

## RESEARCH ARTICLE

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## Key Points:

- Minimum temperature ( $T_{\min}$ ) was a major limiting factor for Amur cork tree growth at regional scales
- The positive effects of summer temperature (precipitation) on Amur cork tree growth decreased (increased) with increasing latitude
- The spatial variability in growth-climate relationships of Amur cork tree may be connected to the range of PDO

## Supporting Information:

- Supporting Information S1
- Data Set S1

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## Spatial Variability in Growth-Climate Relationships of Amur Cork Tree (*Phellodendron amurense*) and Their Connections With PDO in Northeast China

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**Abstract** We used a dendrochronological approach to identify the spatial variability in growth-climate relationships of Amur cork tree (*Phellodendron amurense*), using a network of 12 sites across its natural range in Northeast China. Results showed that the signal-noise ratio, expressed population signal, and mean interseries correlations of the site chronologies decreased significantly with decreasing latitude. Correlation matrix, cluster, and rotated empirical orthogonal function (EOF) analysis all indicated that the 12 chronologies can be classified into two groups, the southern and northern chronologies. Minimum temperature ( $T_{\min}$ ) was a major factor limiting Amur cork tree growth at regional scales. Almost all sites had positive correlations with monthly temperature, while correlation coefficients with precipitation were much lower than minimum temperature correlations, and only a few months (January, April, and July) were significant ( $p < 0.05$ ). The positive effects of summer  $T_{\min}$  on tree growth were significantly decreased with increasing latitude (except BSL site), while positive effects of summer precipitation increased significantly with latitude and longitude and decreased significantly with altitude. The southern nine site chronologies (EOF-1) were significantly positively correlated with the seasonal or annual Pacific Decadal Oscillation (PDO) index of the previous year and the current spring, while the northern three chronologies (EOF-2) showed different relationships, which is consistent with the spatial relationship between PDO and local temperature. The spatial variability in growth-climate relationships of Amur cork tree can be affected by PDO, which can modulate the spatiotemporal variation of spring onset, autumn termination, and the effective accumulated temperature by affecting local temperature.

### 1. Introduction

Global climate change has had significant impacts on the distribution, growth, and reproduction of plants around the world (IPCC, 2013). Forest ecosystems are important parts of the earth's vegetation and are affected by climate change but also affect the climate by altering the radiation balance and hydrological cycle, as well as the global carbon cycle (Bonan, 2008; Thurner et al., 2017). The majority of dendrochronological studies carried out around the world, focused on studying a single site or a wide geographic area (Álvarez et al., 2015; Chavardès et al., 2013; Griesbauer & Green, 2010; Martin-Benito & Pederson, 2015). Inconsistent patterns of tree growth-climate relationships and spatial variability of growth-climate relationships were found in different regions (Chavardès et al., 2013; Griesbauer & Green, 2010; Mäkinen et al., 2002; Martin-Benito & Pederson, 2015; Wang et al., 2016). For instance, trees at the edges of their distribution ranges, such as at high elevation and in high latitudes are usually more sensitive to climate variability than trees in the main range of their distribution (Álvarez et al., 2015; Fritts, 1976; Mäkinen et al., 2002; Martin-Benito & Pederson, 2015). Consequently, it is critical to understand the spatial variability in tree growth-climate relationships for predicting the impact of climate change on species distribution and growth sensitivities.

Many recent tree ring studies have suggested that climate/environmental conditions within the geographical range of a species vary along latitudinal, longitudinal, and altitudinal gradients that influence the spatial

variability of tree growth-climate relationships (Álvarez et al., 2015; Mäkinen et al., 2002; Martin-Benito & Pederson, 2015; Wang et al., 2016). Many studies have focused on the spatial variability of forest/tree growth responses to climate change, but the drivers of large-scale variability in tree/forest growth-climate relationships are still not clear (Bigelow et al., 2014; Chavardès et al., 2013; Mäkinen et al., 2002; Martin-Benito & Pederson, 2015). The identification and understanding of these climate-effect mechanisms can provide valuable information for constructing more realistic models to accurately predict forest responses to future climate change. Thus, analyzing the patterns of spatial variability in tree/forest growth-climate relationships in climate change contexts is important for providing information to better forecast its effect on natural resources (Griesbauer & Green, 2010; IPCC, 2013; Martin-Benito & Pederson, 2015; Thurner et al., 2017). Large-scale climate oscillations, such as the Pacific Decadal Oscillation (PDO), El Niño–Southern Oscillation (ENSO), and Atlantic Multidecadal Oscillation (AMO), can affect local climate and tree/forest growth (Álvarez et al., 2015; Chavardès et al., 2013; Mäkinen et al., 2002; Zhu et al., 2016). Therefore, comprehensive analyses of the spatial patterns of tree growth-climate relationships are needed.

Broadleaf forests in the temperate zone provide ~60% of the global net forest carbon sink (Pan et al., 2011). The mixed broadleaf-Korean pine (*Pinus koraiensis* Sieb. et Zucc.) forests of Northeast China help maintain regional economic and ecological security. Prior dendroclimatological studies in this forest type have concentrated mainly on conifer trees, including *P. koraiensis*, *Abies nephrolepis* (Trautv.) Maxim, *Picea jezoensis* var. *microsperma*, and *Picea koraiensis* Nakai (Wang et al., 2016; Yao, 2013; Yu et al., 2006; Zhu et al., 2016). Studies on tree growth-climate relationships of angiosperms in Northeast China are scarce, especially at the regional and subregional scales (Li & Wang, 2013; Su & Wang, 2017; Zhu et al., 2015). However, they comprise more than 33% of the regional biomass; hence, their response to climate change will strongly influence the dynamics of these forests. Moreover, recent studies suggest that PDO could strongly affect local climate and tree growth in Northeast China (Yao, 2013; Zhu et al., 2016).

