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Different response of earlywood vessel features of *Fraxinus mandshurica* to rapid warming in warm-dry and cold-wet areas

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A R T I C L E I N F O

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A B S T R A C T

Xylem anatomical features are constantly adapting to changing environmental conditions, and are directly related to the key functions and physiological processes of trees. However, little is known about the responses of xylem to recent rapid warming in many areas. Based on the anatomical features of the xylem of *Fraxinus mandshurica* Rupr. from 14 sites in two contrasting areas (warm-dry and cold-wet) of northeast China, the plasticity response and adaptation strategies of radial growth, earlywood vessels (EWV), and hydraulic features of *F. mandshurica* to climate change were studied. Results showed that, compared with the cold-wet area, *F. mandshurica* in warm-dry area had wider rings, larger vessel area, higher number of vessels (VN), larger hydraulic diameters (Dh) and higher theoretical tree-ring hydraulic conductivity (Kh). On the contrary, the vessel density (VD), percentage of EWV (PC) and xylem-specific theoretical hydraulic conductivity (Ks) in warm-dry area was lower than those in cold-wet area. In these two areas, the RW, mean vessel area (MVA), total vessel area (TVA), VN, Dh, and Kh were significantly positively correlated with temperature, and negatively correlated with winter moisture. However, the PC, VD, and Ks were inversely related to climate factors in the two areas. *F. mandshurica* can adjust the density and proportion of EWV by changing the configuration of earlywood and latewood to cope with the interannual climate change and balance the hydraulic efficiency and safety. Rapid warming significantly increased the growing season length and hydraulic efficiency of *F. mandshurica* in warm-dry and cold-wet areas, thus maximizing carbon fixation. This provides a potential physiological explanation for the growth increase and range expansion of the main broadleaf tree species in temperate zone of northeast China in recent years. *F. mandshurica* in warm-dry areas benefits greatly from continuous climate warming, but the risk of hydraulic failure may increase.

1. Introduction

Temperate forests account for a quarter of the world's forests and account for one-third of all forest carbon storage (Pan et al., 2011). Climate change, especially the accelerated warming observed since the 1980s, has widespread impacts on tree growth, species distribution, forest structure, and tree mortality, ultimately affecting the health and carbon sequestration capacity of forest ecosystems (Allen et al., 2010; Babst et al., 2014; IPCC, 2015; Williams et al., 2013).

The period 1981–2020 may be the hottest 40 years of the past 1400

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years in the Northern Hemisphere (IPCC, 2015; Morice et al., 2021). Many studies have been conducted to better understand the sensitivity and growth pattern responses of different tree species to current climate warming (Cao et al., 2018; Harvey et al., 2019; Liu et al., 2013; Zhu et al., 2018a). Most of them showed that phenological changes caused by rapid warming can increase the net carbon absorption of trees (Keenan et al., 2014). Dendrochronological studies have also confirmed that rapid warming will increase tree growth in temperate forests in Asia (Cao et al., 2018), Europe (Harvey et al., 2019), and North America (Salzer et al., 2009). However, a growing number of studies have found that the growth decline around 1980 was caused by temperature-induced drought stress (Beier et al., 2008; Liu et al., 2013). There are many reasons for the difference in the effects of climate warming on tree growth (Zhu, 2019). A variety of factors influence the relationship between tree growth and climate, thus affecting the extent to which the rapid warming affects tree growth. These factors include climatic differences caused by site conditions such as latitude, longitude, and altitude (Castagneri et al., 2020; Harvey et al., 2019; Zhu, 2019; Zhu et al., 2018a; Zhu et al., 2020).

In recent years, quantitative wood anatomy (QWA) has been widely used in dendrochronology. Xylem anatomical features are directly related to the key functions and physiological processes of trees, and are important phenotypic plasticity traits of trees to adapt to environmental changes (Fonti et al., 2010; Sperry et al., 2008; Vaganov et al., 2006; Zhu, 2019). Xylem features record high-resolution environmental information, which is the key to better understand the physiological processes and mechanisms controlling tree growth (Carrer et al., 2015; Fonti et al., 2010; von Arx et al., 2016). Vessel features, especially earlywood vessel (EWV) features, are the most commonly used parameters in QWA of ring-porous species (Balzano et al., 2020; Castagneri et al., 2020; Fonti et al., 2010; Zhu et al., 2020). EWV features (e.g., vessel size and density) determine the potential hydraulic conductivity of tree species (Fonti et al., 2010). The range of differences in vessel features observed in trees growth under contrasting conditions highlights the plasticity of hydraulic structure and vessel function (e.g., hydraulic efficiency VS safety) (Castagneri et al., 2020).

