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ORIGINAL PAPER

# Spatiotemporal evidence of tree-growth resilience to climate variations for Yezo spruce (*Picea jezoensis* var. *komarovii*) on Changbai Mountain, Northeast China

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**Abstract** Global warming-induced changes in tree-growth resilience to climate variations have been widely reported for mid- and high-latitude regions around the world. Most studies have focused on the spatial variability of trees in radial growth–climate relationships on Changbai Mountain in Northeast China, but little is known about temporal changes in tree growth in response to climate. We explored the stability of effect of climate variables on radial growth of Yezo spruce [*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu] at 1200, 1400, and 1600 m above sea level, representing low, middle, and upper ranges of the spruce–fir mixed forest on Changbai Mountain. The results showed that the relation between tree growth and climate did not vary with altitude, but the stability of the tree-growth–climate relationship did vary with altitude as the climate changed. Radial growth of Yezo spruce at all three elevations was influenced primarily by maximum temperature during May (Tmax5) and mean minimum temperature from January to March (Tmin1–3). More specifically, the relationship strengthened significantly at lower elevations, but weakened significantly at higher elevation, and fluctuated at mid elevations since 1980. Increase in Tmin1–3 and decrease in Tmax5 were the main reasons for the decrease in the radial growth at three altitudes. The findings of this study clarified that the decrease in radial growth on Changbai Mountain is not a "divergence problem" of an unexpected decrease in tree growth in response to an increase in mean temperature and provides a reference for using tree-ring data to reconstruct climate patterns and/or predict the growth of trees under various climate change scenarios.

**Keywords** Altitudinal gradient · Changbai Mountain · Ring width · Spatiotemporal stability · Yezo spruce

## Introduction

Global warming has been predicted to significantly impact tree growth (Shao et al. 2003; Shestakova et al. 2016), mortality of dominant trees (Dai et al. 2013), and vegetation distribution at mid to high latitudes in the Northern Hemisphere (Kelly and Goulden 2008). In the context of climatic change in Northeast China, questions have understandably arisen concerning forest composition, survival and growth in response to annual climate variability.

It is widely acknowledged that the effects of climate on tree growth vary along latitudinal and altitudinal gradients (Yu et al. 2006; Griesbauer and Green 2012). In the Northern Hemisphere, trees growing at more northerly latitudes or higher altitudes in their distributional range will

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benefit from climate warming, with faster growth resulting in wider tree rings and the opposite being the case for trees at more southern latitudes and lower altitudes (Shen et al. 2015). This expectation is based on the uniformitarian assumption, which assumes that the relationship between tree growth and limiting climatic variables such as temperature and precipitation remains stable over time as these variables fluctuate within a certain range (Fritts 1976).

Recently, however, many studies have reported that radial growth of some trees at higher latitudes or altitudes in the Northern Hemisphere has been decreasing (Herguido et al. 2016). Such an altered relationship between radial growth and climatic data has been termed the divergence problem, which is defined herein as the tendency in recent decades for tree growth at some previously temperature-limited northern sites to demonstrate a weakening (i.e., decrease) response to mean temperature increase, thus diverging from the expected pattern. This phenomenon is also described as a decrease in climate sensitivity (D'Arrigo et al. 2008). Thus, the pattern of the relationship is changing, i.e., radial growth is either invariable or decreasing with increased temperature instead of increasing with a rise in temperature. These findings suggest that tree growth–climate relationships might be unstable under a regime of climate warming, violating the uniformitarian assumption, and strongly challenges the basic principle of dendrochronology.

Globally, most trees referred to in studies on the divergence problem are conifers, and most are in regions where the climate is becoming warmer and drier. Conifer trees begin their growing season earlier and, compared with deciduous trees, have a longer growth period in which they are exposed to climatic factors (Yu et al. 2006; Wang et al. 2009; Bai et al. 2016; Zhu et al. 2018). The fact that most cases of the divergence problem occurred in warming/drying regions has been attributed to two main causes. One is that climate warming might result in temperatures greater than the maximum endurable limit of tree growth, which shifts the effects of climate on growth from positive to negative. The other is that climate warming might increase water deficits for tree growth, with temperature shifting to the water limit (Jacoby and Jacoby 1995; Wilmking et al. 2005). Given that the divergence problem has been reported more often for conifers in the regions with warming–drying climates, better knowledge of the precise causes of this apparent instability in the climate–growth relationship would enhance understanding of the complex influences of climate change on conifer tree growth for individuals and the forest ecosystems they dominate.

Northeast China has experienced a dramatic change in climate reflected in an obvious warming–drying trend in recent decades (He et al. 2013). The Changbai Mountain, with elevations up to 2700 m above sea level (a s l) are the highest in Northeast China and are renowned for a distinctive vertical zonation of vegetation. They provide an ideal study area to explore the effects of climate change on tree growth. Meteorological records indicate that the climate in the area has clearly warmed during recent decades, but precipitation has not increased over the same period. As a consequence, climate drying may be simultaneous with warming in the area.

