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Topography- and Species-Dependent Climatic Responses in Radial Growth of *Picea meyeri* and *Larix principis-rupprechtii* in the Luyashan Mountains of North-Central China

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Abstract: Dendroecological techniques were used to examine the relationships between topographic aspects, climate factors and radial growth of *Picea meyeri* and *Larix principis-rupprechtii* in Luyashan Mountains, North-Central China. Four sites were selected at timberline and totally 67 trees and 134 cores were collected. Pearson correlation and regression surface analysis were conducted to reveal the growth-climate relationships. The results indicated that the two species both showed significant negative correlations with temperature during preceding November on the two topographic aspects. On both slope aspects, growth of *P. meyeri* exhibited significant negative correlations with precipitation in current June, whereas growth of *L. principis-rupprechtii* showed significant negative correlations with precipitation in preceding September. On north-facing slope, tree growth was limited by low temperature in early growing season, which not shown on south-facing slope. If climate warming continues, *L. principis-rupprechtii* may be more favored and a reverse between relationships with temperature and precipitation maybe occur in growth of trees. Treeline position on the north-facing slope may possess a greater potential for elevation shifting than the

south-facing slope. Our results supply useful information for discussing the potential effect of future climate on the forest growth in North-Central China.

Keywords: Topographic aspect; Interspecific difference; Dendroclimatic response; *Picea meyeri*; *Larix principis-rupprechtii*; Luyashan Mountains

1. Introduction

Dendrochronology methods have been widely used to study the climatic responses of forest trees. Tree-ring data can be useful for analyzing the relations between tree growth and climate [1,2]; however, the ability of tree rings to serve as a proxy for climatic response depends on a variety of factors, such as tree species and site conditions. For example, Oberhuber reported different sensitivities to climate in the growth of *Pinus cembra* L. that was associated with slope aspect in the timberline ecotone of the Central Austrian Alps [3]. Cai and Liu found different climatic responses in the growth of three co-existing tree species, *L. principis-rupprechtii*, *P. meyeri* and *Pinus tabulaeformis*, in the Lüliang Mountains of China [4]. At timberline in the Qinghainan Mountains, on the northeastern Tibetan Plateau, species and site differences both led to variability in the climatic responses of *Sabina przewalskii* Kom. and *Picea crassifolia* Kom. on west-facing and east-facing slopes [5]. These studies demonstrated the complex effects of species and topography on tree growth.

A difference in slope aspect results in reallocation of solar energy, which influences tree growth. At timberline in the Qinghainan Mountains, severe limitation of moisture available for tree growth was found on the relatively dry west-facing slope but not on the wetter east-facing slope [5]. A similar result was reported in dendroecological studies on *Liriodendron tulipifera* L., which showed greater response to drought on the southwest aspect than on other aspects [6]. In addition, some studies reported different responses to low temperature in the growing season for different slope aspects. In the Central Italian Alps, chronologies from the north-facing slopes all showed stable relationships with summer temperature, whereas those from the southwest-facing slopes exhibited decreased sensitivity to temperature [7]. After assessing the multi-scale effects of slope aspect at the upper treeline in the southern Rocky Mountains, Elliott and Kipfmueller claimed that investigation of possible treeline response to climate change should take the impacts of varied slope aspect into account [8].

P. meyeri and *L. principis-rupprechtii* are both indigenous conifers that co-dominate in most of the cold coniferous forests of North-Central China [9]. In previous dendrochronological studies, these two species have proven to be suitable for dendroclimatic research because of their easiness to date and their high sensitivity to climate change [10–13]. As evergreen and deciduous conifer species, respectively, *P. meyeri* and *L. principis-rupprechtii* inhabit different temperature and precipitation niches [14], suggesting the potential for differences in climatic response between these two species. However, they have a similar geographic distribution and frequently co-exist in mixed forests on all topographic slopes, implying that a common growth response may exist [15]. This coexistence provides an opportunity to study the differences and similarities in their growth and growth-climate relationships in the context of topographic differences under harsh timberline environments.

In this study, we used dendroecological methods to investigate the similarities and variation in growth responses of *P. meyeri* and *L. principis-rupprechtii* on two opposite aspects in the Luyashan Mountains. We hypothesized that there would be common climatic responses in the growth of trees but different responses between different slope aspects and different species. To verify these hypotheses, we (a) quantified the relationships between radial growth and climate data, including monthly mean temperature and total monthly precipitation, and (b) identified differences in the climatic responses of *P. meyeri* and *L. principis-rupprechtii* on south-facing and north-facing slopes.

