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Age-Effect Radial Growth Responses of *Picea schrenkiana* to Climate Change in the Eastern Tianshan Mountains, Northwest China

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Received: 22 June 2017; Accepted: 10 August 2017; Published: 26 August 2017

Abstract: The climate changed from warm-dry to warm-wet during the 1960s in northwest China. However, the effects of climate change on the response of radial growth from different age-class trees have been unclear. We assessed the age-effect radial growth responses in three age-classes (ml-old: \geq 200 years, ml-middle: 100–200 years and ml-young: <100 years) of Schrenk spruce (*Picea schrenkiana* Fisch. et Mey.) in the eastern Tianshan Mountains. The primary conclusions were as follows: the developed chronologies of the three age-class trees contained significant climate information and exhibited high similarity as shown by calculating the statistical parameter characteristics and Gleichlaufigkeit index. The three age-class trees were consistent for annual variation trends of radial growth under climate change, showing similar fluctuations, tree-ring width chronology trends, time trends of cumulative radial growth, and basal area increment. In addition, the old and middle trees were found to be more sensitive to climate variability by analyzing Pearson correlations between radial growth from three age-class trees and climate factors. As a result, the drought caused by reduced total precipitation and higher mean temperature was a limiting factor of tree radial growth, and the trees with ages of up to 100 years were more suitable for studies on the growth-climate relationships. Thus, the studies on age-effect radial growth responses of Schrenk spruce can help not only in understanding the adaptive strategies of different-age trees to climate change, but also provide an accurate basis for climate reconstruction.

Keywords: climate change; radial growth response; age-effects; drought stress; eastern Tianshan Mountains

1. Introduction

Tree growth is an irreversible process, and the size and growth rates of trees are affected by external environmental factors, such as climate condition, altitude, location slope, slope direction, and historical interference mechanisms. Growth is also controlled by biological characteristics and genetic factors, including species, life, age, competition, and sensitivity [1,2]. Through the informed choice of sample trees, available settings and a thorough dendroclimatology research process, the effects of noise, such as forest disturbance and competition, on tree growth trends can usually be avoided. The climatic signals of tree-ring chronologies could also be maximally retained, and the age-related growth trends could be extracted by the appropriately detrended methods. This approach could

establish radial growth-climate relationships to explore the effects of climate change on tree growth and the responses of radial growth to the main climate factors [3]. According to study results of tree physiology and biology, age is not only intuitively reflected in tree growth increments, but could also indirectly affect trees responses to environmental factors due to different photosynthesis efficiency, hydraulic conductance, and nutrients transport [4]. In other words, tree age could interfere with the expression of environmental signals related to radial growth, and the age effect is not completely eliminated from the chronologies.

Traditional dendrochronological studies posited that the age-dependent radial growth responses to climate factors did not exist after the raw tree-ring chronologies were detrended. In agreement with this hypothesis, several studies have confirmed that the responses of radial growth from different age-class trees were relatively stable, such as in *Larix lyallii* Parl. in the Banff-Kananaskis area of the southern Canadian Rockies, *Betula lenta* L. in the New England Black Birch, *Sabina przewalskii* Kom. in the Qinghai-Tibetan Plateau, and *Pinus tabulaeformis* Carrière in the eastern Loess Plateau of North China [5–8].

In contrast to this general hypothesis, sensitivity of radial growth to climate depending on age has been reported. For example, the growth responses of Abies lasiocarpa (Hook.) Nutt. from different age-class trees were different depending on climate factors in the Olympic Mountains, WA, USA [9]. Meanwhile, it is still disputed whether young trees or old trees are more sensitive to climate. The old trees of *Pinus sylvestris* L. (>250 years) were more sensitive to climate than the middle-aged and young pines [10]. Fang et al. [11] also found old trees were more sensitive to drought than the young trees over the Chinese Loess Plateau. In contrast, climatic sensitivity decreased with increasing age for *Juniperus thurifera* L. in north-central Spain [12]. The sensitivity of the radial growth response for Araucaria araucana (Molina) K. Koch to climate varies but was the strongest in the rings of young trees from xeric sites in Patagonia, Argentina [13]. Furthermore, the responses of the different-age trees to climate factors are also different. The younger age-class trees for *Pinus bungeana* Zucc. responded better to temperature, but the older and middle-aged trees had a better response to precipitation in the Shennong Mountains of China [14]. Therefore, age-dependent radial growth responses to climate change are still under discussion by scientists [4,9-14]; the growth-climate relationship results of an age-effect may change with different species and different regions, which supports the need for further research on age-effects of climate change [15].

Global warming is a world-wide problem with important implications to forest management [16]. Observed data showed a climatic transition from warm-dry to warm-wet in Xinjiang of northwest China during the 1960s, which was a change that likely affected the dynamics of forest ecosystems in the Tianshan Mountains [17]. It is very difficult to predict the impacts of climate change on forest productivity and stability due to potential disturbances in composition, density and age structure over time [18]. Because the responses of the different-age trees to environmental changes vary due to differences in physiological characteristics, the age-effect of radial growth must be considered in dendroclimatology research [19]. Furthermore, several studies have obtained evidence that younger trees of Schrenk spruce (Picea schrenkiana Fisch. et Mey.) exhibit more significant responses to climate factors than do older trees in western and central Tianshan Mountains [20,21]. However, compared to the western and central Tianshan Mountains, the eastern Tianshan Mountains are the driest regions and are ideal for studying the age-effect radial growth responses [22]. Our studies focused on accurately assessing the stability of the radial growth-climate relationships, understanding the physiological and ecological characteristics of trees under climate change and choosing the appropriate age-class trees to carry out dendroclimatology research in arid and semi-arid areas. The main aims of this study were (1) to develop tree-ring width chronologies from three age-classes of Schrenk spruce and determine the quality of chronologies, (2) to assess the effects of climate change on the radial growth patterns of three age-classes of trees, and (3) to detect age-effects of trees on growth-climate relationships in the eastern Tianshan Mountains.

2. Materials and Methods

2.1. Study Area

The study area is on the north slope of the eastern Tianshan Mountains in northwest China, a region dominated by the cold and drought of the temperate semiarid continental climate with the central Asian westerly circulation (Figure 1). Moisture and heat were synchronous. The total annual precipitation was 188.31 mm, with 70.0% falling from April to September during the years 1959–2012 (Figure 2A). The mean annual temperature was 5.2 °C, the hottest mean month temperature (July) was 23.0 °C, and the coldest mean month temperature (January) was -17.5 °C (Figure 2A). The trend of total annual precipitation and mean annual temperature significantly increased (total annual precipitation: 8.88 mm/10a, *p* = 0.040; mean annual temperature: 0.18 °C/10a, *P* = 0.005) according to linear regression model of recorded climate data over the period 1959–2012 (Figure 2B). Schrenk spruce is an evergreen and dominant species in the study area, occurring on the shady slopes of elevations 1950–2600 m [23]. Meanwhile, Schrenk spruce is also a climate-sensitive species and very suitable for analyzing growth-climate relationships [24,25].