Yezo spruce [*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu] is one of the dominant conifer tree species in the spruce–fir [*Abies nephrolepis* (Trautv.) Maxim] mixed forest, ranging from 1100 to 1700 m a s l in the Changbai Mountain. Previous studies of the area have explored the dynamic relationships between climate variables and spruce radial growth. These showed that the growth–climate relationship varied with altitude, with precipitation more limiting at lower altitudes (Yu et al. 2006, 2011) and temperature more limiting at higher altitudes (Gao and Wang 2011; Li et al. 2011; Yu et al. 2011). In addition, previous work has found that radial growth of spruces at higher altitudes has decreased due to the warming–drying climate (Li et al. 2012) or will decrease under a climate warming scenario (Yu et al. 2011), thus presenting a type of divergence problem (Wang et al. 2017). However, there has been no direct evidence that the climate–growth relationship has varied with time or with climate warming over recent decades.

Given that the divergence problem was caused by the warming–drying climate, exploring the dynamic relationship of climate growth along an altitudinal gradient or over time will help us to understand the stability of spruce growth and the underlying causes of that stability. The present work analyzed tree-ring width based on data for spruce at three elevations along an altitudinal gradient on the Changbai Mountain. The objectives were to (1) explore how climatic variables influence spruce growth on the mountain, (2) examine the altitudinal differences in the climate variables that affect spruce growth, and (3) assess the stability of the observed climate–growth relationship over time.

## Materials and methods

### Study area

The study area is on the northern slope of the Changbai Mountain Natural Reserve in Northeast China (41°31′–42°28′N, 127°9′–128°55′E). The altitudinal vegetation zonation within the study area consists of four divisions: Korean pine (*Pinus Koraienese* Sieb. et Zucc) and broadleaf mixed forest extending from ~ 700–1100 m a s l;

spruce–fir forest from 1100 to 1700 m a s l; Erman's birch (*Betula ermanii* Cham.) forest, which forms the upper limit of forest cover on the mountain, from 1700 to 2000 m a s l; and alpine tundra above 2000 m a s l. We selected sites subject to minimal anthropogenic disturbance, given that the Changbai Mountains have drawn ever more tourists since the 1980s. Moreover, the northern slope of Changbai Mountain is gentle (about 2.4%), providing site conditions with no major obstructions to tree radial growth and adequate for analysis of dendroclimatology.

### Field sampling

Based on a representative distribution range for Yezo spruce in the Changbai Mountain Natural Reserve, three sample sites were selected along an altitudinal gradient at 1200, 1400 and 1600 m a s l. Within each sample site, trees were selected using a typical dendrochronological sampling strategy and randomly sampled to allow a more representative sampling of the forest (Fritts 1976).

### Sample processing

Two cores were extracted from each tree at ~ 1.3 m height using a 5.1-mm increment borer. Cores were taken at 180° to one another on cross-slope positions to acquire samples for deriving the average radial growth. At least 20 trees of Yedo spruce were sampled from the sites to ensure adequate replication.

All cores were air-dried and mounted on grooved boards. The cores were then sanded to a 600-grit polish for visualizing the annual rings (Stokes and Smiley 1968). Ring widths were measured to the nearest 0.01 mm using computer software TSAP of LINTAB 5 and a high-resolution flatbed scanner to permit the extraction of growth trends (Rinn 2003). The computer program COFECHA was then employed for statistics (Holmes 1983).

### Development of chronologies

Steps were taken to reduce the potential bias of standardization effects by introducing artificial divergence in the development of our master tree-ring chronologies. To remove age-related and localized disturbance-related trends, raw ring-width series were detrended using a cubic smoothing spline (Cook and Peters 1981) that preserved 50% of the amplitude over a wavelength of 67% of the series length in ARSTAN (Cook 1985). An autoregressive model was then used to remove autocorrelation present in each tree ring chronology. The standard chronology (STD) and residual chronology (RES, Table 1) were obtained using ARSTAN (Cook 1985). When autoregressive modeling is used to remove the problem of biological persistence in the resulting series, the RES contains more high-frequency signals, which is better for assessing climate–growth relationships (Gazol et al. 2015). To avoid possible "end-effect" bias, the residual chronology is preferred to analyzing the climate–growth relationship (Schneider et al. 2014). In light of the above, we selected the RES for the analysis.