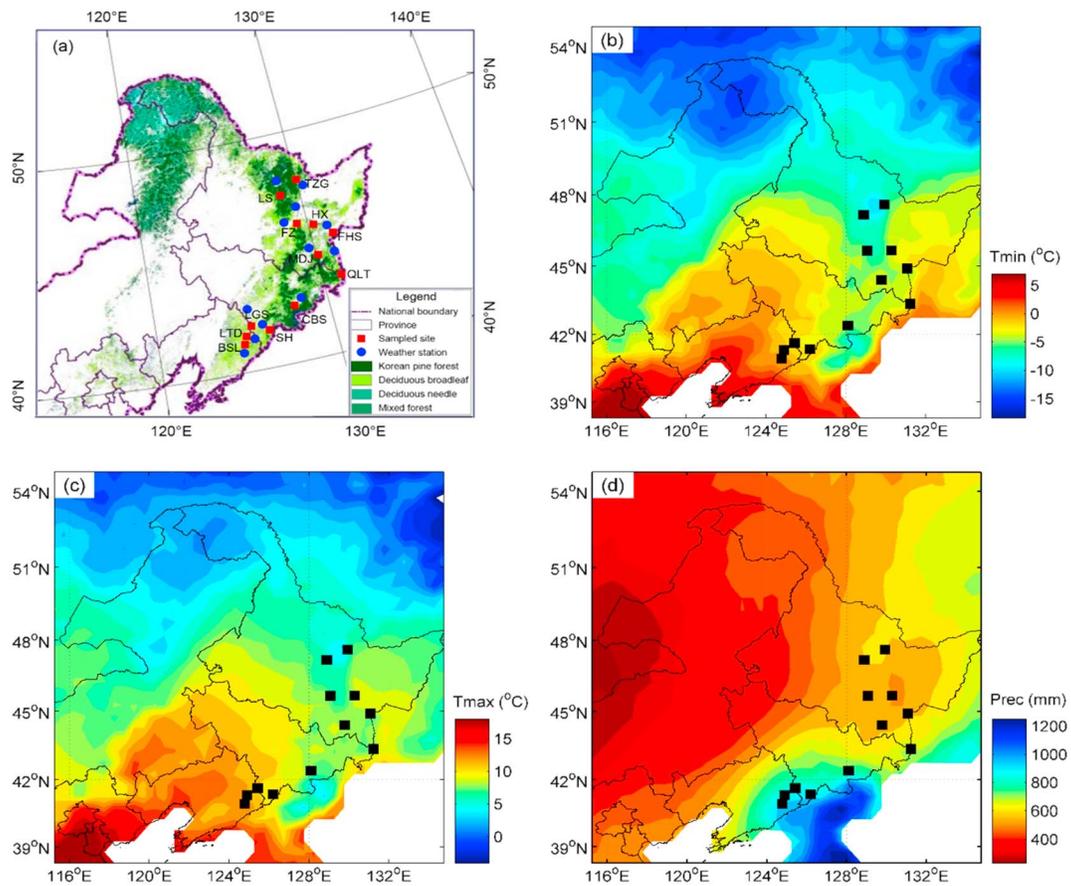
Amur cork tree (*Phellodendron amurense* Rupr.) is an important tree species in temperate broadleaf-Korean pine forests in Northeast China. It is widely distributed in Korea, Japan, northern and Northeast China, and parts of the Russian Far East (<http://www.efloras.org/>). This species not only has important economic and ecological values, but it is also a major source of huáng bò, an important element of traditional Chinese medicine (Li, 1982). In recent decades, the population of Amur cork tree has suffered a sharp decrease, and some protective and restorative work, afforestation, currently being conducted is not successful due to the complex and changeable climate (Li & Wang, 2013; Su & Wang, 2017). Therefore, it is urgent to improve our understanding of the relationship between Amur cork tree growth and climate factors to better protect this rare species. Two previous dendroclimatological studies of Amur cork tree were from a single site or a very small area (Li & Wang, 2013, Su & Wang, 2017), and the broadscale patterns of climatic limitations on its growth are not known. Hence, we carried out a regional dendroecological analysis on Amur cork tree from a network of 12 sites across its range in Northeast China. Our main objectives were to (a) investigate the dominant radial growth patterns of Amur cork tree at different spatial scales; (b) identify the spatial variability of tree growth-climate relationships along latitude, longitude, and altitude gradients; and (c) explore the potential linkage between the spatial variability of dendroclimatological relationships and PDO.

## 2. Materials and Methods

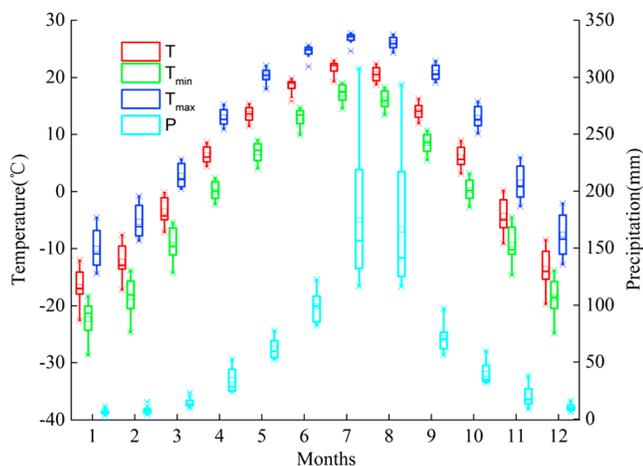
### 2.1. Study Area

Amur cork tree increment cores were collected from 12 sites that across the species' distribution from the northern edge of Xiaoxing'an Mountains (47.60N, 129.92E) to the southern Changbai Mountains (40.91N, 124.79E) in Northeast China (Figure 1). All sampled sites had minimal human disturbance and are typical broadleaf-Korean pine forests, which is the zonal vegetation in the northern temperate subzone of Northeast China. The main tree species include *P. koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurense*, *Juglans mandshurica*, *Tilia amurensis*, *Tilia mandshurica*, *Betula costata*, *Quercus mongolica*, *Ulmus japonica*, *Abies nephrolepis*, *P. jezoensis* var. *microsperma*, and *P. koraiensis*. The main bedrock is granite, and the most common soil type is dark-brown forest soil.