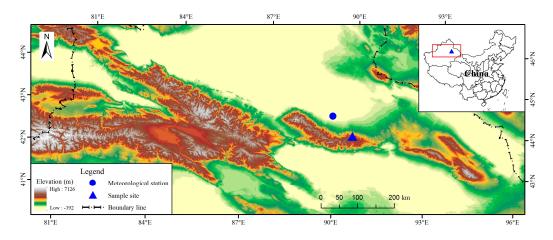


Figure 1. Locations of the study area and the nearest meteorological station (Tianshan Mountains).

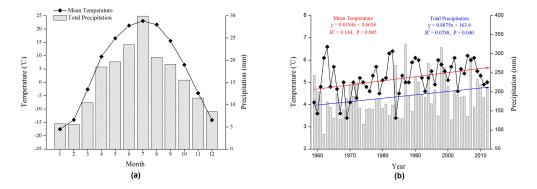


Figure 2. Mean temperature and total precipitation during 1960–2012 using the records from the Qitai meteorological station, northwest China. (**a**) Monthly total precipitation and mean temperature averaged; (**b**) Variation trends of annual total precipitation and mean temperature; the lines with arrows represent the simulated trends by linear regression.

2.2. Climate Data

Precipitation and temperature data were obtained from the Qitai meteorological station (44°01′ N, 89°34′ E, 793.5 m a.s.l.) closest to the study region (approximately 70 km) (Figure 1). Although the values of climate data are different along elevation gradients, the patterns of interannual variability

were mainly controlled by the single climate of westerly circulation, which is suitable for assessing the general tree growth-climate relationships in Tianshan Mountain [26,27]. Based on a number of dendrochronology studies and the principles of tree physiology, tree growth was affected not only by the climatic conditions of the current year but also by those of the previous year [3]; therefore, the monthly climate data from June of the previous year to September of the current year were used for growth-climate relationship analysis. The monthly standardized precipitation evapotranspiration index (SPEI) has advantages over other drought indices, and is calculated using climate data of precipitation, temperature, relative humidity, solar radiation, water vapor pressure, and wind speed with the SPEI calculator [28]. Negative SPEI values correspond to dry conditions and positive represent wet conditions. The relationships between the radial growth of trees and the drought indices of SPEI were analyzed. Positive coefficients indicate better growing conditions without drought, whereas negative coefficients indicate growth increment during dry conditions.

2.3. Field Sampling, Tree Age-Class Divisions and Tree-Ring Chronology Development

The tree-ring samples of Schrenk spruce were collected on the northern slope near the forest line in Mulei Kazakh Autonomous County (43°35.016′ N, 90°14.416′ E), where were the altitude of 2352 m a.s.l., the exposure of north by east 10°, the slope of 10%, the canopy coverage of 20%, the average tree distance of 2.5 m, the average tree height and crown width of 11.8 m and 2.6 m, and the average diameter at breast height of 31.3 cm. The sample trees were allocated to three classes according to the diameter size, with 20 healthy trees located in isolated conditions in each class. Two cores per tree were extracted at a height of 1.3 m at 120° from each other with a 5.15-mm-diameter increment borer. A total of 120 cores from 60 living trees were collected in July 2013.

In the laboratory, tree cores were air-dried, mounted on woody supports, and polished with 120-, 400-, and 600-grit sandpapers until there were clearly visible boundaries of tree-rings for identification. Tree age analysis demands cores that include tree bark vertical to the pith, and two series were excluded from the master chronology because they did not reach the pith. According to the physiological habits of Schrenk spruce and the growth-climate relationship of trees, 100 years was considered to be an ideal classification interval [19,29]. The tree cores collected were divided into three age classes based on 100 years increment: the young class with tree age less than 100 years (Abbr.: ml-young, mean age of 81 years), the middle class with tree age greater than 200 years (Abbr.: ml-middle, mean age of 126 years), and the old class with tree age greater than 200 years (Abbr.: ml-old, mean age of 242 years, Table 1).

Dendrochronological Parameters	ml-old	ml-middle	ml-young
Sample depth (cores/trees)	40/20	40/20	36/18
Chronology length: Starting–End year (Total years)	1684-2012 (329)	1845-2012 (168)	1915-2012 (98)
Mean age	242	126	81
MRW (Mean raw width of chronology)	0.683	1.331	1.788
MS (Mean sensitivity)	0.219	0.212	0.150
SD (Standard deviation)	0.226	0.190	0.131
AC1 (First-Order serial autocorrelation)	-0.132	-0.110	-0.169
R (Mean correlation of all series)	0.365	0.479	0.441
R1 (Within-trees)	0.643	0.645	0.732
R2 (Between-trees)	0.345	0.467	0.417
PC1 (Variance in the first principal comment)	0.413	0.520	0.488
SNR (Signal to noise ratio)	9.209	14.690	11.052
EPS (Expressed population signal)	0.902	0.936	0.917

Table 1. Dendrochronological characteristics of Schrenk spruce tree-ring width chronologies from three age-classes of trees during 1960–2012 in the eastern Tianshan Mountains, northwest China.

Tree-ring width was measured with 0.001 mm resolution using the LINTAB measurement system (TM5, Rinntech, Heidelberg, Germany). The quality of the cross-dating was tested using the COFECHA program [30]. The raw tree-ring width series of three age-classes of trees were detrended by the negative

exponential curve or by linear regression, and the standard chronologies (STD), the residual chronology (RES) and the arstan chronology (ARS) removing non-climatic growth effects were subsequently developed utilizing the ARSTAN program [31]. The tree-ring width chronology containing more high-frequency signals is better in assessing climate-growth relationships [32]. Given the above, we selected the residual chronology for the analysis of the radial growth responses of different age-class trees to climate change. Some dendrochronological statistical parameters were calculated for assessing the quality and reliability of the chronologies from three age-class trees (common period: 1960–2012), including the mean sensitivity (MS), the standard deviation (SD), the first-order serial autocorrelation (AC1), the mean correlation (R), the variance in the first principal comment (PC1), the signal to noise ratio (SNR), and the expressed population signal (EPS, Table 1) [33,34].

2.4. Analysis of Radial Growth Characteristics from Different Age-Class Trees

The radial growth characteristics of different age-class trees could be analyzed by the correlation among the chronologies and the change of growth trend. The correlation could not only compare discrepancies of radial growth characteristics from three age-classes of trees but could also analyze the different physiological processes of the old and young trees. The correlation analysis of three age-class chronologies was calculated with the Gleichlaufigkeit index (GLK), which has advantages in examining the similarity of two time series, and the percentage of total GLK represents the consistency of two chronological curves at a very high frequency [35].

The growth trends could depict the radial growth dynamic patterns and reflect similar or different responses of three age-classes of trees to the climate change, including the time trend of cumulative radial growth, the radial growth rate, the trend of tree-ring width residual chronologies and the basal area increment (BAI, $\text{cm}^2 \text{ yr}^{-1}$). In comparison with tree-ring chronology series, the BAI was suitable for evaluating the long-term radial growth trend of trees with the non-standardized raw measurement ring width data, especially as the decreasing trend in BAI represented an effective decline of tree growth under environmental stress [36,37]. The BAI was calculated [38]:

$$BAI_t = \pi \left(r^2_t - r^2_{t-1} \right), \tag{1}$$

where r_t is a given tree-ring corresponding to radial radius at year t, and r_{t-1} is a given tree-ring corresponding to radial radius at year t - 1.