### Climatic data

Climatic data including monthly total precipitation (*P*), monthly mean minimum temperature (Tmin), monthly mean maximum temperature (Tmax) and monthly mean temperature (*T*) were obtained from the Songjiang Meteorological Station (42°43′N, 128°12′E, 721 m a s l). The station at the foot of the Changbai Mountain, which is close to the research area, has been collecting meteorological data since 1958. The climatic data were extracted from the China Meteorological Data Sharing Service Network (http://data.cma.cn/). The Changbai climate consists of warm, moist, rainy summers and cold, dry winters, with annual mean temperatures between 1.1 and 4.8 °C. From 1980 to 2014, annual mean temperature increased significantly (+ 0.05 °C/year), while precipitation was almost unchanged (Fig. 1). The maximum temperature in the hottest month (July) was 24.6–29.6 °C, and minimum temperatures in the coldest month (January) ranged from − 29.9 to − 20.9 °C (Fig. 2). Annual precipitation was 459.2–920.6 mm (Fig. 1); 44–73% of the total fell in June–August (Fig. 2).

### Climate–growth relationships

The relationships between climate and radial growth of Yezo spruce were analyzed using bootstrapped correlation functions via the software Dendroclim2002 (Biondi and Waikul 2004). The climatic variables included *T*, Tmax, Tmin and *P* from the previous November to current October. To test the temporal stability of the climate–growth relationship, moving correlation functions between the three chronologies and limiting climate variables (temperature, precipitation) were calculated via a 25-year time window using Dendroclim 2002. To precisely calculate the climate–growth relationships with altitude, we took as base meteorological data, the temperature at 700 m a s l, and calculated temperature at other elevations based on that data using a lapse rate of 0.6 °C/100 m (Li et al. 2011).

For validating the temporal stability of the climate–growth relationship, we also determined several linear regression equations via a stepwise regression method, using tree-ring indices as dependent variables and monthly climatic data as independent variables based on the bootstrapped correlation (25-year moving window). R-squares

**Table 1** Characteristics of sample sites and summary statistics for RES chronologies of Yezo spruce

| Elevation (m) | Cores/stems | Time span (SSS = 0.85) | TRW(SD) (mm) | SD | MS | AC1 | SNR | EPS | rbr | PC1 (%) |
|---|---|---|---|---|---|---|---|---|---|---|
| 1200 | 42/23 | 1835–2014 | 1.00 (0.18) | 0.165 | 0.176 | 0.008 | 17.6 | 0.95 | 0.311 | 33.55 |
| 1400 | 54/30 | 1855–2014 | 1.31 (0.33) | 0.133 | 0.153 | 0.006 | 24.0 | 0.96 | 0.343 | 36.44 |
| 1600 | 65/33 | 1790–2014 | 1.12 (0.30) | 0.127 | 0.152 | 0.011 | 29.9 | 0.97 | 0.360 | 37.70 |

*SSS* 0.85 refers to information for subsample signal strength attaining 0.85; *TRW* tree-ring width of raw measurement series; *SD* standard deviation; *MS* mean sensitivity; *AC1* first-order autocorrelation; *SNR* signal to noise ratio; *EPS* expressed population signal; *rbr* mean correlation between trees; *PC1* variance in first eigenvector

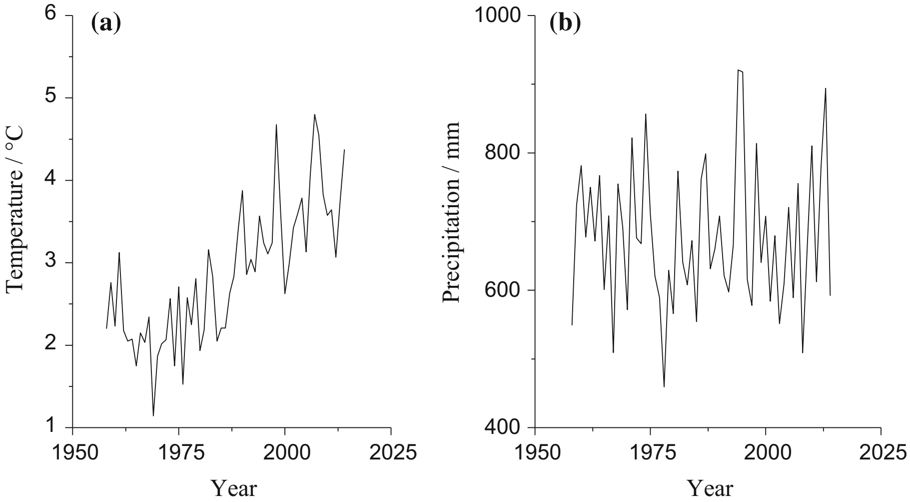

**Fig. 1** Annual mean temperature (**a**) and annual total precipitation (**b**) in the study area from 1958 to 2014, based on records from the Songjiang meteorological station