On the one hand, increasing vessel diameter can maximize the conductivity; on the other hand, it decreases the safety margin to prevent cavitation and embolism under drought stress (Sperry et al., 2008; Tyree and Zimmermann, 2002). For this reason, it is essential to understand the plasticity response and adaptative strategy of tree xylem under different conditions. It is also important to predict the potential response to future climate change (Balzano et al., 2020; Castagneri et al., 2020). Rita et al. (2015) found that the functional anatomical features of European holly (*Ilex aquifolium* L.) in mesic sites were limited by temperature; in drought-prone areas, they were mainly determined by precipitation. Therefore, the climatic driving mechanisms of xylem formation, especially under different climatic conditions, is worthy of further study.

Manchurian ash (*Fraxinus mandshurica* Rupr.) is an important dominant broad-leaved tree species in northeast Asian temperate forests (Wang, 2004). It is very sensitive to climate change and is often used in dendrochronological studies (Cao et al., 2018; Su, 2016; Zhu, 2019; Zhu et al., 2020; Zhu et al., 2015). Previous studies have shown that the growth-climate relationship of *F. mandshurica* has obvious spatial and temporal variability (Cao et al., 2018; Su, 2016; Zhu, 2019). However, previous dendrochronological studies of *F. mandshurica* are almost entirely based on tree-ring width. The response of xylem anatomical features of *F. mandshurica* growing in different environments to rapid warming is unclear.

In this study, we collected the xylem anatomical data of *F. mandshurica* from 14 sites in two different climatic regions in northeastern China. Our goals were to (i) analyze the difference in xylem anatomical features occurring in *F. mandshurica* growing in warm-dry and cold-wet conditions; (ii) explore the differences in the effect of main climatic factors on xylem features between the contrasting conditions; (iii) determine the plasticity response of xylem anatomical features of *F. mandshurica* to rapid warming.

2. Materials and Methods

2.1. Study area and climate

This study was carried out in Changbai Mountains, northeastern China (Fig. 1). The zonal forest here is a typical broad-leaved Korean pine mixed forest, which is often distributed in the temperate zone of northeastern China and Far East Russia. *F. mandshurica* is an important dominant or codominant species of hardwood broad-leaved forest or coniferous broad-leaved mixed forest in northeast Asia. It is distributed between 700 and 2100 m a.s.l, with a height of 30 m and a diameter of 1.5 m (Hu et al., 2008). The soil is mainly dark-brown forest soil with the following characteristics: pH range 5.4-6.6, soil organic matter ~95 g kg^{-1}, total N ~3.4 g kg^{-1}, total phosphorus ~2.6 g kg^{-1}, and soil bulk density (0-9 cm) ~0.7 g cm^{-3} (National Soil Inventory Office, 1998).

This area is characterized by a temperate continental monsoon climate with long, cold winter and warm, rainy summer. Two subsampling areas were set up in the southwestern (SW) and northeastern (NE) Changbai Mountains (Fig. 1). In the SW area, the annual mean temperature is 6.6 °C, and the total annual precipitation is 914 mm. In the NE area, the annual mean temperature is 3.3 °C, and the total annual precipitation is 669 mm (Fig. 2). The coldest and warmest months are January and July, respectively. Compared with the temperature in the SW area, the lower temperatures in the NE area leads to a significant increase in relative humidity (the NE area: 70.2% and the SW area: 57.8%) and lower vapor pressure deficit (the NE area: 0.29 and the SW area: 0.53) (Fig. 2). Therefore, the SW of Changbai Mountains is defined as 'warm-dry', while the NE area is defined as 'cold-wet'. Fig. 2 showed the climate in the SW and NE areas from 1958 to 2015.