2.5. Analysis of Relationship between the Radial Growth from Different Age-Class Trees and Climate Factors

To confirm the key climate factors limiting radial growth of different age-class trees, Pearson correlation coefficients were calculated between the tree-ring width chronologies and climate factors of mean temperature, total precipitation and SPEI from the previous June to the current September (the significant correlation represents p < 0.05) [3]. Moreover, the correlation coefficient variations between the chronologies of three age-classes of trees and the same climate factors were accurately evaluated by the *u* test method. The value of *u* is the quantile of a standard normal distribution [39]:

$$u = \frac{ln\left(\frac{1+r_1}{1-r_1}\right) - ln\left(\frac{1+r_2}{1-r_2}\right)}{2 \times \sqrt{\frac{1}{n_1-3} + \frac{1}{n_2-3}}}$$
(2)

where r_1 and r_2 represent the correlation coefficients between the tree-ring width chronologies and climate factors, and n_1 and n_2 represent the sample numbers in the two age-classes. If |u| > 1.96, the correlation coefficients exhibit significant variations (p < 0.05).

2.6. Testing Differences in Slopes of Regression Curves

In order to more accurately depict and fit the variation trend of climatic factors and the radial growth of trees during 1960–2012, we used linear regression analysis.

3. Results

3.1. Tree-Ring Chronology Characteristics from Different Age-Class Trees

The statistical parameter characteristics of the tree-ring width chronologies among the three age-class Schrenk spruce are shown in Table 1. Mean raw width of chronology (MRW) reflected the biological characteristics of tree growth, showing gradual decline with an increase in tree age. The MS and SD values increased with increasing tree age, that is, old trees were stronger in chronologies with inter-annual fluctuation than young trees. The AC1 values were negative, and ml-young value (0.169) was higher than ml-middle (0.110) and ml-old (0.132), suggesting that the radial growth of Schrenk spruce was easily affected by tree growth in the previous year, and the "lag effect" of climate had more profound effects on the young trees. In addition, the R and PC1 values of ml-middle were higher than ml-young and ml-old, demonstrating that change synchronicity of tree-ring width chronology was better. Additionally, the SNR values were high (ml-old: 9.209, ml-middle: 14.690 and ml-young: 11.052), which meant the three age-class chronologies. Thus, the tree-ring width chronologies from three age-class Schrenk spruce were highly reliable, and the old trees were more sensitive to climate change than young trees.

3.2. Consistency for Annual Variation Trend of Radial Growth from Different Age-Class Trees

3.2.1. Similarity of Tree-Ring Chronologies from Different Age-Class Trees

The similarities of the tree-ring chronologies from different age-class trees were compared by calculating the GLK indices (Table 2). The results indicated GLK values were 82.69% (ml-old and ml-middle, n = 53), 76.92% (ml-old and ml-young, n = 53) and 71.15% (ml-middle and ml-young, n = 53), suggesting that annual variation in trends of radial growth in three age-classes of trees had high similarity and further showing the radial growth in different age-class trees was affected by the same climatic conditions in the eastern Tianshan Mountains, especially in the old and middle-aged trees.

GLK	ml-old	ml-middle	ml-young
ml-old	100%	82.69% ***	76.92% ***
ml-middle		100%	71.15% **
ml-young			100%

Table 2. Gleichläufigkeit (GLK) correlation of chronologies from three age-classes of Schrenk spruce trees during 1960–2012 in the eastern Tianshan Mountains.

** represents significance at the 0.01 level; *** represents significance at the 0.001 level.

3.2.2. Radial Growth Trends from Different Age-Class Trees

The time trend of cumulative radial growth, boxplots of radial growth rate, the tree-ring width chronologies, and BAI from three age-classes of trees from 1960 to 2012 are shown in Figure 3. The time trend of cumulative radial growth of three age-classes of trees had the same significant increased trends and showed the ml-young > ml-middle > ml-old (Figure 3A). The radial growth rates of three age-classes of trees were positive, and the mean values of radial growth rate boxplots showed the ml-young (0.543 mm/10a) > ml-middle (0.377 mm/10a) > ml-old (0.240 mm/10a) (Figure 3B). The tree-ring width residual chronologies of three age-classes of trees had similar fluctuation, especially

in some feature years, such as the relatively wide rings in 1964, 1966, 1973, 1982, 1994, 1996, 2002, 2004, and 2010 and the relatively narrow rings in 1965, 1972, 1981, 1987, 1992, 1995, 2001, 2003, 2008, and 2011 (Figure 3C). The annual variation trends of BAI showed similar growth patterns from three age-classes of trees, which slowly increased at first, rapidly increased thereafter and finally showed the downward trends from 1960 to 2012 (Figure 3D).

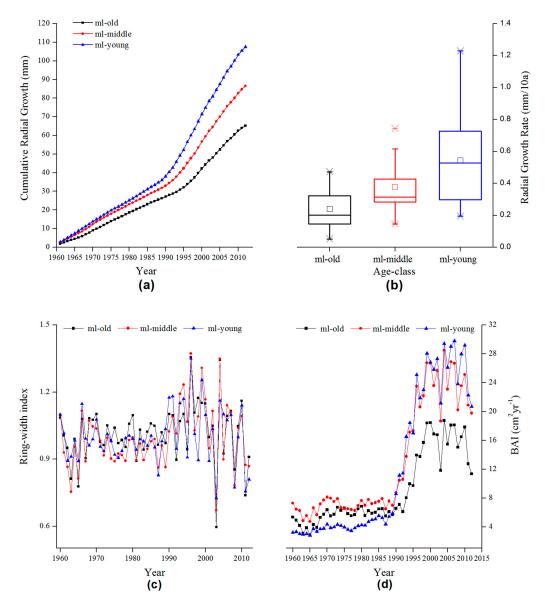


Figure 3. The trend of radial growth from three age-classes of Schrenk spruce trees during 1960–2012 in the eastern Tianshan Mountains (the black lines represent the old age-class of trees; the red lines represent the middle age-class of trees; the blue lines represent the young age-class of trees). (a) the time trend of cumulative radial growth (mm); (b) the boxplots of radial growth rate (mm/10a), the solid lines represent the median and the squares represent the mean radial growth rate; (c) the tree-ring width residual chronologies; and (d) the basal area increment (BAI, cm² yr⁻¹).

Moreover, the radial growth rates of three age-classes of trees were different in the three periods of 1960 to 1987, 1987 to 2004 and 2004 to 2012. The increased rate of BAI for ml-old (0.877 cm²/10a, p < 0.001) was faster than those for ml-young (0.735 cm²/10a, p < 0.001) and ml-middle (0.472 cm²/10a, p = 0.023) from 1960 to 1987; the increase of BAI for ml-young (14.848 cm²/10a, p < 0.001) was faster than those for ml-middle (13.052 cm²/10a, p < 0.001) and ml-old (8.363 cm²/10a, p < 0.001) from 1987 to

2004; but the decline of BAI for ml-middle ($-8.021 \text{ cm}^2/10a$, p = 0.037) and ml-young ($-7.967 \text{ cm}^2/10a$, p = 0.065) was faster than those for ml-old ($-6.665 \text{ cm}^2/10a$, p = 0.034) from 2004 to 2012 by fitting the linear regression equation (Figure 3D). Thus, the different age-class trees had the similar radial growth trends under climate change, but the declines of radial growth rates for young trees were faster than old trees in the recent ten years.