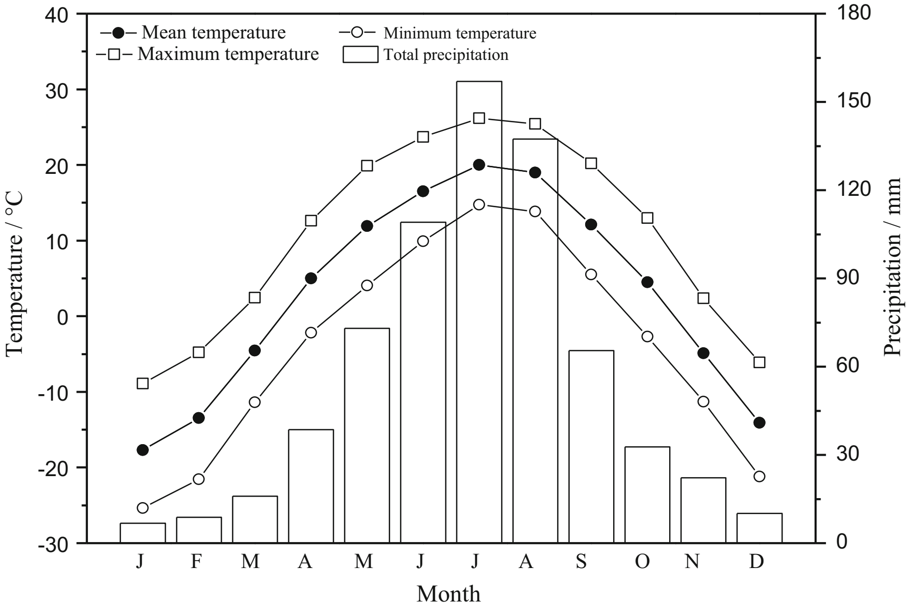

**Fig. 2** Monthly total precipitation, mean temperature, and maximum and minimum temperatures in the study area from 1958 to 2014, based on records from the Songjiang meteorological station

were calculated using a multiple linear model with R software environment, as shown in Eq. (1).

$$\mathrm{Chr} = \beta_0 + \beta_1 \mathrm{Cli}_0 + \beta_2 \mathrm{Cli}_1 + \cdots + \beta_{j+1} \mathrm{Cli}_j + \varepsilon \tag{1}$$

where Chr is the value of chronology, $\mathrm{Cli}_k$ ($k$ = 0, 1,…, j) are the climatic variable that significantly affected tree growth as calculated by DENDROCLIM 2002, $\beta_0$ was set as 0, $\beta_k$ ($k$ = 1,2,…, $j$ + 1) were all set as 1.

## Results

### Chronology character

Yezo spruce varied in age and mean ring width across the three sites. The RES could date back to 1835 at elevation of 1200 m a s l, to 1855 at 1400 m a s l, and to 1790 at 1600 m a s l (Table 1). The mean raw ring width ranged from 1.00 to 1.31 mm, initially increasing with altitude and decreasing afterward. Yezo spruce at 1400 m a s l had the largest mean tree width, and spruce at 1200 m a s l had the largest statistical standard deviation (SD) and mean sensitivity (MS) (Table 1).

The MS and SD of the three chronologies were similar and $< 0.2$. The first-order autocorrelation coefficients (AC1) ranged from 0.006 to 0.011, suggesting that RES chronologies retained less low-frequency information. Common interval analyses revealed that the expressed population signal (EPS) at all sites exceeded 0.85, indicating that the theoretical population for each chronology was well represented. Large values of SNR ($> 15.0$) indicated that the chronologies were of high quality and reliable. Strong reliability of the chronologies was further indicated by mean correlation between trees (rbr), which ranged from 0.311 to 0.360, and also by the large variance for the first principal component (PC1), which varied from 33.55 to 37.70%. This result suggests that the Yezo spruce chronologies contain a large amount of climatic information (Table 1).

### Long-term trends in radial growth

From 1855 to 1979, all ring-width chronologies of Yezo spruce showed similar patterns of variability. Since 1980, however, the three chronologies exhibited different growth trends (Fig. 3). There was a significant decline in radial growth since 1980 at 1400 m a s l ($y = -0.005x + 10.69$, $p = 0.01$) (Fig. 3b), and a slight decline at 1200 m a s l since 1980 ($y = -0.004x + 8.79$, $p = 0.08$) (Fig. 3a). However, there was no significant change detected at the highest altitude of 1600 m a s l ($y = -0.001x + 3.73$, $p = 0.51$) (Fig. 3c). In general, the spruce ring-width index significantly decreased except for the trees at 1600 m a s l on Changbai Mountain.

### Climate–growth relationships

As revealed by the bootstrap correlation for climatic factors for 1958–2014, at all three elevational sites, the radial growth was negatively affected by mean temperature and mean minimum temperature in winter (January–March), and positively affected by mean maximum temperature in May (Tmax5) at all three sites (Table 2). Total precipitation in May is negatively correlated with the tree data at the two lower-altitude sites. Combining the effects of temperature in January to March (Tmin1–3) on radial growth, mean minimum temperature shows the most significant correlation at all three sites (Table 2).