2.2. Sampling, wood preparation, and data measurement

A total of 14 sampling sites were selected in Changbai Mountains, including 7 sites in the SW area and 7 sites in the NE area. The distribution of these sites represents the different growth conditions of *F. mandshurica* across its range of northeast China. More than 20 healthy dominant or codominant trees were selected at each site. One or two incremental tree-ring cores were collected at the breast height using an increment borer with an inner diameter of 5.15 mm for each tree (Table 1).

The cores were air-dried, fixed, and polished with a series of progressively finer sandpaper grades up to 1200 grit. All cores were visually cross-dated using the skeleton-plot method under a microscope (Stokes and Smiley, 1968). The Velmex tree-ring width measurement system (Velmex, Inc., Bloomfield, NY, USA) was used to measure tree-ring widths with an accuracy of 0.001 mm. The accuracy of the cross-dated ring-width series was tested by the COFECHA program (Holmes, 1983). A total of 505 tree-ring cores of 320 *F. mandshurica* individuals were successfully cross-dated (Table 1).

Six evenly aged and undamaged cores were selected from each site for further QWA analysis. The vessel lumina of each core were filled with chalk powder to increase the contrast. Then, a 2400 dpi high-resolution scanner (Epson Perfection V600 Photo Scanner, Seiko Epson Corporation, Suwa, Japan) was used to capture the core digital image. All images were processed using Image-Pro Plus 6.0 (Media Cybernetics, Inc., Rockville, MD 20850 USA). For each ring, the diameter (d) and area (A) of all vessels ($A \geq 5000\ \mu m^2$) in the defined rectangular or parallelogram target area ($RW \times l$, where RW is the ring width and l is the tangent length of the growth ring in a sample, as shown in Fig. 3) were measured by combining automatic detection with manual editing. For each ring in every core, mean vessel area (MVA), vessel number (VN), total vessel lumen area (TVA), percentage of vessel area per ring (PC), vessel density (VD), hydraulic diameter (Dh), tree-ring theoretical hydraulic

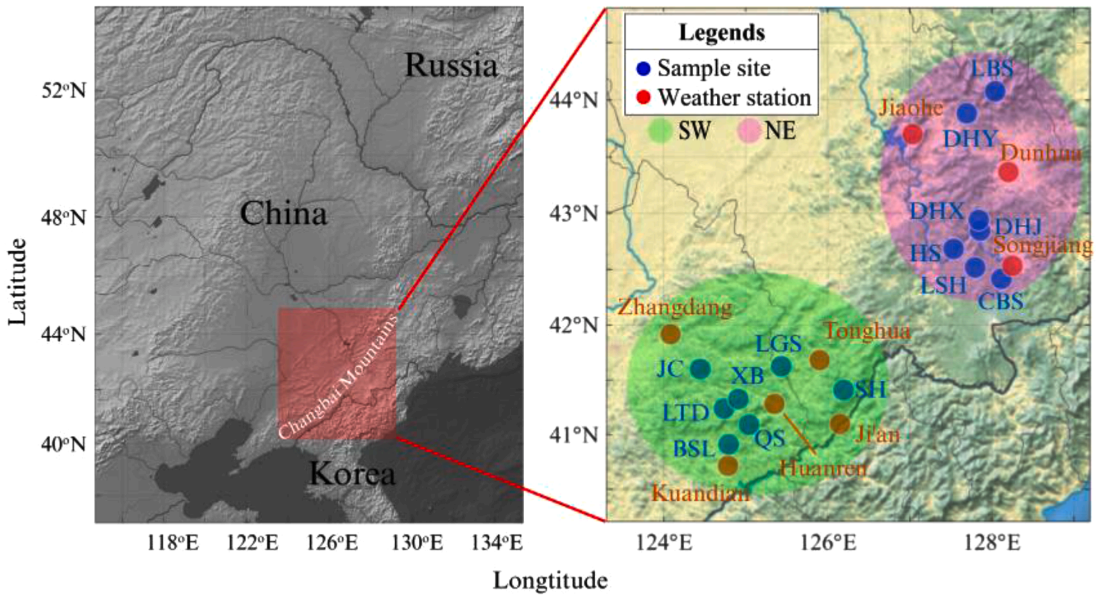

Fig. 1. Distribution of sampling sites in the southwestern (SW) and northeastern (NE) Changbai Mountains, northeastern China.

