Species-specific indication of 13 tree species growth on climate warming in temperate forest community of northeast China

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A R T I C L E   I N F O

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Resistance
Recovery
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A B S T R A C T

Temperate forests in northeast Asia are crucial to maintaining biodiversity conservation and ecological security. Under the background of global warming and drought, it is of great significance to study the special indicator effect of tree growth on climate change. Dendrochronological analysis of different tree species in the same community under climate change can provide valuable information for the adaptive potential of tree species and the species-specific growth indications. Here, we compared the radial growth patterns of 13 co-occurring tree species in a temperate forest community in northeast China. Pearson correlation and moving interval analysis were used to reveal the key climate factors affecting radial growth and the temporal stability of growth-climate relationships, respectively. Results showed that temperature and moisture played a key role in the radial growth of the 13 co-occurring tree species in northeast China. The radial growth of Pinus sylvestris var. mongolica, Picea koraiensis, and Ulmus davidiana increased significantly after rapid warming (around the 1980s), while the radial growth of Pinus koraiensis, Acer mono, and Betula platyphylla decreased slightly. The radial growth of almost all tree species (except P. koraiensis, A. mono, and B. platyphylla) had a positive indication of temperature, especially Juglans mandshurica, Prunus mandshurica, and U. davidiana. The precipitation in the early growing season (May to June) and the relative humidity in the growing season were positively correlated with the growth of most species. Coniferous and diffuse-porous tree species were more resistant and recovery to extreme droughts than semi-ring-porous and ring-porous species (except U. davidiana). The 13 co-occurring tree species, especially conifers, showed low resistance and high recovery to extreme temperature. The differences in the growth-climate relationships among different species may be related to wood properties and ecological habits. If the climate continues to warm, coniferous trees will suffer the most serious impact, so they need protection most. Our results highlight that differentiated strategies are needed for the management and restoration of different tree species due to the species-specific indications of climate warming.

1. Introduction

Forest ecosystems account for about 45% of global terrestrial carbon stocks and play a crucial role in biogeochemical cycles and long-term carbon sinks (Choat et al., 2018; Kang et al., 2021; Köhl et al., 2015; Seidl et al., 2017; Trumbore et al., 2015). The world has warmed rapidly over the past 150 years, particularly at high latitudes in the Northern Hemisphere, including northeast China (IPCC, 2018). Global warming affects the structure and function of forest ecosystems and affects the regeneration, growth, flowering, and fruiting of individual trees, reshaping the geographical distribution of forests, especially in mountain regions (Wang and Yang, 2021). Trees can adapt to climate change...
by changing their structure and functions (Fritts, 1976). Climate models predict that the frequency and duration of droughts and other extreme weather events will increase significantly in the coming decades. These phenomena will have a substantial negative impact on forest productivity and forest health (Cherubini et al., 2021), thereby changing the role of forests in major ecosystem services (Dale et al., 2001; Allen et al., 2010; Wang et al., 2016; IPCC, 2018). The response of tree growth to climate is usually species-specific. A better understanding of this specificity will improve our estimation of the effects of warming on forests (Michelot et al., 2012a; Li et al., 2021). For this reason, an ever-growing number of studies have attempted to assess the adaptability of forests under different climate change scenarios by focusing on the strategies and mechanisms trees use to adapt to changes in temperature and moisture.

The analysis of tree-ring width plays a crucial role in understanding how trees respond to climate change (Fritts, 1976; Dobbertin, 2005; Cherubini et al., 2021) and their response to extreme climate events (Bhuyan et al., 2017; Wang et al., 2019b; Fang et al., 2020). Long-term radial growth changes provide important information for assessing past forest productivity, vegetation dynamics, and tree-species distributions (Fan et al., 2009; Gaspard et al., 2018; Sangiexa-Barreda et al., 2019). In addition, the spatial pattern of global temperature rise is uneven: the increase in temperature is more obvious in the Northern Hemisphere than in the Southern Hemisphere (IPCC, 2018; Johnson et al., 2020). The northern region of China has a large forest area and is greatly affected by global warming, especially the temperate coniferous and broad-leaved mixed forest (Bai et al., 2019; Cao et al., 2019; Li et al., 2020b; Zhu et al., 2020). Species specificity is the main cause of growth-climate response heterogeneity (Lyu et al., 2017; Li et al., 2021).

Coniferous (non-porous) and broad-leaved (diffuse-porous, semi-ring-porous, ring-porous) tree species show clear differences in their growth-climate responses on account of their unique internal morphological traits, physiological mechanisms, and phenological processes (Duan et al., 2019; Islam et al., 2019). Dai et al. (2020) found that ring-porous, diffuse-porous, and coniferous trees in northern China have different strategies to cope with winter embolism. The species composition of the forest stand also plays an important role in determining how each species responds to climate change Cao et al., 2019). Species-specific growth responses to these changes translate into inconsistent growth trends, thereby driving changes in the structure and composition of forest ecosystems (Cao et al., 2019; Rahman et al., 2019). This species-specific response also reshapes the current species distribution (Bhuyan et al., 2017; Li et al., 2021). To understand these changes, it is necessary to study the growth-climate response of different tree species, especially those with different wood properties.