3.3. Relationships between Tree-Ring Width Chronologies of Different Age-Class Trees and Climate Factors

The growth-climate relationships were analyzed by Pearson correlations, which demonstrated that the radial growth rates from different age-class trees were largely driven by the total precipitation in non-growing seasons and the mean temperature in growing seasons (Figure 4).

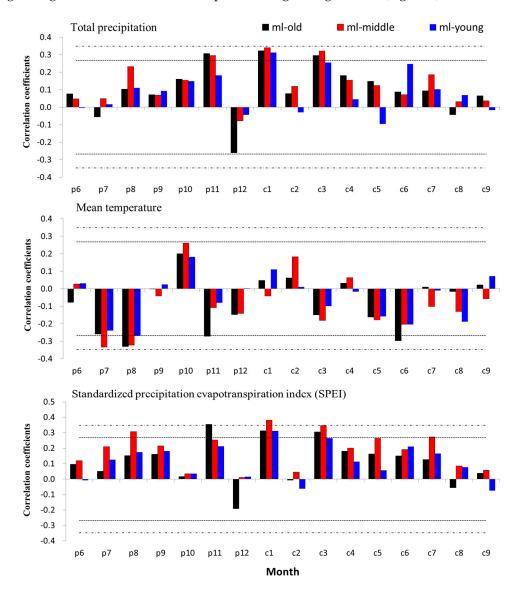


Figure 4. Correlations between tree-ring width chronologies from three age-classes of Schrenk spruce trees and monthly climate factors (total precipitation, mean temperature and SPEI) during 1960–2012 in the eastern Tianshan Mountains (The dotted lines represent significance at the 0.05 level and the straight lines represent significance at the 0.01 level. p: previous year, c: current year, Number: month, e.g., p6 represents June of the previous year and c1 represents January of the current year).

The tree-ring width chronologies for ml-old and ml-middle were significantly positively correlated with the total precipitation in November of the previous year (ml-old: r = 0.307, ml-middle: r = 0.290) and January (ml-old: r = 0.322, ml-middle: r = 0.340) and March (ml-old: r = 296, ml-middle: r = 0.320) of the current year. The tree-ring width chronology for ml-young was only significantly positively correlated with the total precipitation in January of the current year (r = 0.312).

The tree-ring width chronology for ml-old was significantly negatively correlated with mean temperatures in August (r = -0.331), November (r = -0.272) of the previous year and June of the current year (r = -0.297). The tree-ring width chronology for ml-middle was significantly negatively correlated with mean temperatures in July (r = -0.334) and August (r = -0.323) of the previous year. The tree-ring width chronology for ml-young was significantly negatively correlated with mean temperatures in August (r = -0.272) of the previous year.

Meanwhile, the tree-ring width chronology for ml-old exhibited positive responses to SPEI in November of the previous year (r = 0.355) and January (r = 0.313) and March (r = 0.305) of the current year. The tree-ring width chronology for ml-middle exhibited positive responses to SPEI in August of the previous year (r = 0.308) and January (r = 0.381), March (r = 0.347) and July (r = 0.274) of the current year. However, the tree-ring width chronology for ml-young exhibited only positive responses to SPEI in January of the current year (r = 0.313).

There were not significant discrepancies in the correlation coefficients between tree-ring width chronologies from three age-classes of trees and climate factors by u test (p > 0.05), which revealed that the radial growth activities of different age trees were consistent responses with climate change in the eastern Tianshan Mountains (Table 3).

Furthermore, the old and middle trees were more sensitive to climate factors than young trees based on certain response degrees (Figure 4). For example, the tree-ring width chronologies for old and middle trees were significantly positively correlated with the total precipitation in the previous November and the current March. Moreover, the tree-ring width chronology for old trees was also significantly negatively correlated with the mean temperatures in the previous November and the current June. However, young trees were not significantly correlated with climate factors in the previous November nor the current March and June. Thus, the drought was a limiting factor of radial growth from different age trees, and the old trees more suitable for studies than young trees.

3.4. Main Driving Factor of Interannual Variation of Radial Growth

Principal component analysis (PCA) is well-suited for evaluating consistency of climate signals containing chronologies and common growth patterns from different age-class trees because PCA can explain most of the variations with a few variables by compressing data and reducing dimension [8]. Table 4 extracted principal components of chronologies from three age-classes of trees, which showed that the contribution of the first principal component was 87.807%, and the contribution of the second principal component was 7.829%. The first principal component explaining major variations of three age-class chronologies was considered the climate information. The second principal components explained less variation but also embodied the differences between different aged trees.

Age Class	Climate Factor	p ⁴ 6 ⁶	p7	p8	p9	p10	p11	p12	c ⁵ 1	c2	c3	c4	c5	с6	c7	c8	c9
ml-old vs. ml-middle	P ¹ T ² SPEI ³	$0.144 \\ -0.527 \\ -0.119$	-0.525 0.406 -0.804	$-0.669 \\ -0.043 \\ -0.826$	0.013 0.207 -0.279	$0.033 \\ -0.321 \\ -0.098$	$0.062 \\ -0.852 \\ 0.566$	-0.943 -0.032 -1.030	-0.098 0.448 -0.389	-0.214 -0.618 -0.263	-0.136 0.163 -0.232	$0.144 \\ -0.160 \\ -0.102$	0.123 0.079 -0.534	$0.080 \\ -0.497 \\ -0.215$	-0.463 0.558 -0.767	-0.371 0.572 -0.705	$0.150 \\ 0.396 \\ -0.106$
ml-middle vs. ml-young	P T SPEI	$0.258 \\ -0.020 \\ 0.639$	$0.162 \\ -0.519 \\ 0.430$	0.633 -0.291 0.714	$-0.124 \\ -0.331 \\ 0.176$	$0.031 \\ 0.417 \\ -0.005$	$0.605 \\ -0.142 \\ 0.215$	-0.174 -0.723 -0.020	$0.154 \\ -0.768 \\ 0.388$	0.746 0.872 0.537	$0.353 \\ -0.422 \\ 0.451$	0.550 0.401 0.450	$1.109 \\ -0.100 \\ 1.072$	-0.904 0.001 -0.099	$0.422 \\ -0.455 \\ 0.567$	$-0.185 \\ 0.301 \\ 0.038$	$0.265 \\ -0.652 \\ 0.670$
ml-old vs. ml-young	P T SPEI	$0.402 \\ -0.547 \\ 0.521$	-0.363 -0.113 -0.374	$-0.036 \\ -0.334 \\ -0.112$	-0.111 -0.123 -0.103	0.064 0.096 -0.103	0.666 -0.993 0.781	-1.117 -0.755 -1.050	0.057 -0.319 -0.001	0.532 0.254 0.274	$0.217 \\ -0.260 \\ 0.218$	0.694 0.241 0.348	$1.232 \\ -0.021 \\ 0.537$	-0.823 -0.496 -0.315	-0.041 0.104 -0.200	-0.556 0.873 -0.666	$0.415 \\ -0.257 \\ 0.564$

Table 3. Discrepancies in correlation coefficients between tree-ring width chronologies from three age-classes of Schrenk spruce trees and monthly climate factors by calculating the value of u (the quantile of standard normal distribution by u test method) during 1960–2012 in the eastern Tianshan Mountains.