2. Materials and Method

2.1. Study Area

The sampled sites were located at Heyeping, the highest peak of the Luyashan Mountains in North-Central China (Figure 1). The soil under the forest was mountainous brown forest soil, a well-drained sandy loam characterized by 12%–18% clay and 50%–60% fine sand [16]. According to our measurements in August and September 2009, the pH of the topsoil ranged from 6.4 to 7.3. The slope at timberline was 20°.
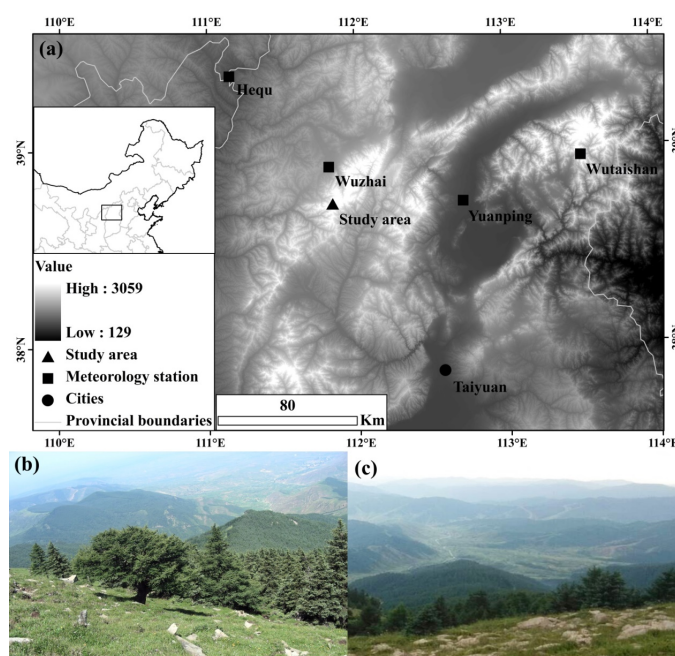

Figure 1. Location of the study area and meteorological stations (**a**), and photographic view of the study sites on north-facing (**b**) and south-facing slopes (**c**).

At high elevations, the climate is characterized as low temperature with relatively plentiful precipitation. Around our study area, there were four meteorological stations (Figure 1), Yuanping (38°44′ N and 112°43′ E at 828.2 m), Hequ (39°23′ N and 110°09′ E at 862 m), Wuzhai (38°55′ N and 111°49′ E at 1401.1 m), and Wutaishan (approximately 38°54′ N and 113°31′ E). Wutaishan differs from the other three stations; it is the only high mountain station and its location migrated in 1998. So the continuous records were kept in two periods, 1958–1997 (2895.8 m) and 1998–2007 (2208.3 m). Based on the climate data from 1958 to 1997 at 2895.8 m, the mean annual temperature

was only −3.8 °C, and the warmest and coldest months were July (approximately 9.7 °C) and January (approximately −17.8 °C), respectively. The annual precipitation was approximately 828.1 mm, and approximately 76% of this precipitation was received during the growing season, May–September.

2.2. Tree-Ring Sampling

According to Wardle [17], timberline is defined as the upper limit of the closed forest. We chose sample sites near and below the upper coniferous forest distribution boundaries on north-facing and south-facing slopes (Figure 1). Sites on north-facing slopes with *P. meyeri* and *L. principis-rupprechtii* were designated as PN (*P. meyeri* on north-facing slope) and LN (*L. principis-rupprechtii* on north-facing slope), respectively; PS (*P. meyeri* on south-facing slope) and LS (*L. principis-rupprechtii* on south-facing slope) represented the sites of corresponding species on the south-facing slope. The elevation of timberline differed between the two opposite slope aspects; therefore, PN and LN were located at 2600–2660 m and PS and LS were located at 2540–2620 m (Table 1).

Table 1. Stand conditions of sampling sites.

I.D.	Tree species	Topographic aspect	Latitude N	Longitude E	Elevation (m)	DBH [a] (cm)	Tree height [a] (m)
PN	*P. meyeri*	North-facing	38°43′14.6″	111°51′16.2″	2600–2660	17.3 ± 4.8	10.0 ± 2.1
LN	*L. principis-rupprechtii*	North-facing	38°43′14.6″	111°51′16.2″	2600–2660	15.9 ± 4.5	8.8 ± 3.2
PS	*P. meyeri*	South-facing	38°42′44″	111°51′33.5″	2540–2620	19.3 ± 4.2	13.4 ± 3.4
LS	*L. principis-rupprechtii*	South-facing	38°42′44″	111°51′33.5″	2540–2620	26.2 ± 4.0	16.0 ± 3.4

[a] Data are presented as the mean ± SD.

The filed work was conducted in the summer of 2009. The trees presumably with oldest ages were selected for sampling at each site. At last, 18 trees were sampled at site PN, 16 at site LN, 17 at site PS and 16 at site LS. From each tree, two increment cores were extracted at breast height (1.3 m above the ground): one core was taken parallel to the contour line and the other core was taken orthogonally to the first. Additionally, three 400 m² plots were surveyed at each site to characterize the stands (Table 1). The diameter at breast height (DBH) and the height of each tree were recorded. Measuring tape and infrared distance measuring sensor were used to survey the diameter at DBH and height, respectively.

2.3. Chronology Development

Tree-ring chronologies were developed using standard dendrochronological techniques. The cores were air-dried, mounted, sanded, visually dated under a microscope and then measured using the LINTAB measuring system, with a resolution of 0.01 mm. The COFECHA program [18] was used to detect potential errors in cross-dating and measuring procedures. All cores with potential errors were rechecked and corrected. All of the tree-ring raw measurement series were standardized using the program ARSTAN [19]. A negative exponential curve was applied to the raw series to remove

age- and size-related signals [20]. Then, each detrended core series was subjected to auto-regressive modeling to remove the temporal auto-correlation and produce a series of independent observations of variation in annual radial growth. At last, the detrended series were averaged by computing the biweight robust mean to remove random signals related to local disturbance [21]. In total, eight RES chronologies were developed based on the sampling. In addition to the four chronologies at each of the four sites, four mixed chronologies were also developed to examine the specific climatic response from the species and topography perspective: one for *P. meyeri* trees (PICEA), one for *L. principis-rupprechtii* trees (LARIX), one for trees on north-facing slope (NORTH) and one for trees on south-facing slope (SOUTH).