### Stability of climate–growth relationships

The comparison between the growth–climate relationships in the two periods (1958–1979; 1980–2014) was complex. The radial growth (1200 m a s l) was significantly correlated with Tmin1–3 ($r = -0.38$, Fig. 4a) and Tmax5 ($r = 0.44$, Fig. 4d) during 1980 to 2014. However, for 1958 to 1979, the correlations between the radial growth and Tmin1–3 ($r = -0.14$, Fig. 4a) and Tmax5 ($r = 0.32$, Fig. 4d) were not as strong.

A significant positive correlation was observed between the radial growth (1600 m a s l) and Tmax5 ($r = 0.47$, Fig. 4f) during 1958–1979, with no significant correlations for 1980–2014 (Fig. 4f). There were no significant correlations between radial growth and Tmin1–3 during 1958 to 1979 (Fig. 4c), but significant negative correlations between that growth and Tmin1–3, with a weakening trend over 1980–2014 ($y = 0.02x - 34.2$, $p < 0.001$, Fig. 4c).

There was significant positive correlation between the radial growth (1400 m a s l) and Tmin1–3 ($r = -0.42$, Fig. 4b) during 1980–2014, but no significant correlation for 1958–1979 (Fig. 4b). The radial growth was significantly positively correlated with Tmax5 ($r = 0.38$, Fig. 4e) during 1958–1979. However, from 1980 to 2014, correlations between radial growth and Tmax5 fluctuated (Fig. 4e).

The stepwise regression method for investigating the variation of growth–climate relationships confirmed the above results from moving correlation functions (Fig. 5). $R^2$ accounted for 15.1% of total variation before the 1980s and 42.7% after the 1980s (Fig. 5a) and, at 1400 m a s l, $R^2$ accounted for 19.2% before the 1980s and 34.5% after the 1980s (Fig. 5b). However, the explanatory power of $R^2$ clearly decreased (from 27.8 to 14.1%) at 1600 m a s l (Fig. 5c).

## Discussion

### Chronological representation

Compared to Yezo spruce in other parts of Northeast China, Yezo spruce on Changbai Mountain with stronger growth and less sensitivity to climate (Table 1). At the three focal altitudes in this study, annual average annual ring widths were $\geq 1$ mm, and the maximum annual

**Fig. 3** RES chronologies of Yezo spruce growing at 1200 m a s l (**a**), 1400 m a s l (**b**), and 1600 m a s l (**c**). Fitted lines indicate the growth trends for 1980–2014 (grey shadow)

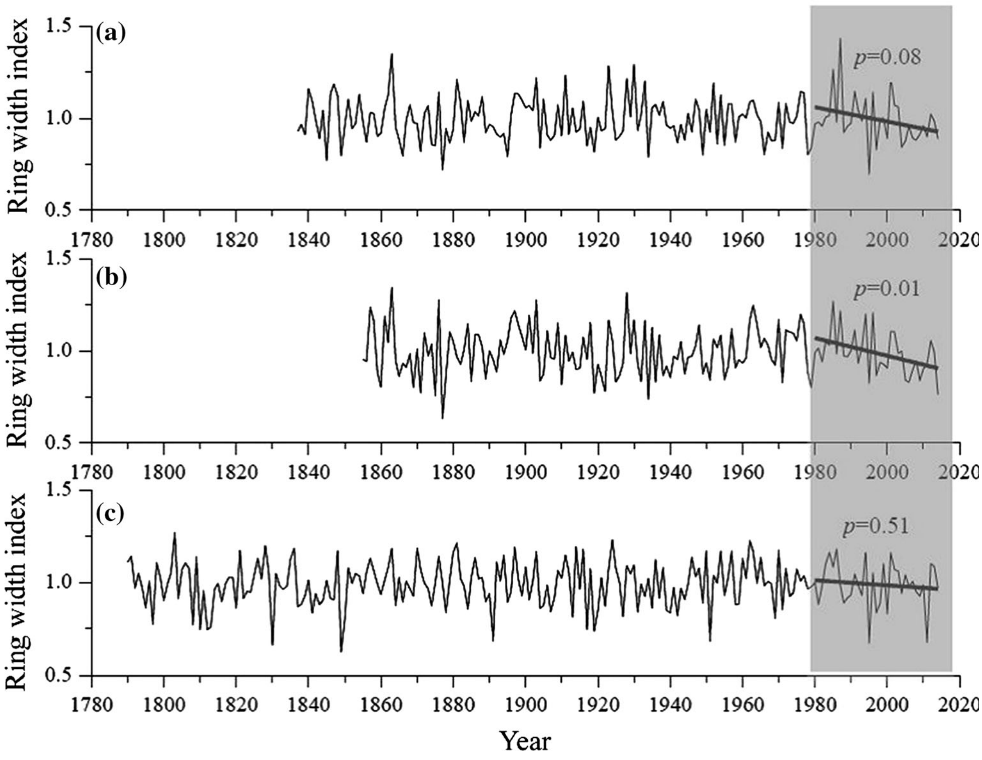

**Table 2** Correlation coefficients (× 100) between residual chronologies and meteorological monthly mean minimum temperature (Tmin), monthly mean maximum temperature (Tmax), mean temperature (*T*) and precipitation (*P*) for 1958–2014, from previous November (p11) to current October (10)