¹ P: Total precipitation; ² T: Mean temperature; ³ SPEI: standardized precipitation evapotranspiration index; ⁴ p: previous year; ⁵ c: current year; ⁶ Number: month, e.g., p6 represents June of the previous year and c1 represents January of the current year.

Table 4. Principal component analysis (PCA) of the tree-ring width chronologies from three age-classes of Schrenk spruce trees in the eastern Tianshan Mountains.

Principal Component	Eigenvalue	Variance (%)	Cumulative Variance (%)			
1	2.634	87.807	87.807			
2	0.235	7.829	95.636			
3	0.131	4.364	100.000			

4. Discussion

4.1. Age-Effect on Tree-Ring Chronology Characteristic Parameters

There is considerable complexity in identifying climate signals with tree-rings, primarily because tree-ring width is controlled by climate variability, as well as trends of biological growth [40]. However, recently, several studies on dendrochronology and tree physiology found that the detrended chronologies would still retain the age signals due to different physiological processes of young and old trees [41,42]. Therefore, it is worthwhile to conduct more research on age-effect radial growth responses to climate change to increase accuracy of climate reconstructions and growth-climate relationships based on tree-ring data.

Dendrochronological characteristics could not only assess the chronology quality but could also describe the high-frequency variation characteristics of chronology with climate fluctuations [3,43]. Because of the drought conditions in the eastern Tianshan Mountains, the chronologies from three age-classes of trees showed higher quality and more climate signals with high SNR and EPS values (Table 1). Although the sample point was located in a high-altitude area, there was relatively small precipitation, high evaporation and poor soil water retention capacity with sparse vegetation [44]. Therefore, the radial growth of trees was limited by the drought stress and sensitivity to climate change in the study area.

The climate sensitivity of Schrenk spruce increased with age increases, showing the higher MS value (0.219) in old trees versus middle (0.212) and young trees (0.150) (Table 1). The main reasons were tree physiological mechanisms and environmental stress [45]. In terms of physiological mechanisms, the old trees were more susceptible to the impacts of climate change, displaying the dual effects of water transport resistance by gravity increase and transportation complexity with increase of height and thickness of trees [46]. At the same time, the water stress could restrict the stomatal conductance and gas exchange with earlier stomata closure, which would cause the radial growth to be more sensitive to climate variability [47]. In terms of environmental stress, the young trees growing in lower shadowlands were more affected by resource competition and had weakened responses to climate variability. Contrastingly, the old trees distributed in the canopy layer had relatively strong adaptive capacity and a lack of intense competition, which were primarily controlled by the climate suitability and sensitivity to climate fluctuations.

4.2. Age-Effect on Tree Radial Growth

Our results provide new evidence to elucidate how age-related growth patterns can predict potential impacts of warming climate. The tree-ring width chronologies from three age-classes of trees were controlled by the same climatic factors, showing basic consistent fluctuation characteristics and highly significant correlations from 1960 to 2012 (Figure 2C and Table 2). The similar time trend of the cumulative radial growth and the basal of area increment from three age-classes of trees also further verified this conclusion (Figure 2A,D). According to the law of limiting factors proposed, biological growth was limited by ecological factors with below- or above-normal needs [48]. The radial growth fluctuations of different age trees were more consistent in the same area when harsh climatic conditions were above or below a certain level [3]. The Schrenk spruce has strong ability for adapting to drought and the different age trees gradually formed relatively consistent responses to drought in the eastern Tianshan Mountains according to the relatively uniform tree-ring width fluctuation and growth trend.

When Schrenk spruce are younger than 100 years, the radial growth rate of trees is faster; but radial growth rate of trees over 100 becomes relatively stable or gradually slows [29]. The results of our study confirmed this conclusion, which showed young trees had a faster growth rate in the same climate condition, suggesting the mean raw chronology width (MRW) of the young trees was approximately 2.62 times that of old trees and the cumulative of radial growth for young trees was more than old trees (Table 1 and Figure 3A). Tree radial growth was also determined by the genetic factor, usually showing the gradually narrowing tree-ring width and slower growth rate with age

increases [3,49]. The auxin activity was stronger in young trees with low height and small canopy, and the initiation and differentiation (enlarging and wall-thickening) time for the cambium cells of young trees was earlier than old trees, but the ending time was the same as the old trees [15,50,51]. In contrast, old trees had a competitive advantage with the bigger diameter and crown, larger root system and more complex forest canopy layers, but their growth gradually slowed due to more survival costs with complicated structure and less water transmission efficiency [7,52,53]. From the perspective of tree physiological ecology, these features confirmed the age-effect in the process of tree growth.

The tree-ring width chronologies and the BAI from three age-classes of trees showed first increased and then decreased growth trends from 1960 to 2012 (Figure 3C,D). The mean annual temperature showed a significant increasing trend, and the total annual precipitation showed a downward trend in the most recent ten years (Figure 2). This finding suggested that the increasing drought had limited the radial growth of Schrenk spruce due to recent significantly increased temperature and declined precipitation in the study area. Long-term drought could increase the water stresses and reduce the photosynthetic efficiency and the accumulation of photosynthetic products for trees. For example, drought influenced a significant growth drop of *Pinus sylvestris* L. in the Eastern Central Alps [54]. The resource allocation strategy of trees would be changed by environmental stress, and nutrients would be given priority to supply plant leaves for adjusting the osmotic pressure to alleviate water deficit, and the remaining nutrients would be assigned to tree radial growth and form a narrow tree ring under the drought year [55,56].

The radial growth from three age-classes of trees all showed declining trends after 2004, but decline rates of middle and young trees were faster than that of old trees (Figure 3). Combined with the variation of mean temperature and total precipitation in the study area, the young trees were particularly vulnerable under worsening long-term drought. Many studies have also found the same conclusions, such as in *Pinus strobus* L. in the southern Appalachian Mountains of western North Carolina, Picea abies (L.) Karst. in northeast Hamburg of northern Germany, Pinus taiwanensis Hayata. in Taiwan, and Pinus cooperi Blanco in the Sierra Madre Occidental of northern Mexico [57–60]. As shown by a controlled experiment on cambial cell sensitivity to rising temperature of Cryptomeria japonica (L. f.) D. Don from different ages, the young tree growth trend would more easily be limited by long-term drought [61]. Compared to the stronger competitive advantage of old trees for resources, the middle and young trees obtained less moisture and nutrition with lower trunk height, shallower root systems and less trunk runoff, were more susceptible to long-term drought, and showed the rapid decline of growth rate [62–64]. Overall, the old trees might be more resilient to long-term drought than young trees due to the ability to absorb deeper water with a stronger root system; this may ease the impacts of long-term drought stress on radial growth in the study area.