The study area climate is temperate continental monsoon, with cold winters and hot rainy summers. Mean annual temperatures range from 0.4 to 7.0°C. Annual precipitation ranges from 537 to 1,108 mm, with ~80% occurring from May to September (Table S1 in the supporting information and Figure 2). Mean



**Figure 1.** Spatial distribution of forest and sampled sites (panel a), annual mean minimum (panel b), and maximum (panel c) temperature and annual total precipitation (panel d) in Northeast China. The red squares and blue circles in panel a indicate the locations of sample sites and weather stations. The black squares in panels b–d indicate the locations of sampled sites. The distribution range of the broadleaf-Korean pine (*P. koraiensis*) forest within China occurs between 40.75°N and 49.82°N latitude and 124.75°E and 135°E longitude. The sampled site code is in Table 1. The climate data used in panels a–c are the CRU TS3.24 data set (0.5° × 0.5°) downloaded from <http://climexp.knmi.nl/>.



**Figure 2.** Box plot of the monthly mean ( $T$ ), minimum ( $T_{\min}$ ), and maximum ( $T_{\max}$ ) temperatures, and mean total monthly precipitation ( $P$ ) averaged for the 12 sites identified in Table S1.

annual temperature and total precipitation increases from north to south (Table 1). Monthly temperature variance in the dormant season (November–March) among all sites is larger than in the growing season, while it is the reverse for monthly precipitation (Figure 2).

## 2.2. Tree Ring Chronology Development

In the early summer of 2012 and 2014, one or two cores per tree were extracted using an increment borer at breast height (~1.3 m) from undamaged dominant or codominant standing trees in all 12 study forests. All cores were pretreated with standard dendrochronological procedures and were air-dried, mounted, and polished allowing each ring to be clearly identified with a binocular microscope. Each core was cross-dated to identify possible absent or false rings and assign accurate calendar years using the skeleton-plot method (Stokes & Smiley, 1968). Ring width was measured to the nearest 0.001 mm using a Velmex tree ring measurement system (Velmex, Inc., Bloomfield, NY, USA). Dating and measurement errors were checked with the COFECHA computer program (Grissino-Mayer, 2001).

**Table 1**  
*Site Characteristics and Statistics of Tree Ring Chronologies Used in This Study*

No.	Site	Lat. (°N)	Long. (°E)	Elev. (m)	MAT (°C)	MAP (mm)	Time span	SNR	MS	AC1	EPS	RBAR	No. T/C
1	TZG	47.598	129.924	381	0.4	619	1920–2013	17.2	0.18	0.70	0.95	0.51	20/40
2	LS	47.180	128.890	427	1.4	661	1950–2011	13.0	0.15	0.56	0.93	0.35	28/46
3	HX	45.672	130.295	582	3.6	556	1929–2013	18.1	0.16	0.80	0.95	0.63	16/31
4	FZ	45.661	129.081	350	2.6	592	1887–2013	4.4	0.21	0.51	0.81	0.30	17/31
5	FHS	44.894	131.084	585	4.0	537	1886–2013	7.7	0.17	0.78	0.89	0.34	17/32
6	MDJ	44.400	129.790	611	3.9	550	1917–2011	11.7	0.18	0.65	0.92	0.38	20/38
7	QLT	43.358	131.238	419	2.7	574	1916–2013	6.6	0.19	0.36	0.87	0.37	17/30
8	CBS	42.400	128.100	718	2.8	679	1790–2013	7.1	0.18	0.48	0.88	0.30	18/33
9	LGS	41.626	125.432	875	6.9	861	1916–2013	7.8	0.15	0.44	0.89	0.29	21/39
10	SH	41.356	126.211	930	5.4	888	1913–2013	11.7	0.18	0.82	0.92	0.38	21/40
11	LTD	41.304	124.897	882	6.7	853	1920–2013	4.2	0.14	0.54	0.81	0.26	17/28
12	BSL	40.913	124.790	1,030	7.0	1,108	1907–2013	2.9	0.15	0.59	0.74	0.18	16/31

Note. MAT = mean annual temperature; MAP = mean annual precipitation; SNR = signal-noise ratio; MS = mean sensitivity; AC1 = first-order autocorrelation; EPS = expressed population signal; RBAR = mean interseries correlation; No. T/C = tree/core numbers.

To remove nonclimate signals related to tree age, cross-dated ring width series were detrended to develop tree ring chronologies using the program ARSTAN (Cook, 1985). We fitted a negative exponential curve or linear straight line with any slope to the raw data series and divided the observed ring widths by the expected growth to obtain tree ring indices (Table 1). The standard chronologies were used in subsequent analyses.

### 2.3. Growth-Climate Relationships

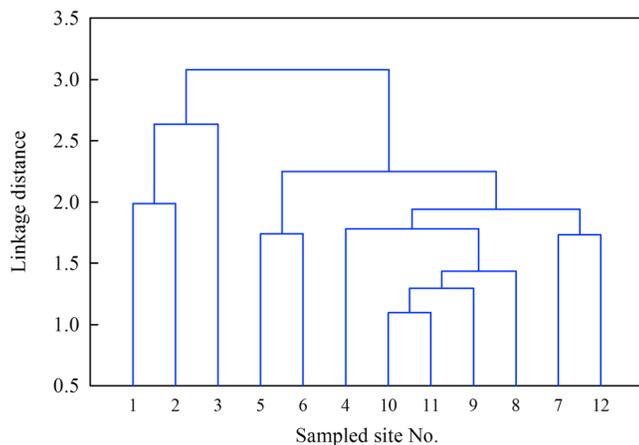
Correlation analysis was used to identify relationships between tree ring chronologies and the climate variables monthly and seasonal mean, minimum and maximum temperatures, and total precipitation from weather stations (<http://data.cma.cn>) nearest the sample sites (Table S1). We also examined the relationships between site tree ring chronologies and current and previous seasonal PDO indices (<http://www.data.jma.go.jp/gmd/kaiyou/data/db/climate/pdo/pdo.txt>) during their common periods. Seasonal timeframes were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

Cluster analysis based on the complete linkage of Euclidean distance was used to organize the 12 tree ring chronologies into groups for their 62-year common period from 1950 to 2011. In addition, rotated empirical orthogonal function (EOF) analysis was conducted for the 12 site chronologies for the common period 1950–2011 to identify their spatial structure and leading time series expansions. Several other regional growth patterns can be justifiably resolved by rotating more EOFs. Here we focus our attention on the well-separated, large-scale patterns of tree growth variability represented by the first two EOFs, which account for a significantly higher proportion of variance (EOF-1: 36.7% and EOF-2: 19.4%). The loadings on the first and second EOFs of the chronologies are shown in the Figure 4. Correlation analysis was conducted between the first and second EOF scores and monthly and seasonal climatic variables during the period 1950–2011.