Northeast China is the core area of the temperate coniferous and broad-leaved mixed forest and is important for maintaining the ecological integrity of northeast Asia. Northeast China is also one of the regions most significantly affected by climate warming. Rapid warming and drought caused by warming have resulted in considerable changes in the structure, function, and productivity of the forests in this region (Lyu et al., 2017; Li et al., 2020a; Li et al., 2020b). In the past 20 years, several dendrochronological studies have been carried out in this area. Existing studies have focused mainly on determining the factors influencing tree growth-climate relationships, such as age, altitude, aspect, latitude (Liu et al., 2013; Wang et al., 2013; Zhu et al., 2018b; Bai et al., 2019; Wang et al., 2019a; Gai et al., 2020; Yu and Liu, 2020), on identifying spatiotemporal variations in growth-climate relationships, and on paleoclimate reconstruction (Gholami et al., 2015; Zhang et al., 2018; Hippler et al., 2020; Li et al., 2020a).

The composition and structure of temperate forest ecosystems in northeast China are complex. Although some studies have attempted to compare the responses of different tree species to climate change (Lyu et al., 2017; Cao et al., 2019; Yasmeen et al., 2019), few studies have examined the differences in growth-climate relationships among species and their relationships with rapid warming at the ecosystem level. Also, with the increasing frequency and intensity of extreme climate events, the resistance and recovery of trees have been a question of wide concern (Duan et al., 2019; Rahman et al., 2019; Fang et al., 2020). Resistance and recovery have been quantified and compared in dendroclimatological studies (Lloret et al., 2011; DeSoto et al., 2020) and many past studies have used the two parameters to describe the recovery of trees to extreme climate (Merlin et al., 2015; Gomes Marques et al., 2018; Rahman et al., 2019; Wang et al., 2019b; Fang et al., 2020). Determining which tree species are more vulnerable to extreme climate is a challenging but important part of understanding how forest ecosystems are responding to climate change (Zhao et al., 2018; Vitasse et al., 2019; Wang et al., 2019b; DeSoto et al., 2020; Sharafati and Pezeshki, 2020).

Maaoershans Mountains in northeast China, rich in tree species, is a typical representative of temperate forests in China. It is also one of the areas with the most significant climate warming. To improve our understanding of accurately assessing the impact of climate change on forest ecosystems in northeast China and predicting the future dynamics of temperate forest vegetation, productivity, and community succession, we need to deeply understand the influence of climatic variables on the growth of different tree species. In this study, we examine the growth-climate responses of 13 representative tree species in temperate forests in northeast China. We aim to: (i) reveal the growth patterns and growth-climate relationships of main co-occurring tree species; (ii) determine whether the growth-climate relationships of major tree species have changed due to rapid warming; (iii) explore the differences in growth resistance and recovery of major tree species to extreme climate events. We provide new data on climate-growth relationships of major tree species in temperate forests.

2. Materials and methods

2.1. Study area and climate

The study area is located in the Maaoershans Mountains (45°24′N, 127°40′E) of northeastern China (Fig. 1a) and has an average elevation of 403 m (Fig. 1c). The existing vegetation types are plantations and the natural secondary forest formed following repeated human disturbances. The natural forest is composed mainly of Pinus koraiensis and various broad-leaved tree species, such as Praxinus mandshurica, Phellodendron amurense, Juglans mandshurica, Betula platyphylla, Quercus mongolica, and Tilia amurensis. The soil in this area is mainly dark-brown forest soil.

The study area is characterized by a temperate continental monsoon climate, with a pronounced seasonality, relatively short, warm, and rainy summers, and long, cold, and dry winters. The mean annual temperature is 2.98 °C, and the annual total precipitation is 659 mm (Fig. 1b). Mean monthly temperatures (1954–2017) range from –19.7 °C in January to 22 °C in July. Precipitation occurs primarily from May to September (80%), with some snowfall in the winter (Fig. 1b). The frost-free period is 120–140 days long. From 1982 to 2017, the annual mean (0.4 °C/decade, $r^2 = 0.51, p < 0.01$) and minimum (0.7 °C/decade, $r^2 = 0.77, p < 0.01$) temperatures showed a significant upward trend. In addition, precipitation, relative humidity, and the standardized precipitation evapotranspiration index (SPEI) decreased significantly from 1954 to 1992, but did not change significantly after 1982 (Fig. 2).