2.4. Climate Data

Unfortunately, Wutaishan station, the only mountainous meteorological station, could not support a long time series because the observation site changed in 1998. For this reason, we also calculated the mean data from Yuanping, Hequ and Wuzhai stations to represent the regional climatic conditions. There was a significant linear relationship between the mean data and the data from Wutaishan station for both monthly mean temperature and total monthly precipitation (Figure 2). Therefore, we utilized the mean from the three stations in the analysis of growth-climate relationships, instead of data from Wutaishan station. The climatic variables contained the monthly mean temperature (TEM) and total monthly precipitation (PRE).
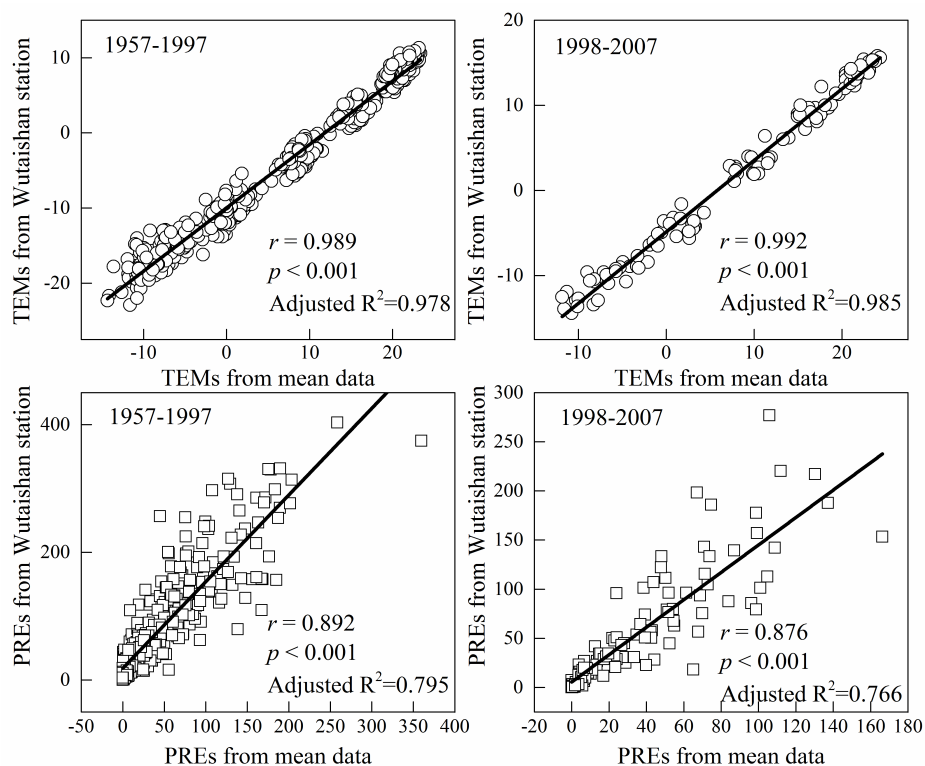

Figure 2. The relationship of monthly mean temperature (TEM) and total monthly precipitation (PRE) data from Wutaishan station and mean data from the other three stations (Hequ, Wuzhai and Yuanping), during the periods 1957–1997 and 1998–2007.

2.5. Data Analysis

Several standard statistics were computed to assess the reliability of the chronologies. Mean sensitivity (MS) is a measurement of relative change in ring width index between consecutive years, and the standard deviation (SD) indicates the variability of the entire series [22]. The mean between-tree correlation (Rbar) and variance expressed by the first principal component (PC1%) were calculated to indicate common signal strength [23]. In addition, the signal to noise ratio (SNR) and the expressed population signal (EPS) were determined to reflect the signal strength of each chronology. An EPS > 0.85 is considered to indicate a chronology of satisfactory quality [24].

The Gleichläufigkeit index (GLK) was calculated to assess the similarity of interval trends between different chronologies. The total GLK across all intervals is a measure of agreement between the two chronologies. Where the intervals for annual ring curves run parallel for many years, it can be assumed that the growth-climate relationships are similar between the two chronologies [25,26].

Pearson's correlation coefficients were calculated for tree-ring chronologies and monthly meteorological data to reveal growth-climate relationships, using the bivariate correlation function in SPSS (version 17.0; SPSS Inc., Chicago, IL, USA). The meteorological data consisted of the monthly mean temperature and total monthly precipitation from the prior September to the current September during the period 1958–2007.

A response surface regression was conducted using STATISTICA (version 7.0; StatSoft Inc., Tulsa, OK, USA) to examine the integrated effect of multiple climate variables. By this method, the different contributions of the same climatic variables to growth between different species and different topographic aspects will be figured out. All pair-wise combinations of climate variables were those indicating the similar or different relationships between the two species and the opposite topographic aspects in the above correlation analysis. The regression equation was as follows:

$$RWI = C_0 + C_1 V_1 + C_2 V_2 + C_3 V_1^2 + C_4 V_2^2 + C_5 V_1 V_2 \tag{1}$$

Where *RWI* is the tree-ring width index, V_1 and V_2 are the climate variables, C_0 is the regression constant, and C_1 through C_5 are the regression coefficients.