4.3. Age-Effect on Tree Growth-Climate Relationships

Analysis of the growth-climate relationship could evaluate the similarities and differences in responses from different age-class trees [19]. The precipitation and drought in non-growing seasons were critical to Schrenk spruce growth, which was further illustrated by tree-ring width chronologies from three age-classes of trees, as chronologies were significantly positively correlated with total precipitation and SPEI in the current January (Figure 4). The total precipitation in non-growing seasons (from the previous November to the current March) was $40.98 \pm 2.20 \text{ mm/a}$, only accounting for 21.89% of total annual precipitation in the study area (Figure 2). However, water could still be available in the early growing seasons with snow and thus provide snow melt water for tree growth in the arid region, relieving the water shortage in spring [65]. Temperatures in growing seasons were also important to tree radial growth, primarily reflecting the negatively correlated relationship between tree-ring width chronologies from three age-classes of trees and mean temperature in the previous August (Figure 4). The negative AC1 values could confirm that the radial growth of Schrenk spruce was easily affected by climate conditions in the previous year (Table 1). The high temperature in

the previous growing seasons could not only increase the evaporation of soil moisture, reduce the preservation of soil available water, increase the tree evapotranspiration, and reduce the accumulation of tree photosynthetic nutrition but also lead to effects on the initiation and vitality of tree cambium cells with increasing drought stress and reductions in tree health [66]. Similar responses of radial growth to climate factors were found in Schrenk spruce from different age-class trees (60–90a, 90–120a and 120–150a) in western and central Tianshan Mountains [67].

Principal component analysis (PCA) of tree-ring width chronologies from different age-class trees demonstrated that the climate was the main factor and age was the secondary factor controlling the radial growth of trees (Table 4). The old and middle trees had common responses with the young trees, showing significant correlation with the total precipitation in the current January and mean temperature in the previous August (Figure 4). However, the old and middle trees were also significantly correlated with total precipitation in the previous November and the current March, and the mean temperatures in the previous November and the current June (Figure 4). Consequently, the old and middle trees were more sensitive to climate change than young trees.

The different physiological processes for old and young trees resulted in the sensitivity discrepancies of radial growth responses to climate [40]. On the one hand, old trees had higher sensitivity to climate factors than the young trees due to gradually increasing the resistances of water supply and lower photosynthetic rates with the increase of tree age [68,69]. On the other hand, the different resource utilization strategies for old trees and young trees could also cause the different response characteristics to climate change [41]. To ensure normal growth and development in the face of short-term adverse climatic conditions or fierce competition, the "overspend" nutrient utilization strategies for young trees could be used to enhance the photosynthetic efficiency and keep higher assimilation efficiency using the lasting induced stomatal opening and declining climate sensitivity but also bringing a greater risk of mortality [19]. The "conservative" nutrient utilization strategies for old trees would reduce photosynthetic efficiency in a short-term adverse environment, but their complex organs would consume more nutrients, making radial growth of old trees more sensitive to climate variability [70]. The same results were also found in *Picea abies* (L.) Karst. in the Austrian Alps, Abies alba Mill. in the Romanian Carpathians, Fagus sylvatica L. in France, Pinus tabulaeformis Carrière on the semi-arid Chinese Loess Plateau, and Abies georgei var. smithii in the southeastern Tibetan Plateau [11,71–74].

5. Conclusions

In conclusion, tree-ring recording of climatic signals in time and spatial scales would also be disturbed by biological signals such as age. Based on the results of our research in the eastern Tianshan Mountains, Schrenk spruce is an ideal tree species for studying dendrochronology due to the tree-ring width chronologies from different age-class trees with the high quality and relatively consistent radial growth patterns under climate change. Furthermore, the drought caused by the lack of precipitation in non-growing seasons and the mean temperature in growing seasons, was a major limiting factor of tree radial growth. However, the trees with ages of up to 100 years were more reliable climatic proxies and more sensitive to climate factors, suggesting the collection of relatively older or larger-diameter trees for study on climate reconstructions and growth-climate relationships in the eastern Tianshan Mountains.

Acknowledgments: This research was supported by the National Natural Science Foundation of China (Projects No. 41630750 and 41361010). We especially thank Xiaolong Shang for sampling work in the field. We are grateful to Yan Wen, Wen Xiao and Ao Shen for their assistance in data analysis and laboratory work. We also thank the anonymous referees for helpful comments on the manuscript.

Author Contributions: Study conception and experimental design: Liang Jiao and Yuan Jiang. Acquisition of samples: Liang Jiao, Mingchang Wang and Wentao Zhang. Analysis and interpretation of data: Liang Jiao, Yuan Jiang and Yiping Zhang. Drafting of manuscript: Liang Jiao and Yuan Jiang.

Conflicts of Interest: The authors declare no conflict of interest.

References

- 1. Martín-Benito, D.; Cherubini, P.; del Río, M.; Cañellas, I. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees* **2008**, *22*, 363–373. [CrossRef]
- 2. Linares, J.C.; Camarero, J.J.; Carreira, J.A. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo. J. Ecol.* **2010**, *98*, 592–603. [CrossRef]
- 3. Fritts, H.C. Tree Rings and Climate; Academic Press: London, UK, 1976.
- 4. Vieira, J.; Campelo, F.; Nabais, C. Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. *Trees* **2009**, *23*, 257–265. [CrossRef]
- 5. Colenutt, M.E.; Luckman, B.H. The dendrochronological characteristics of alpine larch. *Can. J. For. Res.* **1995**, 25, 777–789. [CrossRef]
- 6. Kirkpatrick, M. Spatial and age dependent patterns of growth in New England Black Birch. *Am. J. Bot.* **1981**, *68*, 535–543. [CrossRef]
- 7. Yu, G.; Liu, Y.; Wang, X.; Ma, K. Age-dependent tree-ring growth responses to climate in Qilian juniper (*Sabina przewalskii* Kom.). *Trees* **2008**, *22*, 197–204. [CrossRef]
- 8. Sun, J.; Liu, Y. Age-independent climate-growth response of Chinese pine (*Pinus tabulaeformis* Carrière) in North China. *Trees* **2015**, *29*, 397–406. [CrossRef]
- 9. Ettl, G.J.; Peterson, D.L. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Glob. Chang. Biol.* **1995**, *1*, 213–230. [CrossRef]
- 10. Linderholm, H.W.; Linderholm, K. Age-dependent climate sensitivity of *Pinus sylvestris* L. in the central Scandinavian Mountains. *Boreal Environ. Res.* **2004**, *9*, 307–317.
- Fang, K.; Chen, D.; Gou, X.; D'Arrigo, R.; Davi, N. Influence of non-climatic factors on the relationships between tree growth and climate over the Chinese Loess Plateau. *Glob. Planet Chang.* 2015, 132, 54–63. [CrossRef]
- 12. Rozas, V.; DeSoto, L.; Olano, J.M. Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytol.* **2009**, *182*, 687–697. [CrossRef] [PubMed]
- 13. Hadad, M.A.; Juñent, F.A.R.; Boninsegna, J.A.; Patón, D. Age effects on the climatic signal in *Araucaria araucana* from xeric sites in Patagonia, Argentina. *Plant Ecol. Divers.* **2015**, *8*, 343–351. [CrossRef]
- 14. Peng, J.F.; Liu, Y.Z.; Wang, T. A tree-ring record of 1920's–1940's droughts and mechanism analyses in Henan Province. *Acta Ecol. Sin.* **2014**, *34*, 3509–3518. [CrossRef]
- 15. Rossi, S.; Deslauriers, A.; Anfodillo, T.; Carrer, M. Age-dependent xylogenesis in timberline conifers. *New Phytol.* **2008**, *177*, 199–208. [CrossRef] [PubMed]
- 16. Machar, I.; Vlckova, V.; Bucek, A.; Vozenilek, V.; Salek, L.; Jerabkova, L. Modelling of climate conditions in forest vegetation zones as a support tool for forest management strategy in european beech dominated forests. *Forests* **2017**, *8*, 82. [CrossRef]
- 17. Yao, J.; Chen, Y.; Zhao, Y.; Mao, W.; Xu, X.; Liu, Y.; Yang, Q. Response of vegetation NDVI to climatic extremes in the arid region of Central Asia: A case study in Xinjiang, China. *Theor. Appl. Climatol.* **2017**. [CrossRef]
- Itter, M.S.; Finley, A.O.; D'Amato, A.W.; Foster, J.R.; Bradford, J.B. Variable effects of climate on forest growth in relation to climate extremes, disturbance, and forest dynamics. *Ecol. Appl.* 2017, 27, 1082–1095. [CrossRef] [PubMed]
- 19. Carrer, M.; Urbinati, C. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* **2004**, *85*, 730–740. [CrossRef]
- 20. Wu, G.; Xu, G.; Chen, T.; Liu, X.; Zhang, Y.; An, W.; Wang, W.; Fang, Z.; Yu, S. Age-dependent tree-ring growth responses of Schrenk spruce (*Picea schrenkiana*) to climate—A case study in the Tianshan Mountain, China. *Dendrochronologia* **2013**, *31*, 318–326. [CrossRef]
- 21. Wang, T.; Yu, R.; Yang, M.; Feng, R.; Kang, J. Diameter-dependent growth responses of *Picea schrenkiana* to climate in the middle brae of Tianshan Mountain. *Chin. J. Appl. Environ. Biol.* **2016**, *22*, 579–585. [CrossRef]
- 22. Chen, F.; Yuan, Y.; Yu, S.; Zhang, T.; Shang, H.; Zhang, R.; Qin, L.; Fan, Z. A 225-year long drought reconstruction for east Xinjiang based on Siberia larch (*Larix sibirica*) tree-ring widths: Reveals the recent dry trend of the eastern end of Tien Shan. *Quat. Int.* **2015**, *358*, 42–47. [CrossRef]