2.2. Core sampling and chronology development

The analysis process of the response of different tree species in the same community to climate warming is shown in Fig. 3.

Fieldwork was conducted in May 2017 and a total of 13 co-occurring tree species were sampled: four coniferous species (Larix gmelinii, Picea koraiensis, P. p. koraiensis, and Pinus sylvestris var. mongolica), and nine broad-leaved species (Acer mono, B. platyphylla, F. mandshurica, J. mandshurica, P. amurense, P. davidiana, Q. mongolica,
Fig. 1. (a, c) Location of the sample site (red dot) and weather station (blue dot) in the study area (red rectangle). (b) Variations of monthly mean temperature and precipitation for Shangzhi meteorological station for the period 1954-2017. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. Variations in annual precipitation, minimum ($T_{\text{min}}$), mean ($T_{\text{mean}}$), and maximum ($T_{\text{max}}$) temperature, relative humidity, and standardized precipitation evapotranspiration index (SPEI) at the Shangzhi meteorological station from 1954 to 2017. The asterisk “*” indicates significant correlation at the 0.05 level; Two asterisks “**” indicate significant correlation at the 0.01 level. The bold straight line is a piecewise fitted linear regression line of the meteorological data.
Fig. 3. The flow diagram depicting the species-specific indication of climate warming by the growth of 13 tree species in a temperate forest community in Northeast China.

T. amurensis, and U. davidiana). These species play key roles in the productivity and community succession of temperate forests in northeast China (Table 1). A total of 20–30 mature and healthy trees of each species were cored at the height of 1.3 m with a 5.15-mm diameter increment borer.

In the laboratory, cores were prepared (air-dried, fixed, and gradually polished) until cell or annual ring boundaries were visible. All cores were visually cross-dated under a binocular microscope using the skeleton-plot method (Stokes and Smiley, 1968). Ring widths were then measured to an accuracy of 0.001 mm using the Velmex tree-ring measuring system (Velmx Inc., Bloomfield, NY, USA). The quality of the measurement series of each species was checked using the COFECHA program (Holmes, 1983). The raw tree-ring series were detrended with the ARSTAN program by fitting a negative exponential curve or linear regression function (Cook, 1985). The resulting thirteen standard chronologies (Fig. 2) were then used for subsequent analyses.

2.3. Climatic data and statistical analysis

The instrumental climate data of Shangzhi weather station (45°13′N, 127°58′E, 190 m a.s.l.) (1954–2017) were obtained from the China Meteorological Data Service Center. They included monthly total precipitation (P), mean (Tmean), minimum (Tmin), and maximum (Tmax) temperature, and relative humidity (RH) (http://data.cma.cn; Fig. 1b and Fig. 2). The average temperature and precipitation data were used to calculate the standardized precipitation evapotranspiration index (SPEI, the time-scale of 1 month) with SPEI software (Vicente-Serrano et al., 2010). Seasonal climate variables are defined as follows: previous growing season (PGS, May(previous)–October(previous)), previous non-growing season (PNG, November(previous)–April(current)), current growing season (GS, May(current)–October(current)), and annual (AN, November(previous)–October(current)).

The slopes and the coefficients of the linear models were used to assess the trends of climate change (Fig. 2). Pearson correlation analysis was carried out between tree-ring chronologies and monthly or seasonal climate data. To analyze the temporal stability of the relationships between radial growth and major climate factors, we used Denstroclim2002 to study the moving correlations with a 25-year temporal

Table 1

<table>
<thead>
<tr>
<th>Wood property (code)</th>
<th>Tree species (code)</th>
<th>Leaf traits</th>
<th>Slope position</th>
<th>DBH (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-porous (NP)</td>
<td>Pinus koraiensis (PK)</td>
<td>Evergreen-coniferous</td>
<td>Middle</td>
<td>45.8 ± 1.3</td>
</tr>
<tr>
<td></td>
<td>Larix gmelinii (LG)</td>
<td>Deciduous-coniferous</td>
<td>Middle</td>
<td>31.9 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>Pinus sylvestris var. mongolica (PS)</td>
<td>Evergreen-coniferous</td>
<td>Middle</td>
<td>30.3 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>Picea koraiensis (PC)</td>
<td>Evergreen-coniferous</td>
<td>Valley</td>
<td>31.3 ± 0.6</td>
</tr>
<tr>
<td>Diffuse-porous (DP)</td>
<td>Acer mono (AM)</td>
<td>Deciduous-broadleaved</td>
<td>Upper</td>
<td>35.1 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>Betula platyphlla (BP)</td>
<td>Deciduous-broadleaved</td>
<td>Middle</td>
<td>32.4 ± 1.3</td>
</tr>
<tr>
<td></td>
<td>Tilia amurensis (TA)</td>
<td>Deciduous-broadleaved</td>
<td>Middle</td>
<td>29.9 ± 2.1</td>
</tr>
<tr>
<td></td>
<td>Populus davidiana (PD)</td>
<td>Deciduous-broadleaved</td>
<td>Upper</td>
<td>35.1 ± 1.6</td>
</tr>
<tr>
<td>Semi-ring-porous (SRP)</td>
<td>Juglans mandshurica (JM)</td>
<td>Deciduous-broadleaved</td>
<td>Valley</td>
<td>34.5 ± 2.2</td>
</tr>
<tr>
<td>Ring-porous (RP)</td>
<td>Quercus mongolica (QM)</td>
<td>Deciduous-broadleaved</td>
<td>Upper</td>
<td>37.8 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>Phellodendron amurense (PA)</td>
<td>Deciduous-broadleaved</td>
<td>Middle</td>
<td>33.8 ± 2.2</td>
</tr>
<tr>
<td></td>
<td>Fraxinus mandshurica (FM)</td>
<td>Deciduous-broadleaved</td>
<td>Lower</td>
<td>40.3 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>Ulmus davidiana (UD)</td>
<td>Deciduous-broadleaved</td>
<td>Lower</td>
<td>35.5 ± 1.2</td>
</tr>
</tbody>
</table>