3. Results

3.1. Characteristics of Tree-Ring Chronologies

In general, the SNR (signal to noise ratio) of the eight chronologies ranged from 15.679 to 40.800, and the EPS ranged from 0.940 to 0.976 (Table 2). The EPS (expressed population signal) of the different chronologies all exceeded 0.85, the minimum threshold for a strong climate signal within the tree ring, suggesting that our chronologies were all suitable for growth-climate relationship studies [24].

The chronologies confirmed the potential differences between species and between topographic aspects, although the differences seemed to be more or less modest. First, a consistent difference was observed between species, with PN exhibiting lower values for MS (mean sensitivity), SD (standard deviation), Rbar (mean between-tree correlation) and PC1% (variance expressed by the first principal component) than LN. Similar trends were observed between PS and LS. Second, PN possessed a

higher Rbar value and higher PC1% than PS, suggesting a difference between the two aspects. Similarly, the Rbar and PC1% values of LN and NORTH were higher than those of LS and SOUTH, respectively.

Table 2. Characteristics of tree-ring width chronologies.

I.D.	Trees/Cores	Time span	MS	SD	Rbar	PC1%	SNR	EPS
PN	18/36	1947–2007	0.166	0.134	0.409	49.0	15.679	0.940
LN	16/32	1940–2007	0.171	0.161	0.509	58.0	18.273	0.948
PS	17/34	1909–2007	0.140	0.120	0.365	46.6	18.807	0.950
LS	16/32	1931–2007	0.182	0.164	0.457	51.0	25.178	0.962
PICEA	35/70	1909–2007	0.140	0.120	0.334	41.6	26.999	0.964
LARIX	32/64	1931–2007	0.171	0.160	0.488	52.4	40.800	0.976
NORTH	34/68	1947–2007	0.146	0.126	0.326	38.3	19.381	0.951
SOUTH	33/66	1909–2007	0.133	0.119	0.319	37.5	27.386	0.965

MS: mean sensitivity; SD: standard deviation; Rbar: mean between-tree correlation; PC1%, the variance expressed by the first principal component; SNR: signal to noise ratio; EPS: expressed population signal. The R, PC1%, SNR, and EPS were calculated based on the interval, 1958–2007.

3.2. Similarities and Differences in Radial Growth between Different Species and Topographic Aspects

Comparison of GLK values between different chronologies allowed assessment of topography- and species-dependent growth similarities (Table 3). Results showed that all of the trees exhibited, to some extent, a synchronous growth rhythm, as evidenced by a significance level of at least 95.0% for all pairwise comparisons of GLK values between chronologies. The relatively high GLK values between PN and PS (81.6%), as well as between LN and LS (79.6%), indicated that tree growth was consistent within species. The lower GLK values between LN and PN (67.4%), and between LS and PS (65.3%), indicated a weaker relationship between tree growth and slope aspects. Additionally, the GLK value between the two different species chronologies (PICEA and LARIX) was 67.3%, smaller than the GLK value between the chronologies of the north-facing and south-facing slopes (83.7%), suggesting a greater difference between species than between slope aspects. In other words, the growth similarity was higher for the same species on different slope aspects, than for different species on the same slope aspect.

Table 3. Gleichläfigkeit values (%) between different chronologies.

	LN	LS	PN	PS	PICEA	LARIX	NORTH	SOUTH
LN		79.6 ***	67.4 **	65.3 *	69.4 **	89.8 ***	75.5 ***	75.5 ***
LS			63.3 *	65.3 *	65.3 *	89.8 ***	71.4 **	79.6 ***
PN				81.6 ***	93.9 ***	65.3 *	91.8 ***	79.6 ***
PS					87.8 ***	67.3 **	77.6 ***	85.7 ***
PICEA						67.3 **	89.8 ***	85.7 ***
LARIX							73.5 ***	81.6 ***
NORTH								83.7 ***
SOUTH								

* indicates 95.0% significance, ** indicates 99.0% significance, and *** indicates 99.9% significance.

3.3. Correlations between Radial Growth Chronologies and Climatic Variables

The correlation analysis was conducted between radial growth chronologies and the monthly climatic variables using the data from 1958–2007 (Figure 3). In general, the temperature from prior October to current January significantly correlated with growth of trees in most cases. With the exception of PN, all chronologies exhibited significant negative correlations with monthly mean temperature in the preceding November. The temperature in the previous October and the current January also had an apparent impact on the growth of trees, although the correlation was not significant in most cases.

The association between tree-ring growth and temperature in the early growing season indicated a difference in climatic response related to topographic aspect. LN and NORTH both showed significant positive correlations with monthly mean temperature in May, whereas LS and SOUTH did not. The correlations between growth and monthly mean temperature in June and July also showed similar but non-significant differences between the north-facing chronologies (LN, PN and NORTH) and the south-facing chronologies (LS, PS and SOUTH).