- Jiao, L.; Jiang, Y.; Wang, M.; Kang, X.; Zhang, L.; Zhao, S. Responses to climate change in radial growth of *Picea schrenkiana* along elevations of the eastern Tianshan Mountains, northwest China. *Dendrochronologia* 2016, 40, 117–127. [CrossRef]
- 24. Zhang, R.; Yuan, Y.; Gou, X.; Zhang, T.; Zou, C.; Ji, C. Intra-annual radial growth of Schrenk spruce (*Picea schrenkiana* Fisch. et Mey) and its response to climate on the northern slopes of the Tianshan Mountains. *Dendrochronologia* **2016**, *40*, 36–42. [CrossRef]
- 25. Chen, F.; Yuan, Y.; Yu, S. Tree-ring indicators of rainfall and streamflow for the Ili-Balkhash Basin, Central Asia since CE 1560. *Palaeogeogr. Palaeoclimatol.* **2017**. [CrossRef]
- 26. Guo, Y.Y.; Liu, H.Y.; Ren, J.; Zhan, X.F.; Cao, S.P. Responses of tree growth to vertical climate gradient in the middle section of the Tianshan Mountains. *Quat. Sci.* **2007**, *27*, 322–331. (In Chinese)
- 27. Wu, X.; Liu, H.; He, L.; Qi, Z.; Anenkhonov, O.A.; Korolyuk, A.Y.; Yu, Y.; Guo, D. Stand-total tree-ring measurements and forest inventory documented climate-induced forest dynamics in the semi-arid Altai Mountains. *Ecol. Indic.* **2014**, *36*, 231–241. [CrossRef]
- Vicente-Serrano, S.M.; Beguería, S.; López-Moreno, J.I. A multiscalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index. J. Clim. 2010, 23, 1696–1718. [CrossRef]
- 29. Forests in Xinjiang Editorial Board. *Forests in Xinjiang*; Xinjiang People's Press: Urumqi, China; China Forestry Press: Beijing, China, 1990. (In Chinese)
- 30. Grissino-Mayer, H.D. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* **2001**, *57*, 205–221.
- 31. Cook, E.R. A Time-Series Analysis Approach to Tree-Ring Standardization. Ph.D. Thesis, University of Arizona, Tucson, AZ, USA, 1985.
- 32. Gazol, A.; Camarero, J.J.; Gutiérrez, E.; Popa, I.; Andreu-Hayles, L.; Motta, R.; Nola, P.; Ribas, M.; Sangüesa-Barreda, G.; Urbinati, C.; et al. Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J. Biogeogr.* **2015**, *42*, 1150–1162. [CrossRef]
- 33. Fritts, H.C.; Shatz, D.J. Selecting and characterizing tree-ring chronologies for dendroclimatic analysis. *Tree-Ring Bull.* **1975**, *35*, 31–46.
- 34. Wigley, T.M.; Briffa, K.R.; Jones, P.D. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol.* **1984**, *23*, 201–213. [CrossRef]
- 35. Schweingruber, F.H.; Briffa, K.R.; Nogler, P. A tree-ring densitometric transect from Alaska to Labrador. *Int. J. Biometeorol.* **1993**, *37*, 151–169. [CrossRef]
- Rodríguez-Catón, M.; Villalba, R.; Srur, A.M.; Luckman, B. Long-term trends in radial growth associated with *Nothofagus pumilio* forest decline in Patagonia: Integrating local- into regional-scale patterns. *For. Ecol. Manag.* 2015, 339, 44–56. [CrossRef]
- Altman, J.; Doležal, J.; Čížek, L. Age estimation of large trees: New method based on partial increment core tested on an example of veteran oaks. *For. Ecol. Manag.* 2016, 380, 82–89. [CrossRef]
- 38. Monserud, R.A.; Sterba, H. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *For. Ecol. Manag.* **1996**, *80*, 57–80. [CrossRef]
- Wang, H.; Shao, X.M.; Jiang, Y.; Fang, X.Q.; Wu, S.H. The impacts of climate change on the radial growth of Pinus koraiensis along elevations of Changbai Mountain in northeastern China. *For. Ecol. Manag.* 2013, 289, 333–340. [CrossRef]
- 40. Szeicz, J.M.; Macdonald, G.M. Age-dependent tree ring growth response of subarctic white spruce to climate. *Can. J. For. Res.* **1994**, *24*, 120–132. [CrossRef]
- 41. Bond, B.J. Age-related changes in photosynthesis of woody plants. *Trends Plant Sci.* **2000**, *5*, 349–353. [CrossRef]
- 42. Konter, O.; Büntgen, U.; Carrer, M.; Timonen, M.; Esper, J. Climate signal age effects in boreal tree-rings: Lessons to be learned for paleoclimatic reconstructions. *Quat Sci. Rev.* **2016**, *142*, 164–172. [CrossRef]
- 43. Rolland, C. Tree-ring and climate relationships for *Abies alba* in the internal Alps. *Tree-Ring Bull.* **1993**, *53*, 1–11.
- Xu, G.B.; Liu, X.H.; Qin, D.H.; Chen, T.; Wang, W.Z.; Wu, G.J.; Sun, W.Z.; An, W.L.; Zeng, X.M. Tree-ring δ¹⁸O evidence for the drought history of eastern Tianshan Mountains, northwest China since 1700 A.D. *Int. J. Climatol.* 2014, 34, 3336–3347. [CrossRef]
- 45. Szeicz, J.M.; Macdonald, G.M. Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling. *Quat. Res.* **1995**, *44*, 257–266. [CrossRef]