Notes: DBH: diameter at breast height (mean ± SE). Because Latin abbreviations of Pinus koraiensis and Picea koraiensis are both PK, PC is used as the code for Picea koraiensis.
window (Biondi and Waikul, 2004).

Climate change is expected to increase the frequency or the intensity of drought events in temperate forests during the early growing season (IPCC, 2018). We therefore further quantified the response of tree growth to extreme weather events using resistance (Rt) and recovery (Rc) indices adopted from Lloret et al. (2011). The two indices were calculated as follows:

\[ Rt = Dr/PreDr \]  
\[ Rc = PostDr/Dr \]  

The “Dr” variable refers to the tree-ring-width index in dry or cold years. The values of “PreDr” and “PostDr” were calculated by averaging the tree-ring width index over the 5 years before and after an extreme event. We defined the ten years with the lowest precipitation from May to July during 1954–2017 as extreme drought years. These are 1954, 1958, 1959, 1965, 1969, 1972, 1976, 1978, 1979, 1982, 1999, 2007, and 2010. Similarly, the ten years with the lowest minimum temperature from May to July are defined as extreme minimum-temperature years, i.e., 1954, 1959, 1965, 1969, 1972, 1976, 1982, 1987, 1989, and 1992.

3. Results

3.1. Tree-ring chronology characteristics of 13 co-occurring tree species

Details regarding the chronology characteristics of the 13 main coniferous and broad-leaved tree species in the Maoershan Mountains are shown in Table 2. The shortest and longest chronologies are 43 (Picea koraiensis) and 163 years (U. davidiana) long, respectively. The high values of the mean correlation coefficients among all series (MC) and the high expressed population signal (EPS) of the chronologies confirm that our chronologies are suitable for dendroclimatological analysis (Wigley et al., 1987).

The correlation matrix of the 13 chronologies indicates that the semi ring-porous chronology is similar to the ring-porous tree chronology (Fig. 4, Table 3). The chronology of Picea koraiensis is positively correlated with non-porous and diffuse-porous trees and negatively correlated with semi ring-porous and ring-porous trees. There is a significant negative correlation between the chronology of A. mono and F. mandshurica (r = 0.34, p < 0.01). The correlations between the other chronologies are positive (Table 3).

3.2. Relationships between radial growth and main climatic factors

The relationships between radial growth and climate variables vary among the different species (Fig. 5, c). Temperature is the main factor limiting the radial growth of Pinus koraiensis, A. mono, B. platyphylla, J. mandshurica, F. mandshurica, and U. davidiana (Fig. 5b, Fig. S1). In almost all seasons (PGS, PNG, GS, MJJ, ASO, and AN), minimum temperature (T_min) is significantly negatively correlated with the radial growth of Pinus koraiensis, A. mono, and B. platyphylla, and significantly positively correlated with the radial growth of J. mandshurica, F. mandshurica, and U. davidiana (Fig. 5b).

The radial growth of P. sylvestris var. mongolica, Picea koraiensis, T. amurensis, P. amurensis, and Q. mongolica is controlled mainly by moisture conditions (Fig. 5a and 5c). Previous non-growing season precipitation has a significant positive effect on P. sylvestris var. mongolica (p < 0.05), but precipitation during the previous growing season and relative humidity in the non-growing season are negatively affected correlated with growth (Fig. 5a and 5c). Picea koraiensis is significantly positively correlated with precipitation of the previous growing and non-growing seasons, the current growing season, and the whole year, and with relative humidity of the previous and current growing seasons. The growth of T. amurensis is significantly and positively affected by the relative humidity of the current growing season (especially in MJJ) (Fig. 5c). The relationship between the growth of L. gmelinii and P. davidiana and climate factors is less clear (Fig. 5, Fig. S1).