The response of growth to precipitation suggested a difference in annual growth dynamics between the two species. The three chronologies of *P. meyeri* (PN, PS and PICEA) all showed significant negative correlations with total monthly precipitation in the current June. Both LN and LARIX exhibited significant negative correlations with total monthly precipitation in the preceding September, suggesting an influence of the previous growing season on growth of *L. principis-rupprechtii*.

Month	TEM								PRE							
	LN	LS	PN	PS	PICEA	LARIX	NORTH	SOUTH	LN	LS	PN	PS	PICEA	LARIX	NORTH	SOUTH
SEP									○					○		
OCT		○						○								
NOV	○	○		○	○	○	○	○								
DEC																
jan				○	○			○								
feb																
mar																
apr																
may	●						●									
jun											○	○	○		○	○
jul														○		
aug																
sep																

Figure 3. Pearson correlation coefficients between tree-ring chronologies and monthly climate data (monthly mean temperature, TEM, and total monthly precipitation, PRE). The white circles represent significant negative correlation, whereas black circles represent significant positive correlation. Significant level is 95% ($p \leq 0.05$). The capitalized months denote months belonging to the previous year.

3.4. Variation in the Integrated Influence of Climate Factors on Radial Growth

In the above correlation analysis, temperature in prior November (T_{p11}) showed similar correlations with growth of trees. Temperature in current May (T_5) exhibited different correlations with growth of trees between the two topographic aspects. The different correlations of precipitation during prior September (P_{p9}) and current June (P_6) with chronologies indicated the varied climatic responses of growth between the two species. Response surface analysis was compulsively conducted using the common T_{p11} and each of the other three different variables to see the contributions of these climate factors to growth (Figure 4). The significant regression equations and statistical parameters were as follows:

$$LN = 0.9113 - 0.1101\ T_{p11} + 0.0036\ P_{p9} - 0.0016\ T_{p11}{}^2 + 0.0016\ T_{p11}\ P_{p9} - 0.00003\ P_{p9}{}^2$$
$$\text{(Adjusted } R^2 = 0.243,\ p = 0.004)$$
(2)

$$LS = 0.8827 - 0.1353\ T_{p11} + 0.0044\ P_{p9} - 0.0022\ T_{p11}{}^2 + 0.002\ T_{p11}\ P_{p9} - 0.00004\ P_{p9}{}^2$$
$$\text{(Adjusted } R^2 = 0.245,\ p = 0.003)$$
(3)

$$PN = 1.2368 - 0.0239\ T_{p11} - 0.0063\ P_6 - 0.0062\ T_{p11}{}^2 - 0.0003\ T_{p11}\ P_6 + 0.00003\ P_6{}^2$$
$$\text{(Adjusted } R^2 = 0.206,\ p = 0.009)$$
(4)

$$PS = 1.1061 + 0.0188\ T_{p11} - 0.0019\ P_6 + 0.0016\ T_{p11}{}^2 - 0.0012\ T_{p11}\ P_6 - 0.00001\ P_6{}^2$$
$$\text{(Adjusted } R^2 = 0.378,\ p < 0.001)$$
(5)

$$LN = 3.1717 + 0.0627\ T_{p11} - 0.3116\ T_5 + 0.0007\ T_{p11}{}^2 - 0.006\ T_{p11}\ T_5 + 0.0108\ T_5{}^2$$
$$\text{(Adjusted } R^2 = 0.146,\ p = 0.033)$$
(6)

$$PN = 0.9246 - 0.4351\ T_{p11} - 0.0417\ T_5 - 0.0028\ T_{p11}{}^2 + 0.0244\ T_{p11}\ T_5 + 0.0028\ T_5{}^2$$
$$\text{(Adjusted } R^2 = 0.140,\ p = 0.038)$$
(7)

The results of this analysis supported the results of correlation analysis. On the one hand, a consistent significant contribution of temperature in the preceding November to all of the chronologies was found ($p \leq 0.038$). On the other hand, between the chronologies of different species and slope aspects, the other significant climatic factors were inconsistent, indicating the varied growth responses. Precipitation in the preceding September was significant in the regression of LN and LS ($p \leq 0.004$) but not in the regression of PN and PS. The regressed surface showed that at the two aspects, the tree-ring width index of *L. principis-rupprechtii* was significantly correlated with both precipitation and temperature, and the highest ring width index occurred in conjunction with climatic conditions that included both mean monthly temperatures of −4 °C to −3 °C and total monthly precipitation values of 0 to 50 mm (represented by the red area of the response surface shown in Figure 4a). As shown by the regression surface (Figure 4b), precipitation in the current June was significantly responsible for PN and PS ($p \leq 0.009$), however not for the LN and LS. In Figure 4c, the temperature in May contributed significantly to the growth of trees on the north-facing slope ($p \leq 0.038$), but the contribution to trees on the south-facing slope was not significant. When temperature in the current May ranged between 18 °C and 19 °C and temperature in the previous November ranged between −4 °C and −2 °C, growth