| Month | Tmin | | | Tmax | | | *T* | | | *P* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1200 | 1400 | 1600 | 1200 | 1400 | 1600 | 1200 | 1400 | 1600 | 1200 | 1400 | 1600 |
| Previous Nov | | | − 22 | | | | | | | | | |
| Previous Dec | | | − 33 | | | | | | − 29 | | | |
| Jan | − 34 | − 42 | | − 29 | − 28 | | − 32 | − 41 | | | | |
| Feb | | − 28 | | | | | | − 26 | − 24 | | | |
| Mar | − 28 | − 41 | − 39 | | | − 30 | − 26 | − 35 | − 37 | | | |
| Apr | | | | | | | | | | | | |
| May | | | | 41 | 43 | 32 | 30 | | | − 36 | − 31 | |
| Jun | | − 37 | | | | 23 | | | | | | |
| Jul | | | | | | | | | | | | |
| Aug | | | | | | | | | | | | |
| Sep | | | | | | | | − 22 | | | | |
| Oct | | − 30 | | | | | | − 34 | | | | |
| Jan to Mar | − 31 | − 49 | − 31 | | − 27 | − 29 | − 27 | − 43 | − 31 | | | |

Only significant coefficients ($p < 0.05$) are shown

growth increment at altitude 1400 m was 1.31 mm. The growth increment, SD and MS at altitude 1200 m were significantly greater than at 1600 m, which may indicate that growth of Yezo spruce is more enhanced in cool and moist conditions at high altitudes and is more limited by climate at lower altitudes. This finding is consistent with previous studies (Gao and Wang 2011; Yu et al. 2011; Zhuang et al. 2017). In comparison, the chronologies at all three altitudes showed lower average sensitivities (< 0.2) (Table 1), similar to the results of previous studies (Yu et al. 2011). A low MS was also found in a study of *Pinus koraiensis*, a dominant coniferous species at low altitude (740–1100 m) on the north slope of the Changbai Mountain (Wang et al. 2016). This low MS is likely attributable to less variation in tree-ring width resulting from the relatively mild and humid climate in the Changbai Mountain (Fig. 2) (Yu et al. 2006) or possibly to a weaker response to climate as a result of a greater density of virgin