In all seasons except PNG, the growth of J. mandshurica, F. mandshurica, and U. davidiana is significantly positively correlated with T_min (Fig. 5b). Precipitation during prophase of the current growing season has a positive influence on the growth of Q. mongolica, P. amurensis, and F. mandshurica, but negatively impacts the growth of U. davidiana. Relative humidity in the current season (especially in MJJ) has a positive and significant correlation with Q. mongolica (Fig. 5c). The growth of Q. mongolica, P. amurensis, and F. mandshurica is significantly positively correlated with precipitation (Fig. 5a).

3.3. Responses to climate warming

The moving correlation between the radial growth of non-porous, diffuse-porous, semi-ring-porous, and ring-porous trees and climate factors showed an opposite trend before and after warming around the 1980s (Fig. 6). With the increase of warm and dry conditions, ring-porous species maintain hydraulic conductivity by increasing vessel size and density, while reducing the number of vessels to reduce the risk of embolism and cavitation, thus limiting the growth at the macro level. The relationship between the growth of almost all non-porous and diffuse-porous trees and the current growing season precipitation (P_c) changes from negative before the 1980s to positive after the 1980s (Fig. 6a). However, the moving correlations between the growth of semi-ring-porous and ring-porous trees (J. mandshurica and U. davidiana) and T_min in growing season (T_minGS) change from significantly positive before the 1980s to not significantly positive or negative after the 1980s (Fig. 6b).

Table 2
Major statistical characteristics of the standard chronologies of the thirteen temperate tree species in northeast China.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Time span</th>
<th>Cores/trees</th>
<th>Eigenvalue of standard chronology</th>
<th>Common interval analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>MS</td>
<td>SD</td>
</tr>
<tr>
<td>PK</td>
<td>1877–2017</td>
<td>34/27</td>
<td>0.20</td>
<td>0.34</td>
</tr>
<tr>
<td>LG</td>
<td>1965–2017</td>
<td>35/22</td>
<td>0.16</td>
<td>0.22</td>
</tr>
<tr>
<td>PS</td>
<td>1970–2017</td>
<td>45/29</td>
<td>0.23</td>
<td>0.27</td>
</tr>
<tr>
<td>PC</td>
<td>1975–2017</td>
<td>41/27</td>
<td>0.25</td>
<td>0.32</td>
</tr>
<tr>
<td>AM</td>
<td>1871–2017</td>
<td>32/24</td>
<td>0.19</td>
<td>0.37</td>
</tr>
<tr>
<td>BB</td>
<td>1867–2017</td>
<td>36/23</td>
<td>0.28</td>
<td>0.29</td>
</tr>
<tr>
<td>TA</td>
<td>1930–2017</td>
<td>39/24</td>
<td>0.16</td>
<td>0.28</td>
</tr>
<tr>
<td>PD</td>
<td>1948–2017</td>
<td>36/22</td>
<td>0.19</td>
<td>0.20</td>
</tr>
<tr>
<td>JM</td>
<td>1933–2017</td>
<td>34/24</td>
<td>0.17</td>
<td>0.26</td>
</tr>
<tr>
<td>QM</td>
<td>1945–2017</td>
<td>32/21</td>
<td>0.20</td>
<td>0.17</td>
</tr>
<tr>
<td>PA</td>
<td>1918–2017</td>
<td>40/23</td>
<td>0.18</td>
<td>0.34</td>
</tr>
<tr>
<td>TM</td>
<td>1915–2017</td>
<td>44/27</td>
<td>0.17</td>
<td>0.25</td>
</tr>
<tr>
<td>UD</td>
<td>1858–2017</td>
<td>32/23</td>
<td>0.17</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Notes: See Table 1 for the tree species codes. MS = Mean sensitivity; SD = Standard deviation; MC = Mean correlation coefficients among all series; ACI = first order autocorrelation; SNR = signal-to-noise ratio; EPS = expressed population signal; VFE (%) = variance in the first eigenvector (%).
The relationships between the growth of non-porous and diffuse-porous trees (except for *P. sylvestris* var. *mongolica*, which has a negative to positive relationship) and *T*$_{\text{min}}$ during the current growing season show positive to negative responses (Fig. 6b). In contrast, the moving correlation coefficients of semi-ring-porous and ring-porous trees and *T*$_{\text{minGS}}$ exhibit a trend of diminishing positive significance until the correlations become non-significantly positive or negative after the 1980s (Fig. 6).