Spatial correlations between the annual average (January–December) PDO index in the previous and current year and the annual averaged (January–December)  $0.5 \times 0.5$  gridded CRU TS3.24 minimum temperatures in the current year during the period 1950–2004 were performed to examine the influence of PDO on local temperature. Spatial correlations were calculated using the KNMI climate explorer (<http://climexp.knmi.nl>). Maps with filled  $p$  values  $>0.05$  were masked out.

## 3. Results

Descriptive statistics, commonly used in dendrochronology, provide a useful comparison of chronologies among sites (Table 1). The signal-noise ratio (SNR), expressed population signal (EPS), and mean interseries correlations (RBAR) showed that the 12 chronologies were a suitable sample for dendroclimatology analysis (Fritts, 1976). The first-order autocorrelation indicated that the previous year's climate conditions may affect Amur cork tree growth in the current year. Interestingly, the SNR, EPS, and RBAR of the site chronologies decreased significantly with decreasing latitude.



**Figure 3.** Cluster diagram for the 12 Amur cork tree chronologies based on the complete linkage of Euclidean distances. Sample site numbers are arranged according to latitude from north to south as in Table 1.

Intersite correlations among all 12 tree ring chronologies ranged from 0.11 to 0.71 (Table S2) and revealed spatial patterns. The northern chronologies (TZG, LS, and HX) did not correlate well with the southern ones (FZ, FHS, MDJ, QLT, CBS, LGS, SH, LTD, and BSL), while their internal correlations were significant (Table S2).

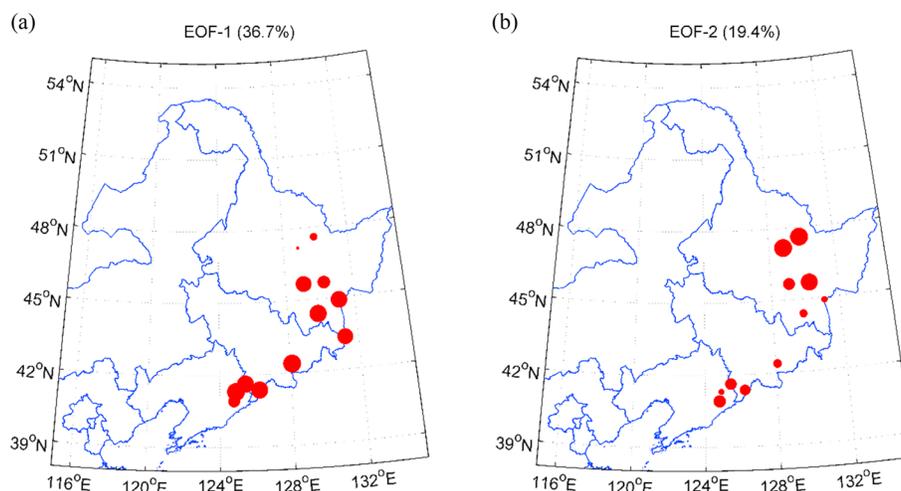
Cluster analysis indicated that the 12 chronologies can be classified into two groups, the northern and southern chronologies, at a linkage distance of 3.0 (Figure 3). These results agreed with the orthogonal relationship between the northern and southern chronologies noted in the correlation matrix (Table S2). As with cluster analyses, the loadings of the first two EOFs showed that the three northern site chronologies behave differently from the southern sites (Figure 4).

Growth-climate relationships of the 12 sites showed that mean monthly minimum temperature was the crucial limiting factor for Amur cork tree radial growth. Almost all sites had positive correlations with monthly temperature (Figure 5). Higher correlation values ( $r > 0.4$ ) were found with February, May, and August to October temperatures. Correlation coefficients with precipitation were much lower than minimum temperature correlations, and only a few months (January, April, and July) surpassed the 95% significance level (Figure 5). Climate sensitivity is not uniform over the study area (Figures 5 and 6). Correlation with minimum temperatures in summer (June–August) were not significant at the northern (TZG, LS) and southern (BSL) distribution edges, while precipitation was only significant ( $p < 0.05$ ) at FZ site (Figure 6).

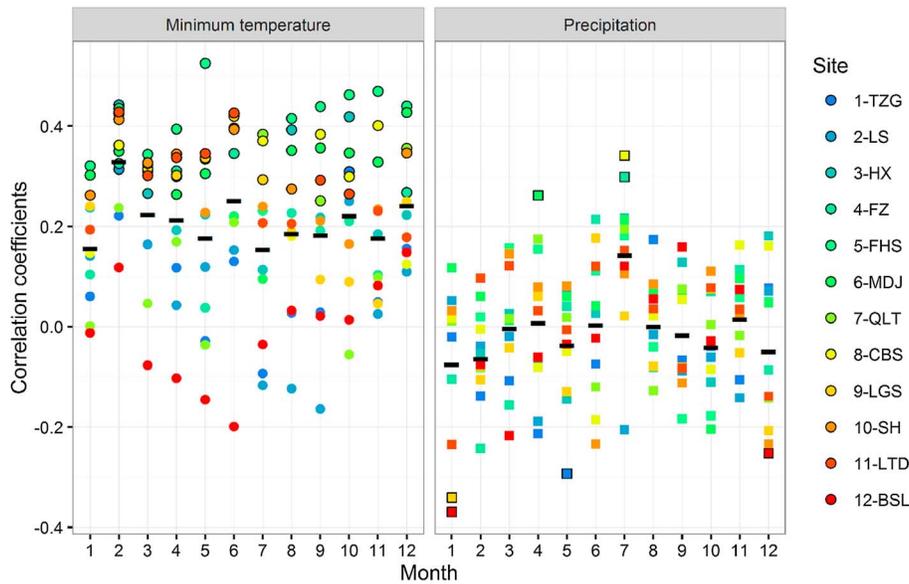
When examining all sites, no significant latitude (Figures 7a and 7d), longitude (Figures 7b and 7e), or altitude (Figures 7c and 7f) effects were found. However, a significant decrease (increase) of the relationship between growth and mean minimum summer temperatures was observed with increasing latitude (altitude) if the southernmost site was excluded (Figures 7a and 7c). On the contrary, correlation coefficients with summer precipitation increased significantly with latitude (Figure 7d) and longitude (Figure 7e) and decreased significantly with altitude (Figure 7f). These were also revealed by the monthly correlation analysis (Figures 5 and 6).