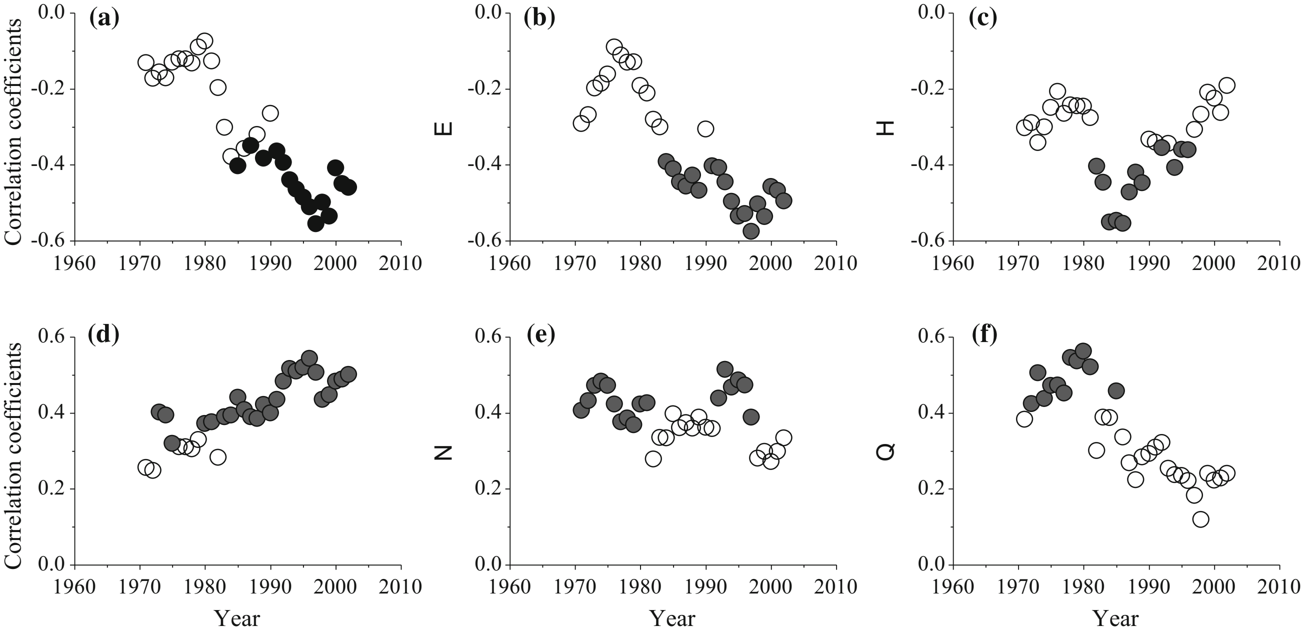

**Fig. 4** Twenty-five year moving correlation coefficients of RES chronologies and climate factors. Monthly mean minimum temperature from January to March with chronologies of 1200 m a s l (**a**), 1400 m a s l (**b**) and 1600 m a s l (**c**); monthly mean maximum temperature in May with chronologies of 1200 m a s l (**d**), 1400 m a s l (**e**) and 1600 m a s l (**f**). Solid points indicate significance above 95% confidence level

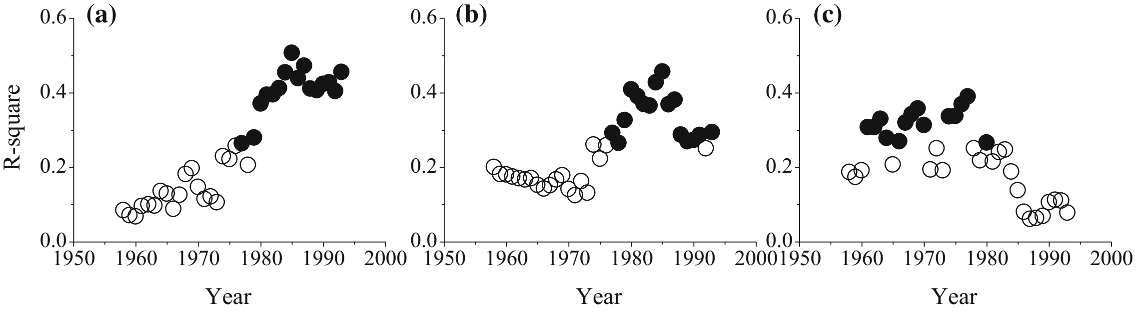

**Fig. 5** The R-square values dynamics for the 25-year moving window stepwise regression method of Yeza spruce radial growth and monthly mean minimum temperature from January to March, monthly mean maximum temperature in May: 1200 m a s l (**a**), 1400 m a s l (**b**) and 1600 m a s l (**c**). Solid points indicate correlations significant at the 95% confidence level

forest trees. However, the relatively large EPS and SNR indicate that tree rings are representative and can be used for a climatic analysis using dendrochronology.

## Altitude change trends of growth–climate relationships

The relationship between chronology and climate at the three focal altitudes in this study was clearly consistent (Table 2). The radial growth of Yezo spruce was all significantly affected by Tmin in winter (January–March) and Tmax in May through the early growing season. An increase in Tmin in winter may increase tree respiration rate and nutrient consumption (Yu et al. 2006). Moreover, increased winter Tmin may boost the survival probability of overwintering pests and the risk of tree pests and diseases, affecting tree growth. The large-scale death of spruces and firs in the Changbai Mountain Nature Reserve during recent years may also be related to this possibility. May marks the beginning of tree growth, which may begin early in a warm May, extending the growing season and increasing overall growth. In addition, the early part of the growing season is the stage of fastest spruce radial growth (Lebourgeois 2000). More than half the ring width is formed at this stage (Schweingruber 1996), and the warm daytime in May favors the growth of annual rings (Dolezal et al. 2015).

Study results suggest that precipitation in May has little effect on tree growth at high altitude, but greatly inhibits trees at low and medium altitudes (Table 2). A tree-ring study of Yezo spruce at 1050–1200 m a s l (Gao and Wang 2011) also showed that precipitation in May can substantially inhibit tree growth. Snowmelt in May results in sufficient soil moisture, and greater precipitation can alter the water environment of the soil. Thus, a decrease in daytime temperature and light intensity and duration may be unfavorable to tree growth. The Yezo spruce at high altitude (1600 m a s l) was not closely related to precipitation, which in turn may be related to the late growth of trees at that altitude.

In general, the radial-growth–climate relationship did not differ significantly among the three altitudes in this study. It is not negatively correlated with temperature or positively correlated with precipitation at low altitude (Makinen et al. 2002), but it is positively correlated with temperature at high altitude, as shown by studies in other areas (Salzer et al. 2014). Studies of Yezo spruce on Changbai Mountain found that even spruces growing sporadically at 900 and 1800 m a s l did not yield the same results as elsewhere, perhaps due to the mild and humid environment of those mountains or to the lower sensitivity of the spruce–fir forest to climate because of its higher stand density.