3.4. Resistance and recovery of tree growth to extreme climate

Differences in the growth resistance and recovery of the 13 co-occurring tree species to two extreme climate events are shown in Fig. 7. Under extreme drought conditions, the growth of *U. davidiana*, *T. amurensis*, and *Picea koraiensis* show the strongest resistance to stress, followed by *L. gmelinii* and *B. platyphylla* (Fig. 7). The stress resistances of other tree species are relatively low, especially for *Pinus koraiensis*, *J. mandshurica*, and all ring-porous species except *U. davidiana*. However, *Picea koraiensis* and *T. amurensis* show high resistance (Fig. 7a) and recovery (Fig. 7b), and *A. mono* shows low resistance and recovery. *Pinus koraiensis*, *P. sylvestris* var. *mongolica*, *P. davidiana*, and *P. amurense* are more resilient than other species during average drought events (Fig. 7a and 7b).

None of the 13 species shows strong resistance to extreme minimum temperature, although *L. gmelinii*, *Picea koraiensis*, and *U. davidiana* have the highest resistance (Fig. 7c). As in extreme drought, species with
lower resistance to extreme minimum temperature have a higher recovery rate (Fig. 7d). Of all the studied tree species, coniferous tree species show the highest resistance. *A. mono*, *J. mandshurica*, *P. amurense*, and *U. davidiana* recover poorly after extreme climate events (Fig. 7).

4. Discussion

4.1. Species-specific limits to radial growth

Although both temperature and precipitation drive xylem formation in the main temperate tree species in northeast China, our results indicate that temperature is the main limiting factor. This result is consistent with those of previous studies (Wang et al., 2013; Lyu et al., 2017; Wang et al., 2019a; Zhang et al., 2019; Zhu, 2019). Temperature can directly or indirectly affect xylogenesis through various physiological and ecological pathways, such as by adjusting the start, duration, and end of the cambial activity (Vaganov et al., 2006; Abrantes et al., 2013). These processes affect photosynthesis and respiration, determine the accumulation, consumption, and distribution of assimilates, and hence affect tree growth (Barbaroux and Breda, 2002). Our study reveals a clear species-specific growth-climate response pattern by examining individuals from radial growth, similar to other studies (Kim et al., 2017; Martínez-Sancho et al., 2018; Espinosa et al., 2018; Cao et al., 2019; Pacheco et al., 2019). The growth of *P. koraiensis*, *A. mono*, and *B. platyphylla* decrease slightly since the 1980s, whereas the growth of *P. sylvestris* var. *mongolica*, *P. koraiensis*, and *U. davidiana* increase significantly. The other species show little change in their growth trends.

The specific response of species to climate warming is reflected in the growth-climate relationship. Multiple species traits, especially interspecies physiological differences, generally lead to the use of different strategies to cope with climate changes (McDowell et al., 2008; Lyu et al., 2017; Li et al., 2021). Except *P. koraiensis*, *A. mono*, and *B. platyphylla*, *T_min* promoted the growth of almost all tree species. The three tree species responded positively to precipitation and relative humidity in most seasons (Fig. 5 and Fig. S1). *P. koraiensis* is a shallow-rooted heliophile (Yu et al., 2013; Lyu et al., 2017) with strict soil moisture requirements (Wang et al., 2013; Omelko et al., 2016; Park et al., 2018). Due to the increase in respiration and the decrease in carbohydrate availability for growth, the carbon loss during the growing season is higher for this species (Lavigne and Ryan, 1997; Wang et al., 2019a). On the contrary, the growth of *B. platyphylla* is limited by winter

<table>
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Notes: See Table 1 for the tree species codes. Two asterisks “***” indicate that correlation is significant at \( p < 0.01 \) (2-tailed). The asterisk “*” indicates that the correlation is significant at \( p < 0.05 \) level (2-tailed).

Fig. 5. Correlation relationships between the tree-ring indices of the thirteen tree species in Moaershan Mountains of northeast China and seasonal precipitation (P) (a), minimum temperature (\( T_{\text{min}} \)) (b), and relative humidity (RH) (c). The asterisk “*” indicates that the correlation is significant at the 0.05 level. PGS = previous growing season; PNG = previous non-growing season; GS = current growing season; MJJ = May to July; ASO = August to October; AN = annual. See Table 1 for the tree species codes.
Fig. 6. Moving correlation analysis between the standard chronologies of the thirteen temperate tree species and (a) precipitation and (b) minimum temperature in the current growing season in Maoershan Mountains, northeast China. The asterisk "*" indicates that the correlation is significant at the 0.05 level. See Table 1 for the tree species codes. The gray areas indicate that there is no value due to the short chronologies.