The EOF-1 representing the nine southern sites was positively and significantly correlated with temperature, especially minimum temperature, while the EOF-2 representing the three northern sites was negatively and significantly correlated with winter-spring precipitation (Figure 8). The common variance accounted for by the first two components suggests that there were large-scale environmental factors influencing the whole study area. The southern nine site chronologies were significantly correlated with the seasonal or annual

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**Figure 4.** Spatial patterns of the first (EOF-1) and second (EOF-2) empirical orthogonal functions (EOFs) of tree ring chronologies from 1950 to 2011. Red circles represent the positive EOF loading of each site, and the circle size is proportional to its magnitude.

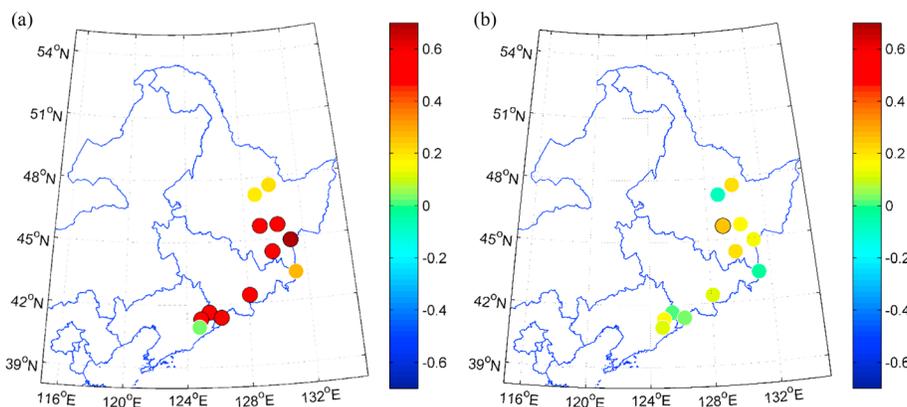


**Figure 5.** Correlation coefficients between tree ring chronologies and monthly mean minimum temperature (circle) and total precipitation (square) at each site. The north-south locations of study sites are indicated by cool to warm colors. Sites with significant ( $p < 0.05$ ) correlation are denoted by black frames. The mean value of correlation coefficients at each month is represented by a black horizontal bar.

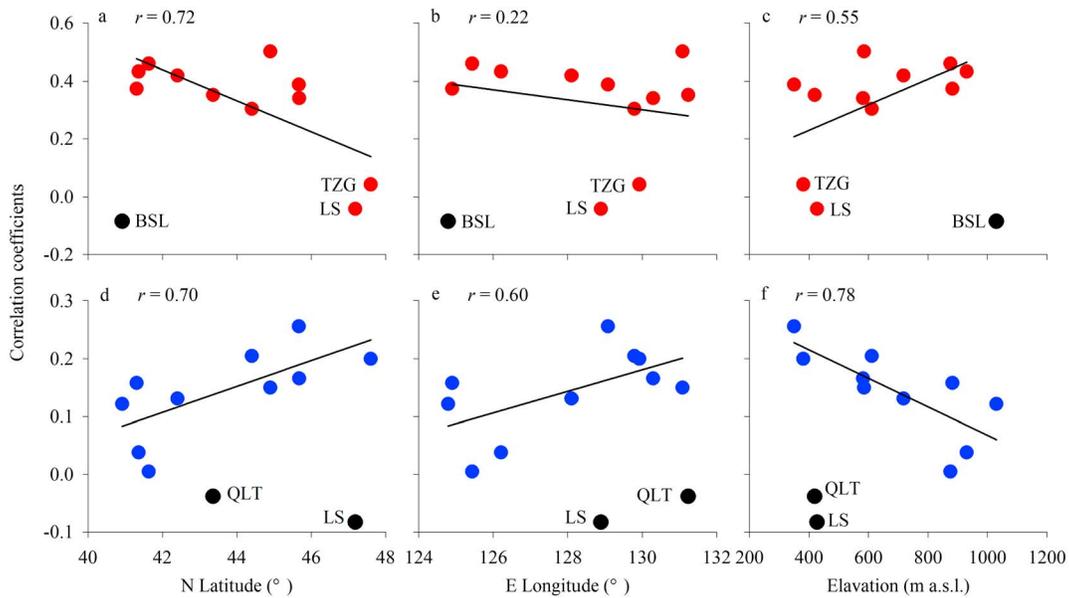
PDO index of the previous year and the current spring, while the northern three chronologies had different relationships (Table 2). This was also confirmed by the correlation analysis between the EOF-1 ( $r = 0.40$ ,  $p < 0.01$ ) and EOF-2 ( $r = 0.12$ ,  $p = 0.34$ ) scores and the PDO index in the previous year (Figure 9). Therefore, the spatial variability in growth-climate relationships of Amur cork tree could be connected to the influence of PDO (Figure S1).

#### 4. Discussion

The SNR, EPS, and RBAR of site chronologies were significantly related to latitude, perhaps due to climate stress having a greater effect on limiting tree growth and providing a more consistent climate signal (Fritts, 1976). We found a stronger effect of  $T_{\min}$  in the south than the north and a stronger effect of precipitation in the north than the south. This suggests that climate is often thought to have less influence on tree growth in the center a species' geographical range, while trees are more climatically limited at their range margins (Fritts, 1976). The growth of Amur cork tree was similar throughout most of the region during the common period 1950–2011 ( $0.11 < r < 0.71$ ; Figure S2 and Table S2), suggesting a common mechanism is