of the two species on the north-facing slope both reached their highest values (red area of the surface in Figure 4c).
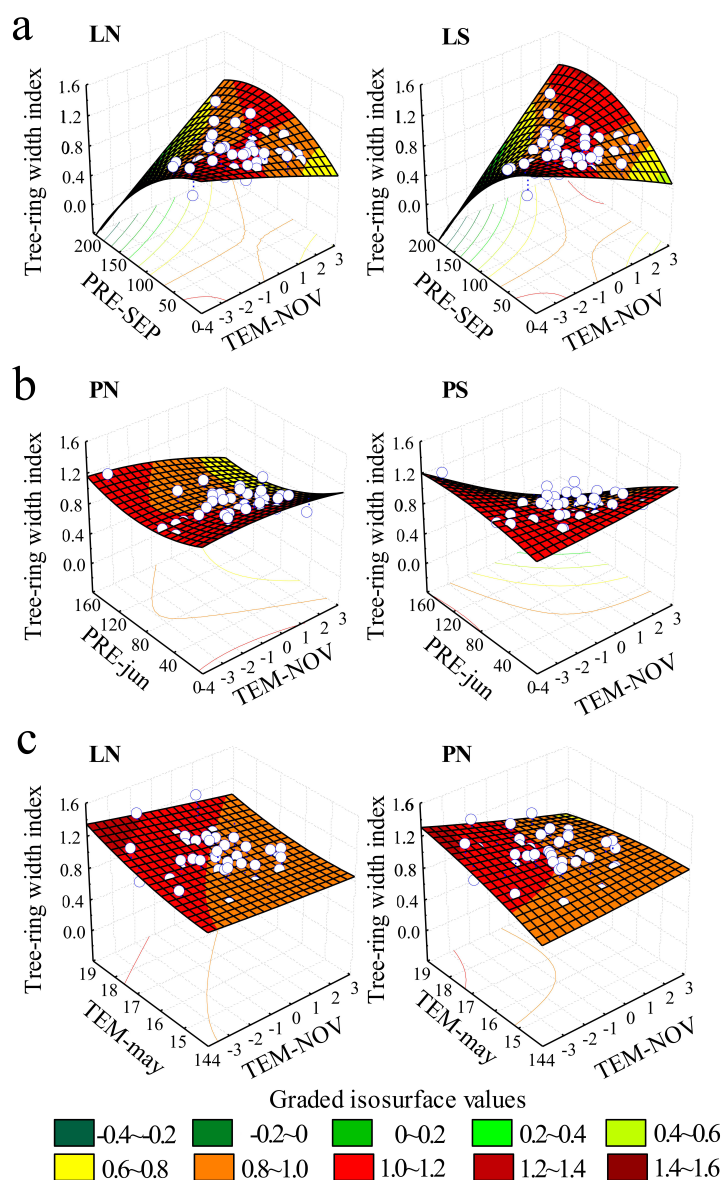

Figure 4. Results of response surface analysis for the two species on opposite slope aspects. The white points represent the tree-ring width index data for each year from 1958 to 2007. The capitalized months denote months belonging to the previous year. The prefix "PRE" indicates total monthly precipitation and "TEM" indicates monthly mean temperature.

4. Discussion

4.1. Common Relationships between Growth and Climate at Timberline

The GLK values between each pair of chronologies all reached the 95.0% significant level, supporting the suggestion of a synchronous growth rhythm for all of the trees within this timberline

ecotone (Table 3). The timberline supplied a harsh environment, which constrained the growth of trees belonging to two different species, and on two different topographic aspects. The synchronous growth rhythms implied the similar adaptation in growth and consequently deduced a common climatic response of trees in this timberline ecotone.

The significant correlation between monthly mean temperature in the preceding November and radial growth demonstrate this type of common climatic response (Figure 3). This result was confirmed by the significant contributions from monthly mean temperature in the preceding November to all of the chronologies derived from the response surface regressions (Figure 4). Our results were different with the previous studies that showed positive correlations of tree growth with temperature in the prior winter, which indicates the detrimental effect of low temperature to the shoot and bud of trees [27,28]. The underlying mechanism that caused high temperatures in winter to have negative effects on the tree-ring width is still unclear although some results like ours were presented. The negative effect of temperature on the growth of *P. meyeri* and *L. principis-rupprechtii* was reported by Cai and Liu in the Lüliang Mountains [4]. Similarly, at treeline of the Changbai Mountains in Northeast China [29] and the Norikura Mountains in central Japan [30], the growth of both *Larix olgensis* and *Betula ermanii* were negatively correlated with December temperatures. The most possible cause mechanism is that high temperatures enhance respiration rates, which could decrease the storage of carbohydrates produced. However, this reason is inappropriate because the temperature in early winter has become below freezing at our sites, under which conditions the respiration of frozen trees is very low. The cause-effect mechanism of this negative correlation between temperature in winter and growth still need more deep investigation.

4.2. Species-Dependent Growth in Response to Climate

According to the correlation analysis of tree-ring chronologies and monthly precipitation, growth of *P. meyeri* showed a significant relationship with precipitation during the current June, whereas growth of *L. principis-rupprechtii* was significantly associated with precipitation during the previous September (Figure 3). The variation in dendroclimatic response reflected differences in growth behavior and phenology between the two species. Unlike *P. meyeri*, *L. principis-rupprechtii* is a deciduous coniferous tree species. Its growth relies more on production during the prior growing season than that of the current season [31,32]. Based on our observations of phenology, defoliation of *L. principis-rupprechtii* happens during October. The energy and materials produced in the growing season before defoliation are stored for the next growing season. Because *L. principis-rupprechtii* can only add biomass through photosynthesis after foliation, energy from the prior year will be very crucial for initiating growth. At the end of the preceding growing season, less precipitation prior to defoliation can bring about more light input for photosynthesis, resulting in more net primary production stored for the next growing season. The negative effects of precipitation during autumn of the previous year on growth of this species have also been reported in the Wutai and Lüliang Mountains, both approximately 150 km from our study area [4,33].