Fig. 7. Comparison of growth resistance and recovery of thirteen temperate tree species to extreme drought and minimum temperature. (a) $P \sim Rt$, resistance to extreme precipitation (drought); (b) $P \sim Rc$, recovery from extreme precipitation (drought); (c) $T_{min} \sim Rt$, resistance to minimum temperature; (d) $T_{min} \sim Rc$, recovery from extreme minimum temperature. See Table 1 for the tree species codes.
warming. Because it has less developed main root systems, sufficient water availability at the beginning of the growing season will be more critical for its survival (Gradel et al., 2017; Podlaski, 2021; Yan et al., 2021). A similar relationship is found in Betula ermanii growing in the Changbai Mountains of northeastern China (Yu et al., 2005). Water availability during the prophase of the current growing season is crucial for the growth of A. mono (Fritts, 1976; Li et al., 2020b), which is distributed along dry upper slopes. The changes in precipitation cannot compensate for the adverse effects of warming during the growing season (Wang et al., 2019a). Compared with other tree species, J. mandshurica, F. mandshurica, and U. davidiana grow in a relatively humid environment. The increase of temperature in the growing season promotes water evaporation and tree transpiration, and intensifies the drought stress caused by warming (Wang et al., 2019a). To adapt to short-term drought stress, trees can reduce the formation of xylem vessels, thereby reducing water loss (Martínez-Sanchez et al., 2017).

In addition to the characteristics of tree species, tree age may be another important factor in the response of different tree species to climate warming. Many physiological processes are also influenced by tree age. With climate warming, older trees usually have foliar efficiency (Sass-Klaassen et al., 2011) and lower photosynthetic rates (Rossi et al., 2008) due to small hydraulic constraints and stomatal limitations (Wang et al., 2019a). This phenomenon potentially leads to a negative indication of temperature (Wu et al., 2018). The absolute growth rate of older trees decreases significantly with the increase of temperature. The negative effects of temperature rise on the growth of old trees is greater than that of young trees. In older trees, increased cell (tracheid/vessel) area, reduced hydraulic efficiency may reduce radial growth and increase temperature sensitivity (Labuhn et al., 2014; Wang et al., 2019a). At the same time, the carbon gain of older trees decreases with the increase of temperature, and the xylem differentiation is slow and short (Rossi et al., 2008; Maxwell et al., 2020). This is why the effect of warming on the growth of old trees is greater than that of young trees.

The growth of Picea koraiensis is mainly limited by precipitation, as also shown for Picea jezoensis, which can be found at low elevations in northeast China (Zhu et al., 2018a). When water is sufficient in the growing season, tracheid division, elongation, and cell wall thickening can proceed fully and rapidly. In the case of water deficit, the leaves wilt, stomata close, and the trees can proceed fully and rapidly. In the case of water deficit, the leaves wilt, young trees.

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Climate warming causes changes in precipitation or soil moisture is often accompanied by increased temperatures and atmospheric evaporation demand (Choat et al., 2018; Keyimu et al., 2020; Zhu et al., 2018b). Scientists have noted that the divergence between tree growth and temperature in summer and growing season in recent decades (Wang et al., 2019a; Yuan et al., 2019; Zhu, 2019; Shen et al., 2020). High temperature in summer and growing season leads to drought stress by increasing evapotranspiration (Choat et al., 2012), which will lead to the decrease of net photosynthetic rate and the increase of dark respiration, thus limiting the accumulation of organic matter and higher nutrient loss. In addition, climate warming may also increase the demand for water vapor in the atmosphere, reduce the stomatal conductance of leaves, thus retarding the flow of steam sap and limiting growth (He et al., 2018; Wang et al., 2019a; Li et al., 2020b). The radial growth of diffuse- porous species is positively correlated with T_{min} during the growing season. Although diffuse-porous species maintain hydraulic conductivity by increasing the area and density of their vessels under drought stress, climate warming weakens the increasing trend in the number of diffuse-porous wood, thereby inhibiting radial growth at the macro-level (Islam et al., 2018). The relationships between T_{min} and radial growth of coniferous tree species (except P. sylvestris var. mongolica) during the growing season changes from positive to negative in the 1980s. Following rapid warming, photosynthesis was blocked due to increased respiration (Fritts, 1976; Fonti and Babushkina, 2016); at the same time, the increase in temperature and the transpiration of soil moisture leads to a decline in soil moisture, inhibiting tree growth (Lêvesque et al., 2014). The positive correlation between T_{min} during the growing season and the radial growth of U. davidiana is relatively stable over the length of the climate data. However, U. davidiana grows at the foot of wet hillside and has a more stable water supply than trees further up the slope. For this reason, higher temperatures are likely to accelerate its radial growth (Yoshida and Kamitani, 1999; Han, 2018; Zhu, 2019). Quercus mongolica, which grows on the upper slopes of dry hillside, is more vulnerable to changes in precipitation and temperature, namely drought stress (Lyu et al., 2017; Cao et al., 2019; Han, 2018; Zhu, 2019). The growth of Q. mongolica is favoured by wetter springs, as it requires a larger supply of spring moisture to support its transpiration demands during summer, especially in the context of rapid warming (Lyu et al., 2017).