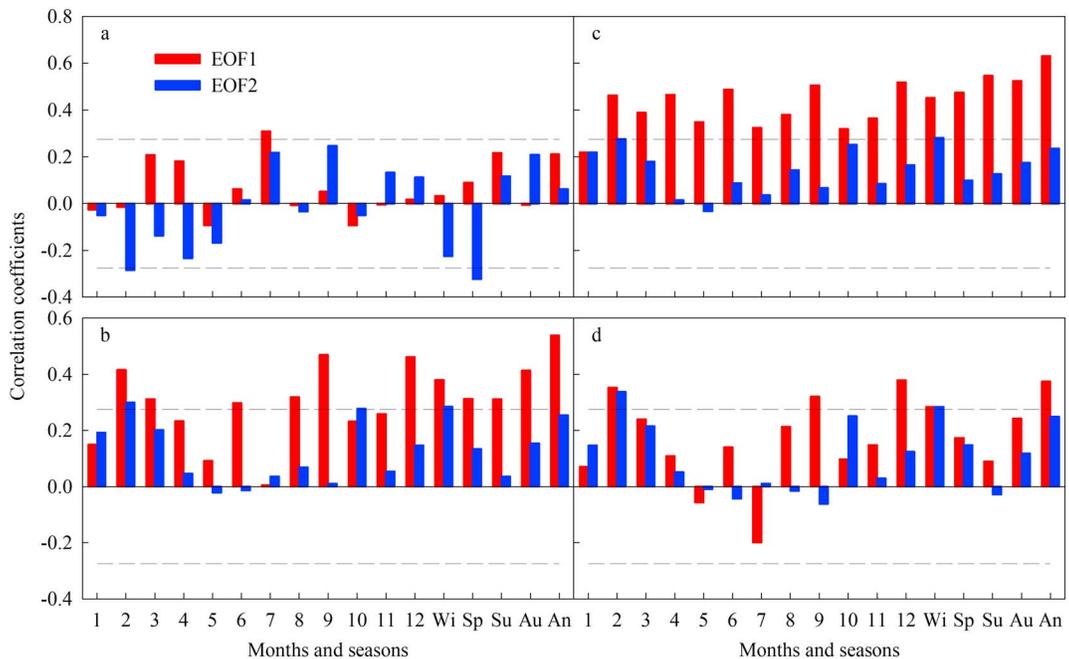


**Figure 6.** Relationships between Amur cork tree growth and summer climate. Colors represent Pearson's correlation coefficients between tree ring chronologies and mean minimum temperature (panel a) and total precipitation (panel b) in summer (June–August). Positive (negative) coefficients are represented by red (blue) colors and circles with black edge (greater than 0.275 or less than  $-0.275$ ) are significant at  $\alpha = 0.05$ .



**Figure 7.** Spatial variation of Amur cork tree growth-climate relationship in Northeast China. Correlation coefficients between tree ring chronologies and mean minimum temperature (red circle; a–c) and total precipitation in summer (blue circle; d–f) plotted as functions of site latitude (a and d), longitude (b and e), and altitude (c and f). Black circles indicate outliers that were not used for linear fitting.

influencing the species' growth response to climate.  $T_{min}$  is the main climate factor broadly limiting the growth of Amur cork tree at ecosystem to regional scales in the temperate broadleaf-Korean pine forests of Northeast China. Minimum temperatures have long been shown to limit the radial growth of trees at most high-altitude locations or in high-latitude regions, including eastern Asia (Lv & Zhang, 2013; Zhu et al., 2015), northern Europe, and North America (Bigelow et al., 2014; Fritts, 1976). Our investigation supports prior work at smaller scales (Li & Wang, 2013; Su & Wang, 2017) but also identifies a similar pattern of climatic sensitivity at a large spatial scale.



**Figure 8.** Correlation coefficients between the first (red bar) and second (blue bar) EOF scores and monthly and seasonal precipitation (a), mean temperature (b), mean minimum temperature (c), and mean maximum temperature (d) for the period 1950–2011. The short dash line represents the  $p$  value at 0.05. Wi, Sp, Su, Au, and An represents winter, spring, summer, autumn, and annual, respectively.

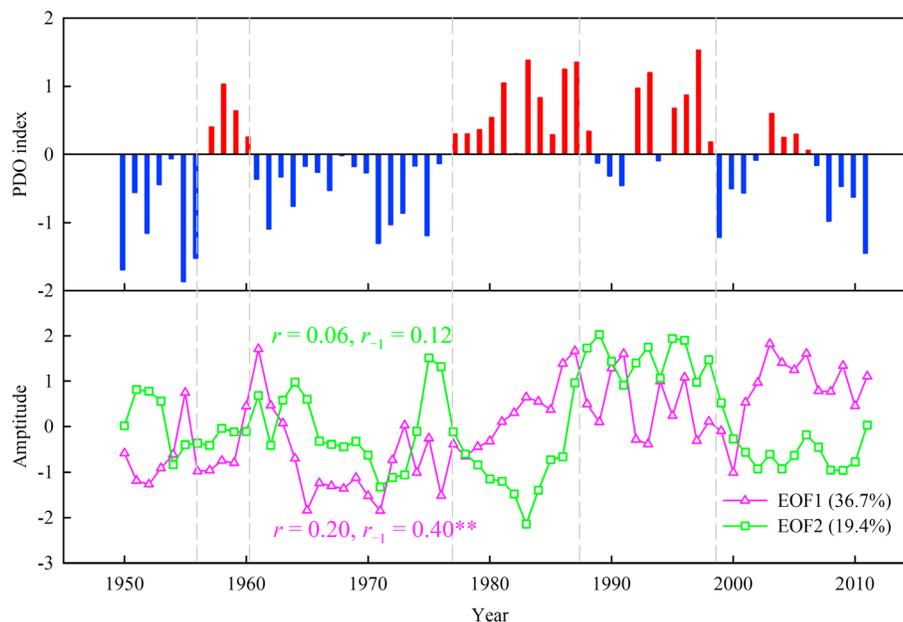
**Table 2**  
Correlation Coefficients Between Amur Cork Tree Ring Chronologies and Seasonal PDO Index During Their Common Periods

	Previous year					Current year			
	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Annual
BSL	0.29	0.31	0.23	0.27	0.31	0.20	0.08	0.01	0.14
CBS	0.19	0.20	0.09	0.26	0.19	0.21	0.03	-0.20	0.06
QLT	0.36	0.30	0.20	0.33	0.34	0.25	-0.07	-0.15	0.08
LTD	0.34	0.25	0.01	0.29	0.25	0.23	0.11	-0.11	0.13
LGS	0.33	0.32	0.16	0.33	0.30	0.34	0.18	0.00	0.23
SH	0.31	0.28	0.16	0.35	0.28	0.27	0.08	-0.15	0.13
FZ	0.55	0.45	0.39	0.40	0.52	0.54	0.38	0.19	0.44
FHS	0.43	0.37	0.22	0.37	0.42	0.35	0.20	0.00	0.24
HX	0.15	0.09	-0.06	-0.06	0.06	0.00	-0.05	-0.17	-0.09
LS	0.21	0.19	0.12	0.10	0.19	0.15	0.10	0.03	0.10
MDJ	0.30	0.27	0.02	0.12	0.24	0.15	0.11	-0.09	0.07
TZG	0.14	0.10	0.20	0.13	0.15	0.13	0.10	0.05	0.11

Note. The red figures represent the significance at  $p < 0.05$ .