- 46. Ryan, M.G.; Yoder, B.J. Hydraulic limits to tree height and tree growth. Bioscience 1997, 47, 235–242. [CrossRef]
- 47. Kolb, T.E.; Stone, J.E. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine-oak forest. *Tree Physiol.* **2000**, *20*, 1–12. [CrossRef] [PubMed]
- 48. Blackman, F.F. Optima and limiting factors. Ann. Bot. 1905, 19, 281–295. [CrossRef]
- 49. Looney, C.E.; D'Amato, A.W.; Fraver, S.; Palik, B.J.; Reinikainen, M.R. Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra*, stands. *For. Ecol. Manag.* **2016**, *375*, 238–248. [CrossRef]
- Aloni, R. Foliar and axial aspects of vascular differentiation: Hypotheses and evidence. *J. Plant Growth Regul.* 2001, 20, 22–34. [CrossRef]
- 51. Deslauriers, A.; Morin, H.; Begin, Y. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). *Can. J. For. Res.* **2003**, *33*, 190–200. [CrossRef]
- 52. Nash, T.H.; Fritts, H.C.; Stokes, M.A. A technique for examining non climatic variation in widths of annual tree rings with special reference to air pollution. *Tree-Ring Bull.* **1975**, *35*, 15–24.
- Hunt, E.R.; Lavigne, M.B.; Franklin, S.E. Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. *Ecol. Model.* 1999, 122, 151–164. [CrossRef]
- 54. Oberhuber, W.; Gruber, A. Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. *Trees* **2010**, *24*, 887–898. [CrossRef] [PubMed]
- 55. Chartzoulakis, K.; Noitsakis, B.; Therios, I. Photosynthesis, plant growth and carbon allocation in Kiwi, cv Hayward, as influenced by water deficits. *Acta Hortic.* **1993**, *335*, 227–234. [CrossRef]
- 56. Chaves, M.M.; Maroco, J.P.; Pereira, J.S. Understanding plant responses to drought-from genes to whole plant. *Funct. Plant Biol.* **2003**, *30*, 239–264. [CrossRef]
- 57. Vose, J.M.; Swank, W.T. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. *For. Ecol. Manag.* **1994**, *64*, 25–39. [CrossRef]
- 58. Van den Brakel, J.A.; Visser, H. The influence of environmental conditions on tree-ring series of *Norway spruce* for different canopy and vitality classes. *For. Sci.* **1996**, *42*, 206–219.
- 59. Ruiz-Benito, P.; Madrigal-González, J.; Young, S.; Mercatoris, P.; Cavin, L.; Huang, T.J. Climatic stress during stand development alters the sign and magnitude of age-related growth responses in a subtropical mountain pine. *PLoS ONE* **2015**, *10*, e0126581. [CrossRef] [PubMed]
- 60. Pompa-García, M.; Hadad, M.A. Sensitivity of pines in Mexico to temperature varies with age. *Atmósfera* **2016**, *29*, 209–219. [CrossRef]
- 61. Begum, S.; Nakaba, S.; Oribe, Y.; Kubo, T.; Funada, R. Cambial sensitivity to rising temperatures by natural condition and artificial heating from late winter to early spring in the evergreen conifer Cryptomeria japonica. *Trees* **2010**, *24*, 43–52. [CrossRef]
- 62. Jacquart, E.M.; Armentano, T.V.; Spingarn, A.L. Spatial and temporal tree responses to water stress in an old-growth deciduous forest. *Am. Midl. Nat.* **1992**, *127*, 158–171. [CrossRef]
- Kloeppel, B.D.; Abrams, M.D.; Kubiske, M.L. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. *Can. J. For. Res.* 1993, 23, 181–189. [CrossRef]
- 64. Pichler, P.; Oberhuber, W. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *For. Ecol. Manag.* **2007**, 242, 688–699. [CrossRef]
- 65. Lévesque, M.; Saurer, M.; Siegwolf, R.; Eilmann, B.; Brang, P.; Bugmann, H.; Rigling, A. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Glob. Chang. Biol.* **2013**, *19*, 3184–3199. [CrossRef] [PubMed]
- Jiao, L.; Jiang, Y.; Zhang, W.T.; Wang, M.C.; Zhang, L.N.; Zhao, S.D. Divergent responses to climate factors in the radial growth of *Larix sibirica* in the eastern Tianshan Mountains, northwest China. *Trees* 2015, 29, 1673–1686. [CrossRef]
- 67. Qi, Z.; Liu, H.; Wu, X.; Hao, Q. Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains, Northwestern China. *Glob. Chang. Biol.* **2015**, *21*, 816–826. [CrossRef] [PubMed]
- 68. Mencuccini, M.; Martínez-Vilalta, J.; Vanderklein, D.; Hamid, H.A.; Korakaki, E.; Lee, S.; Michiels, B. Size-mediated ageing reduces vigour in trees. *Ecol. Lett.* **2005**, *8*, 1183–1190. [CrossRef] [PubMed]

- Li, X.; Liang, E.; Gričar, J.; Prislan, P.; Rossi, S.; Čufar, K. Age dependence of xylogenesis and its climatic sensitivity in smith fir on the south-eastern Tibetan Plateau. *Tree Physiol.* 2013, 33, 48–56. [CrossRef] [PubMed]
- 70. Meinzer, F.C.; Lachenbruch, B.; Dawson, T.E. *Size- and Age-Related Changes in Tree Structure and Function*; Springer: Dordrecht, The Netherlands, 2011.
- 71. Mérian, P.; Lebourgeois, F. Size-mediated climate-growth relationships in temperate forests: A multi-species analysis. *For. Ecol. Manag.* **2011**, *261*, 1382–1391. [CrossRef]
- 72. Schuster, R.; Oberhuber, W. Age-dependent climate-growth relationships and regeneration of *Picea abies* in a drought-prone mixed coniferous forest in the Alps. *Can. J. For. Res.* **2013**, *43*, 609–618. [CrossRef] [PubMed]
- 73. Primicia, I.; Camarero, J.J.; Janda, P.; Čada, V.; Morrissey, R.C.; Trotsiuk, V.; Bače, R.; Teodosiu, M.; Svoboda, M. Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. *For. Ecol. Manag.* 2015, 354, 77–86. [CrossRef]
- Liu, B.; Wang, Y.; Zhu, H.; Liang, E.; Camarero, J.J. Topography and age mediate the growth responses of Smith fir to climate warming in the southeastern Tibetan Plateau. *Int. J. Biometeorol.* 2016, 60, 1577–1587. [CrossRef] [PubMed]



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