4.3. The adaptability of different tree species to extreme climate

Coniferous and broadleaved trees have different woody structures that are related to their different water- and nutrient-use strategies throughout the growing season (Michelot et al., 2012b). Compared with the non-porous (coniferous) and diffuse-porous species, most ring-porous (except U. davidiana) species have a lower resistance to extreme drought, as has been shown in other studies (Rahman et al., 2019). This difference in growth response to extreme drought may be related to species-specific phyiology, such as xylem anatomical characteristics, intrinsic plant physiological adaptations, and water-use efficiency (Pérez-de-Lis et al., 2016; Islam et al., 2019). Ring-porous trees form large earlywood vessels before budburst to restore the water flow pathway before transpiration resumes, which enables trees to acquire enough water to produce new leaves but they also cavitate more easily.
(Breda and Granier, 1996; Sass-Klaassen et al., 2011). This special need for water at the beginning of the growing season and being prone to cavitation may make ring-porous species more susceptible to early drought than coniferous or diffuse-porous species.

Similarly, Choat et al. (2012) reported that coniferous species are more resistant to drought-induced cavitation than broadleaved species and have higher hydraulic safety thresholds. However, the recovery time of coniferous species from drought-induced embolism is more challenging to ascertain. In contrast, broad-leaved trees have a low resistance to cavitation but are more resilient (Pacheco et al., 2019). We can reasonably infer that coniferous species are more vulnerable to extreme drought, while broadleaved species are more susceptible to frequent drought. Our study emphasizes that broad-leaved species are less resistant to extreme minimum temperature than coniferous species (except *P. sylvestris* var. *mongolica*). This may be due to the coupling differences between leaf and wood phenology, cell (vessel/tracheid) density, or anatomical structure (Vitasse et al., 2019; Tan et al., 2020). Tracheids of conifers are superior to vessels of angiosperm trees in avoiding freeze-thaw-(extreme minimum temperature) induced embolism (Sperry et al., 1994; Dai et al., 2020). The radial growth of most broad-leaved species is strongly dependent on leaf photosynthesis. In cases of extreme minimum temperature, trees show a low growth rate and reduced resistance due to insufficient leaf development. More specifically, most evergreen coniferous trees are more resistant to extreme minimum temperatures early in the growing season because the alternation of old and new needles compensates for photosynthesis when new needles are damaged (except in the case of *L. gmelinii* (Vitasse et al., 2019; Zas et al., 2020). Our results also suggest that the resistance of semi-ring-porous species to extreme minimum temperature is significantly lower than that of other tree species (Table S2). The vessel area of semi-ring-porous species and ring-porous species may be more susceptible to cavitation at low temperatures (Islam et al., 2018).

In addition to internal factors, the resistance and recovery of tree growth to extreme drought and minimum temperature depend on the species, competition, and tree age and size (Pretzsch et al., 2013). With the intensification of climate change, the species composition of forests may change, resulting in changes in forest structure and productivity (Duan et al., 2019; Rahman et al., 2019).

5. Conclusion

The 13 co-occurring, temperature tree species studied here show species-specific responses to climate change. Temperature is the main factor controlling the radial growth of these species, followed by precipitation. The effects of warming-induced drought during the growing season have been recorded in almost all non-porous or diffuse-porous species. In contrast, the ring-porous species are currently less affected or not affected by drought. The temporal variations in the growth-climate relationships of the different tree species may be related to the warming-induced drying that increased rapidly in the 1980s. The resistance of coniferous and diffuse-porous trees to extreme drought is higher than that of semi-ring-porous and ring-porous trees (except *U. davidiana*). The recovery rate of coniferous tree species is higher than that of other tree species. The resistance of broadleaved trees to extreme minimum temperature is lower than that of coniferous species, but their recovery rate is higher. If climate warming continues, the decline of conifer species (except *P. sylvestris* var. *mongolica*) and diffuse-porous tree species (*Juglans mandshurica*) may be more prominent. Our results are of great significance for accurately evaluating the impact of climate change on temperate forests of northeast China. The species-specific responses of radial growth to rapid warming should be considered in the future carbon cycle and forest management. In addition, it is necessary to further study the physiological response mechanism of different tree species to climate change on a regional scale.

CRediT authorship contribution statement

**Danyang Yuan**: Conceptualization, Investigation, Data curation, Writing – original draft. **Liangjun Zhu**: Investigation, Writing – review & editing. **Paolo Cherubini**: Writing – review & editing. **Zongshan Li**: Methodology, Writing – review & editing. **Yuandong Zhang**: Investigation, Writing – review & editing. **Xiaochun Wang**: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108389.

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