Previous studies have suggested that drought is the primary limitation of broadleaf tree growth at large scales (LeBlanc & Terrell, 2011, LeBlanc & Stahle, 2015; Martin-Benito & Pederson, 2015; Pederson, 2005; Stahle & Hehr, 1984, Williams et al., 2010). It is unusual for a broadleaf species, such as Amur cork tree, in the temperate zone of the Northern Hemisphere to be limited by growing season  $T_{min}$ . Cool temperatures have been shown to limit broadleaf tree growth in the eastern United States, Northeast Asia, and Europe but only during winter months for a few broadleaf species at a large spatial scale (Hollesen et al., 2015; Martin-Benito & Pederson, 2015) or prior October or current July at a few sites or at the regional scale (Pederson, 2005; Pederson et al., 2004). The limitation of Amur cork tree growth by cool growing season temperatures at a large spatial scale seems to be distinctive.

Lower  $T_{min}$  can limit tree growth during the summer via several pathways. Cool temperatures strongly limit the activity of tree roots with soil microbes significantly decreasing the efficiency of water and inorganic ion uptake (Alvarez-Uria & Körner, 2007; Pregitzer et al., 2000) as well as the availability of nutrients and minerals (Bragazza et al., 2013). Minimum temperatures are also a critical factor affecting cambial activity, and a higher



**Figure 9.** Variation comparison between (a) PDO index and (b) the first and second empirical orthogonal functions (EOFs) of the tree ring chronologies from 1950 to 2011. The  $r$  and  $r_{-1}$  represent the correlation coefficients between the EOF score and the PDO index in the current and previous year, respectively.  $**p < 0.01$ . PDO = Pacific Decadal Oscillation.

$T_{\min}$  means a longer growing season, which directly determines the formation of a wider or narrower ring by affecting the accumulation of photosynthetic products (Fritts, 1976; Lv & Zhang, 2013; Zhu et al., 2015). Many studies have found that temperature, especially  $T_{\min}$ , has a direct impact on cell division, differentiation and enlargement of vessel and tracheid elements of broadleaf trees (Fonti et al., 2010; Fritts, 1976; Zhu et al., 2017). A higher daily  $T_{\min}$  in the early (May) or late (August and/or September) growing season can directly reduce the occurrence of freezing injury (Fritts, 1976; Kidd et al., 2014). In the dormant season, even though cambial activity has stopped, phloem sap may still be at risk of freezing damage caused by low  $T_{\min}$  (Kimmins, 1987). At the same time, higher winter and early spring  $T_{\min}$  could also protect tree roots and soil microbes from freezing damage, which may enable increased growth during the subsequent growing season (Fritts, 1976; Pederson et al., 2004). The impact of cool temperatures on tree growth is complex and needs further investigation on temperate broadleaf species.

We detected important differences between the northern and southern chronologies in our network. In the southern sites (EOF-1), tree growth was more positively correlated with climate than in the north (EOF-2), which further verifies the previous finding that tree growth is not necessarily limited by cold temperature at a species' northern distributional limit (Griesbauer & Green, 2010; Martin-Benito & Pederson, 2015; Tardif et al., 2006). A significant decrease was found in the relationship between tree growth and summer  $T_{\min}$  with increasing latitude (except BSL site; Figures 7a and 7c). In addition, the altitude-related trends of  $T_{\min}$  limitation on trees are stronger at lower elevations. The responses of tree growth to  $T_{\min}$  significantly decreased/increased with increasing latitude/altitude, which might result from a higher effective accumulated temperature, an earlier onset and later termination of growth at lower latitudes/altitudes (Fonti et al., 2010; Fritts, 1976). The influence of  $T_{\min}$  on trees agrees with the finding that the influence of temperature on trees was strongest at higher elevations in the southern region, a cooler area within the southern warm region, and a warmer area within the northern cool region (Martin-Benito & Pederson, 2015).

However, we found a positive effect of summer precipitation with increasing latitude and longitude and decreasing with altitude. This agrees with previous studies of Korean pine along latitudinal gradients (Wang et al., 2016) and Yeddo spruce (*P. jezoensis*) along altitudinal gradients (Yu et al., 2006) in Northeast China. The latitude and longitude response to precipitation is related to the spatial distribution of precipitation (Figure 1). Precipitation patterns in the region produce more severe water stress along a gradient from north to south, and east to west (Figure 1) and from high to low elevation (Yao et al., 2016). The lower total precipitation in the cooler north or east increase drought sensitivity despite lower evapotranspiration rates (Figures S3a and S3d). Similarly, precipitation limitations decreased with increased altitude. In contrast, we found that the tree's southern distribution may be strongly influenced by heat stress or water availability despite abundant precipitation. This was confirmed by the spatial response of Amur cork tree to the standardized precipitation-evapotranspiration index that showed a stronger drought stress in the north and the edge of the south, especially in winter and spring (Figure S3). However, the spatial pattern of drought effects in other seasons did not have a clear trend. This difference of tree growth-climate relationship in space or season could result from (a) the microclimate characteristics caused by elevation, topography, soil type, and land cover; (b) the ages/sizes of trees sampled; (c) local weather conditions; and (d) forest disturbance history, stand structure, and species competition. Water/drought stress might be a secondary codriving factor limiting Amur cork tree growth in the northern or eastern sites (Figure S3). Growth limitations should shift from low temperature to drought; unfortunately, it is difficult to quantify the shift from low temperature to drought with the number of sample sites. Nonetheless, the effect of future climate change on Amur cork tree might be decided by the temperature-precipitation balance across the latitude, longitude, or altitude gradients (Figures 7 and S3), as occurs in eastern North America (Martin-Benito & Pederson, 2015).