As an evergreen, coniferous species, *P. meyeri* needs photosynthate directly from photosynthesis during the current growing season. Zhang *et al.* have reported that sunlight in the summer months is crucial to the growth of this species [34]. At higher elevations, abundant rainfall is generally

combined with increased cloudiness, reduced radiation input and lower temperature, which constrain tree growth [35].

4.3. Topography-Dependent Growth in Response to Climate

A significant, positive correlation between radial growth and temperature was found in the early growing season (May) on north-facing slopes but not on south-facing slopes (Figure 3). The significant positive correlations between temperature during the growing season and growth of *P. meyeri* and *L. principis-rupprechtii*, were also reported for north-facing slopes in other studies [4,34]. These climatic responses imply a limiting effect of cool summer months on tree growth, typical at high elevations in a semi-humid mountainous area [29,36]. At relatively high elevations in the Changbai Mountains of China, growth of *Pinus koraiensis* and *Larix olgensis* showed significant positive correlations with temperature in August and June, respectively. However, similar relationships were not found on south-facing slopes. The south-facing slope experiences a warmer microclimate because it receives more solar radiation; hence, its trees do not experience the constraint of low temperature. This phenomenon confirms the important effect of topographic aspects on the distribution of temperature and the limitation on tree growth, which is pronounced under semi-humid climatic conditions, regardless of the tree species. Another conifer tree species in the Luyashan Mountains, *Pinus tabulaeformis*, also showed significant positive correlations between tree growth and mean temperature in June and July, on a north-facing slope at relatively high elevations [37].

4.4. Possible Errors in the Climate and Growth Relationships

Summing up all the correlations between climate variables and radial growth of trees at timberline, growth of trees always showed significant positive correlations with temperature variables and significantly negative correlations with precipitation variables in prior year and current season. This phenomenon implied that both of the two conifer tree species were more temperature limited than water limited. This result just corresponded to the climatic conditions at high elevations with relatively plentiful precipitation and low temperature. However, there still had another possible error in the analysis of climate-growth relationships. Because of no meteorological station at high elevations, we used the spatially averaged data from low elevation stations. The precipitation correlations are statistically significant but the precipitation at low elevations only can account for about 76%–80% of the variation in high elevation precipitation (Figure 2), much smaller than that of temperature (approximately 98%). Although use the spatially averaged climate data was the best that can be done and can underestimate correlative relationships between temperature and montane tree-ring data [38], the increased error in researching growth-precipitation relationships was unavoidable.

4.5. Topography- and Species-Dependent Growth Trends under Climate Change

The relationships between tree growth and climate is an important aspect of treeline dynamic studies, because the potential impacts from climate change on tree growth, regeneration dynamics and consequently on the forest structure and treeline position [39]. Generally, it is hypothesized that tree growth at the upper treeline is normally controlled by temperature [40]. However, in our studies, the

response to temperature varied with species and topographic aspect. Based on the ANOVA analysis of climate data between 1958–1995 and 1996–2007, the mean value of regional annual temperature after 1996 was significantly higher than that before 1996 in the Luyashan Mountains, whereas the precipitation was decreased after 1996, although not significantly (Figure 5). At the same time, we used a three-year average method to detect the radial growth trend of trees. After 1996, although most of the growth trends increased synchronously, there was less consistency in growth trends between different species and different topographic aspects. With regard to species, the growth trend of *L. principis-rupprechtii* chronologies (LN, LS and LARIX) all showed a higher ratio than those of *P. meyeri* (PN, PS and PICEA) (Figure 6). This difference in response implied that trees of *L. principis-rupprechtii* may benefit more from climate change than *P. meyeri*. If this climate-warming trend continues, *L. principis-rupprechtii* might be more favored in the future than *P. meyeri*. At the same time, growths of both species are more temperature and possibly light limited than water limited. As the substantial warming continues, the relative importance of these limitations may reverse. A "divergent growth" has been proved in the growth of *P. meyeri* at this site by Zhang *et al.* [41]. With regard to topographic aspect, the increased ratio of tree chronologies on the north-facing slope (PN, LN and NORTH) appeared to be greater than those on the south-facing slope (PS, LS and SOUTH) (Figure 6). This suggested that trees on the north-facing slope will grow better than those on the south-facing slope, if the current trend in climate change continues. Many studies have demonstrated the altitudinal shift of treeline position in response to climate warming [42]. Moreover, variation in the magnitude of this shift among different slope aspects was also found in some studies [43]. In the Luyashan Mountains, based on the different climatic response of tree growth on the two opposite slope aspects, the potential of an elevation shift may be greater for the north-facing slope than for the south-facing slope.
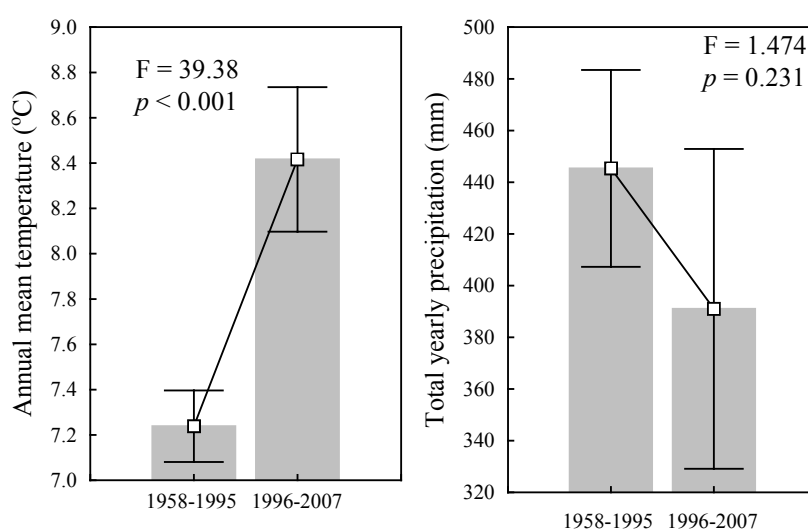