## Temporal trends of growth–climate relationships

Since the 1980s, the growth of Yezo spruce growth has clearly trended downward at low and medium altitudes, but has not changed much at high altitude (Fig. 3). The Changbai Mountain is at medium and high latitudes and have a humid, cold climate. It is one of the regions of greatest climate warming in China. Studies have shown that climate warming and drying are the main factors that reduce tree growth on Changbai Mountain (Yu et al. 2013). With respect to climatic factors that affect tree growth, annual average temperature has rapidly increased since the 1980s, but annual precipitation has not increased (Fig. 2a, b). At the same time, average minimum temperature in January–March has increased rapidly (+ 0.12 °C/year, $p < 0.01$) since 1980, but the monthly average maximum temperature in May has trended downward (− 0.05 °C/year). There has been little change in precipitation during May. Minimum temperatures inhibit increase in the growth of Yezo spruce, while maximum temperatures in May cause growth reduction. The combination of these factors constitutes the major cause of decline in tree growth at mid and low altitudes in the Changbai Mountain. In other words, differences in the pattern of monthly climate change reduce tree growth. This result was not caused by temperature-induced warming and drying.

Numerous studies have demonstrated that the sensitivity of tree-growth–climate relationships has declined at high altitudes in mid and high latitudes (Jacoby and Jacoby 1995; Yu et al. 2013). This study showed a marked intensification of the relationship between tree growth and climate at low and mid altitudes (Fig. 4). The impact of average minimum temperature during January–March on tree growth at medium and low altitudes has increased significantly in recent years (Fig. 4a, b). Thus, the impact of climate warming during this stage at low altitude has strengthened. The correlation with average maximum temperature in May significantly increased at low altitude and fluctuated at mid altitude (Fig. 4d, e), indicating that decrease in maximum temperature in May strengthens the climatic constraints on tree growth at low altitudes. However, at high altitudes, the correlation between the two climatic factors has been declining in recent years (Fig. 4c, f), consistent with studies at high altitudes and/or at high latitudes areas in the world (Büntgen et al. 2005; Zhuang et al. 2017); however, the mechanisms of influence differ. The period from January to March showed a negative correlation with tree growth. However, an increase of winter minimum temperature is often related to insect pests and other factors, but does not act directly on tree growth. At high altitude (1600 m, with average monthly maximum temperature in May of 14.5 °C) trees begin their growing season in late May. A decrease in average maximum temperature in May can delay tree growth and further impact the strength of the relationship between tree growth and climate.

The sensitivity change in tree growth to climate is reflected in the change in the correlation coefficient between tree-ring width and climatic factors, which is ultimately expressed as a variation in annual-ring width explained by those factors. Therefore, by fully considering the variance in the annual-ring width variation of Yezo spruce that is explained by the average minimum temperature in January–March and average maximum temperature in May, we can investigate variations in climate sensitivity of this species. In general, from 1958 to 2014, variance variations in annual-ring width in Yezo spruce that was explained by the three altitude temperatures exceeded 0.15 ($R^2$ for 1200, 1400 and 1600 m a s l of 0.21, 0.33 and 0.15, respectively), indicating that they contain substantial climate information. In recent years, there has been a significant increase in spruce radial growth at low altitude and a significant decrease at high altitude (Fig. 5a, c), but no consistent trend at mid altitude (Fig. 5b). This result shows that the climate sensitivity of Yezo spruce at high altitude has indeed declined in recent years, consistent with previous findings. Moreover, previous studies have suggested that the radial growth and climate sensitivity of high-altitude Yezo spruce greatly decreased in recent years, revealing the divergence problem described earlier (Yu et al. 2013; Li et al. 2012; Gao and Wang 2011). Nonetheless, no evidence of the divergence problem was found in our study. The relationship between high-altitude Yezo spruce and average maximum temperature in May changed from significant to nonsignificant (Fig. 4f). However, the temperature in May did not increase, and we did not find that the average rise in temperature in other months exceeded the threshold beyond which trees can adapt. We found no water deficit caused by climate warming and drying, while the correlation with precipitation changed from insignificant to significant. The main reason for the decline of spruce climatic sensitivity may be related to the outbreak of pests and diseases in high-altitude spruce–fir forests on Changbai Mountain during recent years. Rising temperature improves to the overwintering survival of pests and pathogens, seriously impacting high-altitude spruce–fir forests and greatly increasing spruce mortality.

## Conclusions

Our results confirm the general conclusion that the tree-growth–climate relationship of Yezo spruce did not vary with altitude, while the stability of the tree-growth–climate relationship varied with altitude as climate changed. Yezo spruce chronologies have low MS in the Changbai Mountain region of Northeast China. Despite a comparatively moderate and humid climate, the monthly mean maximum temperature in May and mean minimum temperature during January–March were the limiting factors for radial growth of Yezo spruce at all three altitudinal sites. The decrease in growth at the two lower altitudes was induced by an increase in January–March minimum temperature and decrease in May maximum temperature. Thus, while the tree-growth resilience to climate variations changed significantly with time, there was no obvious evidence of the climate divergence problem. The present findings provide a reference for using tree-ring data to reconstruct climate and/or predicting tree growth under various climate change scenarios.

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