Most large-scale climate oscillations, such as PDO and ENSO, have been statistically linked with the spatial variability of growth-climate relationships along climatic, latitudinal, or altitudinal gradients (Álvarez et al., 2015; Chavardès et al., 2013; Nakawatase & Peterson, 2006; Wang et al., 2016). In this study, much of the variance in tree growth could be explained by PDO, which confirmed that the spatial variability in growth-climate relationships might be affected by the PDO. Our study area was close to the Pacific Ocean and most previous regional dendroclimatological studies have revealed that the PDO significantly affects the climate and tree growth in Northeast China (Wang et al., 2016; Yao, 2013; Zhu et al., 2016). The weak linkage between PDO index and the northern tree ring chronologies might be because the northern sites are farther from the

Pacific Ocean, where the impact of PDO is weaker. The teleconnection between the PDO index and local temperature confirmed our explanation (Figures S1 and S1b). In addition, composite maps of the 500-hPa vector wind composite mean during the period 1948 to 2017 (Figure S1c) shows the mean 500-hPa winds exhibited northwesterly flow Pacific Ocean over most regions of Northeast China. This large-scale atmospheric circulation is consistent with the teleconnection between temperature and PDO (Figure S1a). Temperature can affect the spatiotemporal patterns of physiological activities and accumulation of organic matter in trees. In our study, the spatial patterns of growth season length (the starting [spring onset] and ending [autumn termination] time of tree growth) and the effective accumulated temperature along latitudinal gradients influenced tree growth (Figure S4). Previous studies in North America and Eurasia have confirmed that the PDO can modulate the spatiotemporal variation of spring onset by affecting atmospheric circulation patterns and temperature variability (Ault et al., 2011; Belmecheri et al., 2017; McCabe et al., 2012). The positive anomalies of PDO indicated high pressure over the northern part of our study region and low pressure in the south that favored warm air advection in the northwest and resulted in earlier leaf onset, later leaf loss, a longer growing season, and higher effective cumulative temperature associated with PDO (Figure S5). Negative anomalies on the other hand are associated with later leaf onset, earlier leaf loss, a shorter growing season, and lower effective accumulative temperature in the northwest and earlier in the south (Figure S5). In addition, during the positive phase of PDO with high temperature, the cold air masses in the north made the positive effect of high temperature weaken, while during the negative phase of PDO with low temperature, the warm air masses made the negative effect of low temperature weaken (Figure S5). This helps explain why the radial growth of Amur cork tree in the south has a high positive correlation with temperature, while trees in the north do not. Therefore, the different effects of PDO in space could be a reason for the spatial variability in growth-climate relationships of Amur cork tree.

Our results have important implications for managing forests in northeastern China and can be used to forecast forest dynamics and estimate forest productivity and carbon storage under future climate change. To improve the survival of Amur cork tree, afforestation should be given priority in high-elevation sites of the southern region, while in northern sites irrigation or other nurturing measures are needed at the sapling stage to alleviate severe water/drought stress. If the existing climate continues to warm, the distribution range of Amur cork tree could expand northward, and its growth rate may increase especially at higher elevations of the southern region. Amur cork tree growth in broadleaf-Korean pine forests could be a huge potential carbon sink. At the same time, water/drought stress on Amur cork tree will increase in the north and the southern edge. We also found a significant positive effect of temperature or climate change (warming) on broadleaf tree species, for example, Amur cork tree (this study), *F. mandshurica* and *J. mandshurica* (Li & Wang, 2013; Su & Wang, 2017; Zhu et al., 2015), was opposite of conifer species in the broadleaf-Korean pine forests, such as the *P. koraiensis* (Wang et al., 2016; Zhu et al., 2016), *P. jezoensis* var. *microsperma* (Yu et al., 2006), *Abies nephrolepis*, and *P. koraiensis* (Wang et al., 2016; Yao, 2013; Zhu et al., 2016). Whether such opposite effect of temperature/warming on the growth of conifer versus broad-leaved species exists throughout the broad-leaved Korean pine forest requires further study. However, it is very important for forecasting future trends in the floristic composition of broad-leaved Korean pine forests.

Furthermore, a wider, more precise replication covering the complete distribution ranges of Amur cork tree would allow an improved understanding of its physiological threshold (shift of low temperature to drought). It would help clarify the geographic boundaries of the temperature-precipitation balance as well as other large-scale factors/driving that control tree growth-climate relationship in the north. The effects of PDO on the spatial variability of Amur cork tree growth-climate relationships need to be further understood and verified. Only in this way can we fully understand the spatial variability of Amur cork tree growth-climate relationships as well as the forest dynamics or response of Amur cork tree to future climate change.

## 5. Conclusions

In this study, we found that  $T_{\min}$  was the main factor limiting Amur cork tree growth at regional or ecosystem scales. The positive responses of growth to  $T_{\min}$  significantly decreased/increased with increasing latitude/altitude. This might result from a higher effective accumulated temperature, an earlier onset or later termination of growth at lower latitudes/altitudes. However, the positive effect of summer precipitation with increasing latitude and longitude is coordinated with the spatial distribution of precipitation

patterns. Moreover, drought stress was a secondary codriving factor limiting tree growth of Amur cork tree in the north and the edge of the south, especially in winter and spring. The effect of future climate change on Amur cork tree might be affected by the temperature-precipitation balance across latitude, longitude, or altitude gradients.

The spatial variability in growth-temperature relationships of Amur cork tree coupled with the effects of PDO on tree growth, as well as the impact of PDO on surface temperature in northeastern China confirmed that the PDO can be a major large-scale factor affecting the spatial variability of tree growth-climate relationships. The PDO can modulate the spatiotemporal variation of spring growth onset, autumn termination, and the effective accumulated temperature. In addition, a wider, more precise replication of this study across the entire distribution range of Amur cork tree would allow an improved clarification of the species' physiological threshold or geographical boundaries of the temperature-precipitation balance as well as other large-scale factors that control tree growth-climate relationships in the north.

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