Figure 5. Comparison of annual mean temperature and total yearly precipitation between 1958–1995 and 1996–2007 by ANOVA.
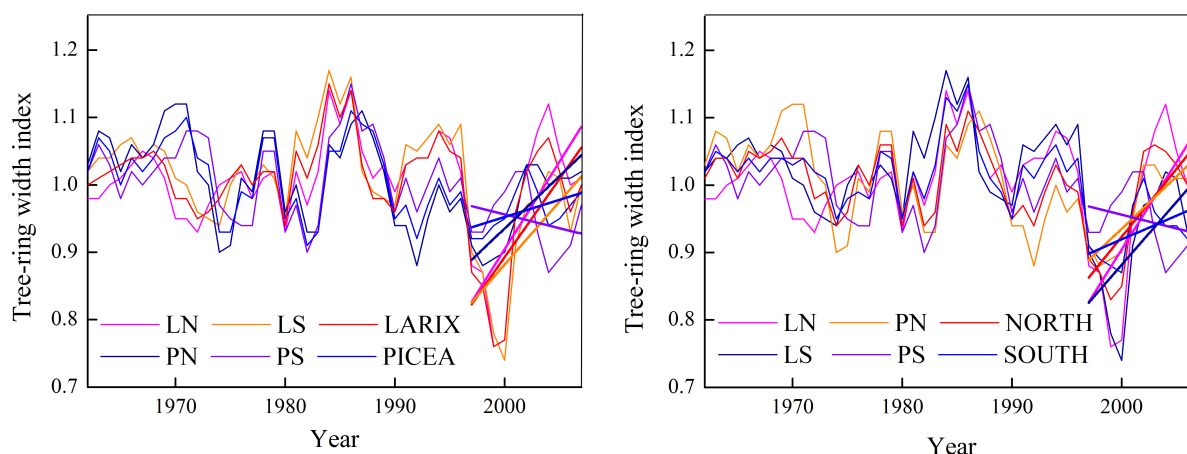
Figure 6. Trends of the eight chronologies using a three-year average.

5. Conclusions

In our study, the climatic responses of radial growth were investigated for two indigenous tree species, *P. meyeri* and *L. principis-rupprechtii*, growing on north-facing and south-facing slopes in the timberline ecotone of the Luyashan Mountains. The results showed that growth of the two species generally displayed significant negative correlations with temperature during the preceding November on both topographic aspects, showing a synchronous response to climate. Second, *P. meyeri* exhibited a significant negative correlation with precipitation during the current June, whereas *L. principis-rupprechtii* growth was significantly negatively associated with precipitation in the preceding September, suggesting a difference in phenology between the growth behavior of the two species. Third, the different temperature conditions between the two slope aspects produced a different climatic response in tree growth. Tree growth was significantly limited by low temperature in the early growing season on the north-facing slope, but this limitation did not appear on the south-facing slope. Based on the different growth trends, growth of *L. principis-rupprechtii* may be more favored than growth of *P. meyeri*, if the climate-warming trend continues. In addition, the north-facing slope may possess greater potential for an elevation shift of treeline position than the south-facing slope. Besides, both species at treeline are more temperature limited than water limited. However, the relative importance of these limitations may reverse as the substantial warming. This study demonstrated variation in climatic responses and growth trends between different tree species and different topographic aspects, and discussed the potential dynamics of treeline based on these relations. In the future, an investigation of tree regeneration would be a beneficial supplement to this work, when researching the detailed changes in forest structure and treeline positions.

Author Contributions

Wentao Zhang and Yuan Jiang were responsible for the research design and the editing coordination of the paper. Data preparation and analysis were partitioned as follows: site inventory and sample collection (Wentao Zhang, Mingchang Wang and Manyu Dong); tree-ring width measurement (Wentao Zhang, Mingchang Wang and Lingnan Zhang); tree-ring growth and climate relationship analysis (Wentao Zhang, Yuan Jiang and Manyu Dong). Wentao Zhang and Yuan Jiang contributed in editing and reviewing the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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