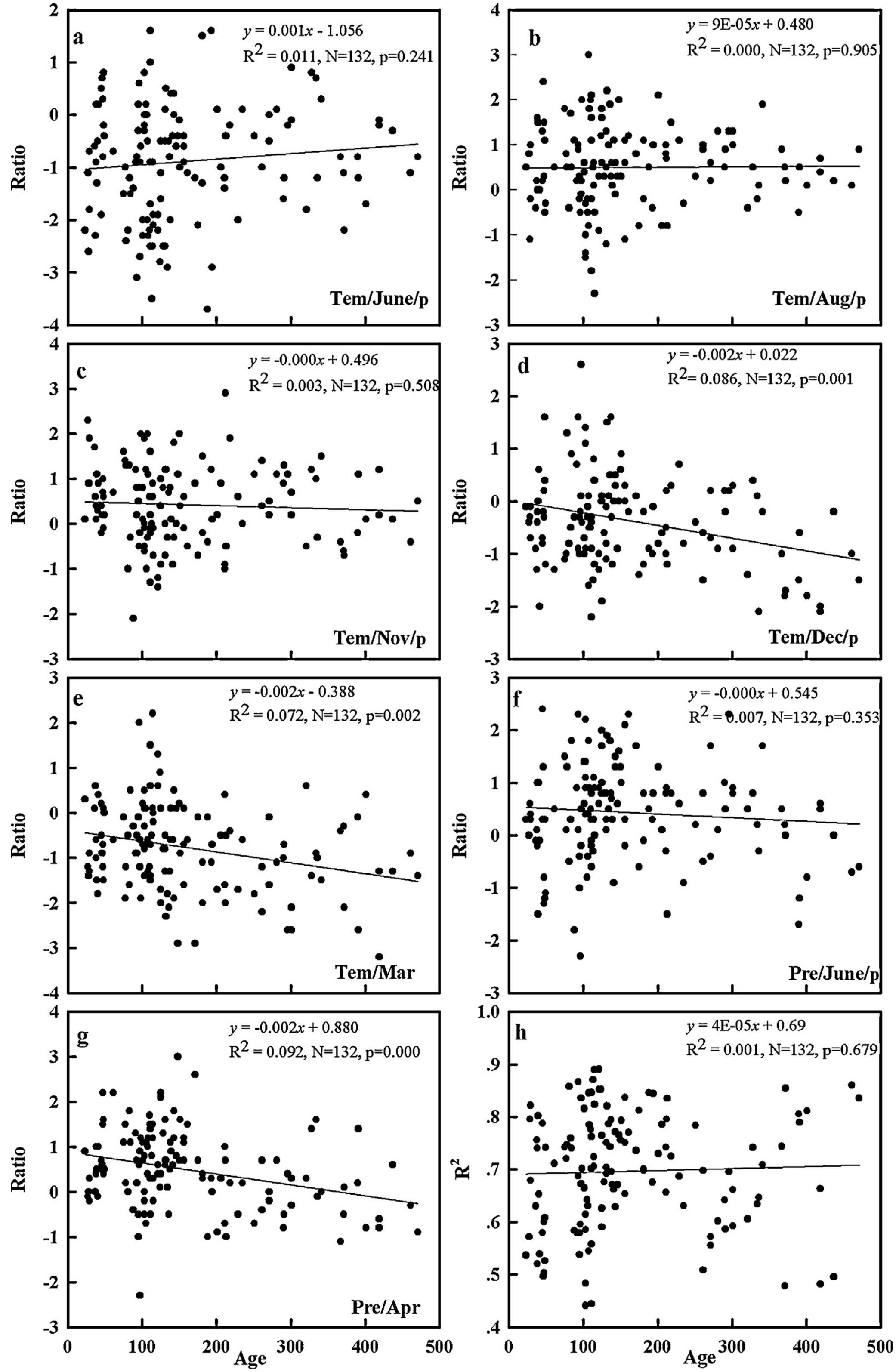

Fig. 5. Scatter plot for tree age versus response function relationships. Response function parameter (*r*/*s*) of selected temperature variables in a–e, selected precipitation variables in e and f and coefficient of determination (R^2) in h (tem: temperature, pre: precipitation, *r*/*s*: the partial regression coefficients divided by their standard deviations obtained after the 1000 bootstrap replications).

significantly positively correlated with low temperature before the growing season. Low temperature could ensure that snow persists longer into spring and reduce nutritive loss caused by respiration, thus guaranteeing ample water and nutrition resource needed for old trees' growth.

Both the standard and residual chronology analysis demonstrates that differences in climate–growth relationships exist in the four age classes. The standard chronology indicates that long-term variation impacts differentially on the changing growth potential of trees with increasing age (Fritts, 1976). In terms of high-frequency variation, the residual chronology displays homogeneity on common changes in the groups. The chronology characteristics and correlation matrix demonstrate (Tables 1 and 2) that the residual chronology contains considerable common environmental information than the standard chronology. However, the response function analysis shows that climate factors before the growing season may both influence the high-frequency and low-frequency variations in tree-ring growth in this region (Fig. 4). Consequently, the different response patterns in the four age classes may indicate that radial growth–climate relationships change with the increasing age.

Scatter plot and linear regressions analysis for individual trees (Fig. 5) indicated a generally negative trend for the climate variables with increasing age, which may be coincident with the mean chronology response results. However, in each linear regression analysis the slope and R^2 (coefficient of determination) is relatively low (Fig. 5), indicating that age variance explanation may weaken in the climate–growth relationship for per tree. It may be that the natural ontogenetic dynamics of trees influence the ability to record climatic variability in tree-ring sequences (Carrer, 2011). Individual tree may deviate markedly and systematically from the mean chronology due to differences in soil factors, competition, microclimate and other factors (Fritts, 1976). The results may explain why mean age–class chronology has divergence on response results but in core chronology the age effect is weak.

In conclusion, climate–growth relationships were partially controlled by age. Compared with older trees, we observed that younger trees generally exhibit a greater climate response, in contrast to previous studies (Carrer and Urbinati, 2004; Yu et al., 2008; Wang et al., 2009; Copenheaver et al., 2011). Furthermore, different responses to temperature and precipitation were observed in the four age classes. Young trees (<210a) sensitive to drought-stressed conditions are a strong climate signal indicator of precipitation. For the oldest age classes, a lower temperature before the growing season has significant impacts on radial growth. The interpretation of this complicated growth pattern suggests that a uniform age effects model is inappropriate, and that age-dependent climate response was the integration of the age-related genetic controls and microclimate. In order to be exploited as a valid indicator of climate change, the ecology of tree-ring growth needs to receive more attention (Zhang and Shao, 2007). In addition, caution should be taken in applying models to other regions or species because of different living environments for various tree species. As with climate change, different species in different habitats are likely to have adapted to the changes associated with increasing age through diverse strategies (Day et al., 2002), which may lead to different age effects on climate responses. Consequently, space-specific age effect patterns may influence both the prediction of climate change and the accuracy of reconstructed climate data.

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