conductivity (Kh), and xylem-specific theoretical hydraulic conductivity (Ks) (Tyree and Zimmermann, 2002) were calculated for all years. The l of different rings or samples varied with the size of the polished section and the inner diameter of increment borer. Since VN, TVA, and Ks depend on the tangential width (l), we normalized these parameters into a fixed frame with a tangential width of 1000 μm (Castagneri et al., 2020). We used the R package 'dplR' (Bunn, 2008) to detrend the age-related growth trend of ring width and vessel features with negative exponential curves or simple linear regression lines.

$$VN = (1000\mu m * n)/l \tag{1}$$

Where VN is vessel number in a 1000-μm tangent length tree ring, n is the number of vessels, and l is the tangent length of each ring (μm).

$$MVA = \frac{1}{n}\sum_{i=1}^{n} A_i \tag{2}$$

Where MVA is the mean vessel area (μm^2), and A_i is the i^{th} vessel area (μm^2).

$$TVA = \frac{1000\mu m}{l}\sum_{i=1}^{n} A_i \tag{3}$$

Where TVA is total vessel lumen area in a 1000-μm tangent length tree ring (μm^2).

$$PC = \frac{TVA}{1000\mu m * RW} \times 100\% \tag{4}$$

Where PC is the percentage of vessel area to total ring rectangular area (%); RW is ring width (μm).

$$VD = VN/(1000\mu m * RW) \tag{5}$$

Where VD is the vessel density of each ring (number/μm^2).

$$Dh = \sum d^5 \Big/ d^4 \tag{6}$$

Where Dh is the hydraulic diameter of each ring (μm) and d is the vessel diameter (μm).

$$Kh = \frac{10^{-24}\pi\rho * 1000\mu m}{128\eta l}\sum_{i=1}^{n} d_i^{\,4} \tag{7}$$

Where Kh is the tree-ring theoretical hydraulic conductivity (kg•m•Mpa^{-1}•s^{-1}), ρ is the density of water at 20°C (998.2 kg/m^3), and η is the viscosity of water at 20°C (1.002×10^{-9} Mpa•s).

$$Ks = Kh/(1000\mu m \cdot RW) \tag{8}$$

Where Ks is the xylem-specific theoretical hydraulic conductivity (kg•m^{-1}•Mpa^{-1}•s^{-1}).

2.3. Climate data

The instrumental climate data were obtained from China Meteorological Data Service Center (http://data.cma.cn/). Data regarding the monthly mean temperature (T), monthly minimum (T_{min}) and maximum (T_{max}) temperatures, monthly mean relative humidity (Rh), and monthly total precipitation (P) of the nearest weather station from each sampling site were used in this study (Table S1). Regional T, T_{min}, T_{max}, P, and Rh in the SW and NE areas were synthesized by simple average method. Then, the monthly VPD of each area was calculated from the monthly mean temperature and relative humidity data using the following formula.

$$VPD = 0.61078 \times e^{\frac{17.27 \times T_a}{T_a + 237.3}} \times (1 - Rh) \tag{9}$$

where T_a and Rh are the monthly air temperature and relative humidity, respectively.

Seasonal climate variables were defined as follows: previous growing season (PGS) = previous June to October; previous non-growing season (PNG) = previous November to current April; beginning of growing season (BGS) = current May to June; middle of growing season (MGS) = current July to August.

2.4. Statistical analysis

Regional RW, EWV, and hydraulic features of each area (SW and NE) were calculated using the arithmetic average. The t-test and principal component analysis were used to test the difference of RW, EWV, or hydraulic features of trees between the SW and NE areas. Pearson correlation analysis was used to explore the relationship between RW and each EWV feature of trees in two areas.

Correlation function analysis was performed using the R package 'treeclim' (Zang and Biondi, 2015) to determine the relationship between climate and growth (xylem features). The relationship between monthly climate (from the previous May to the current October) and growth in each site were analyzed. We divided the xylem growth

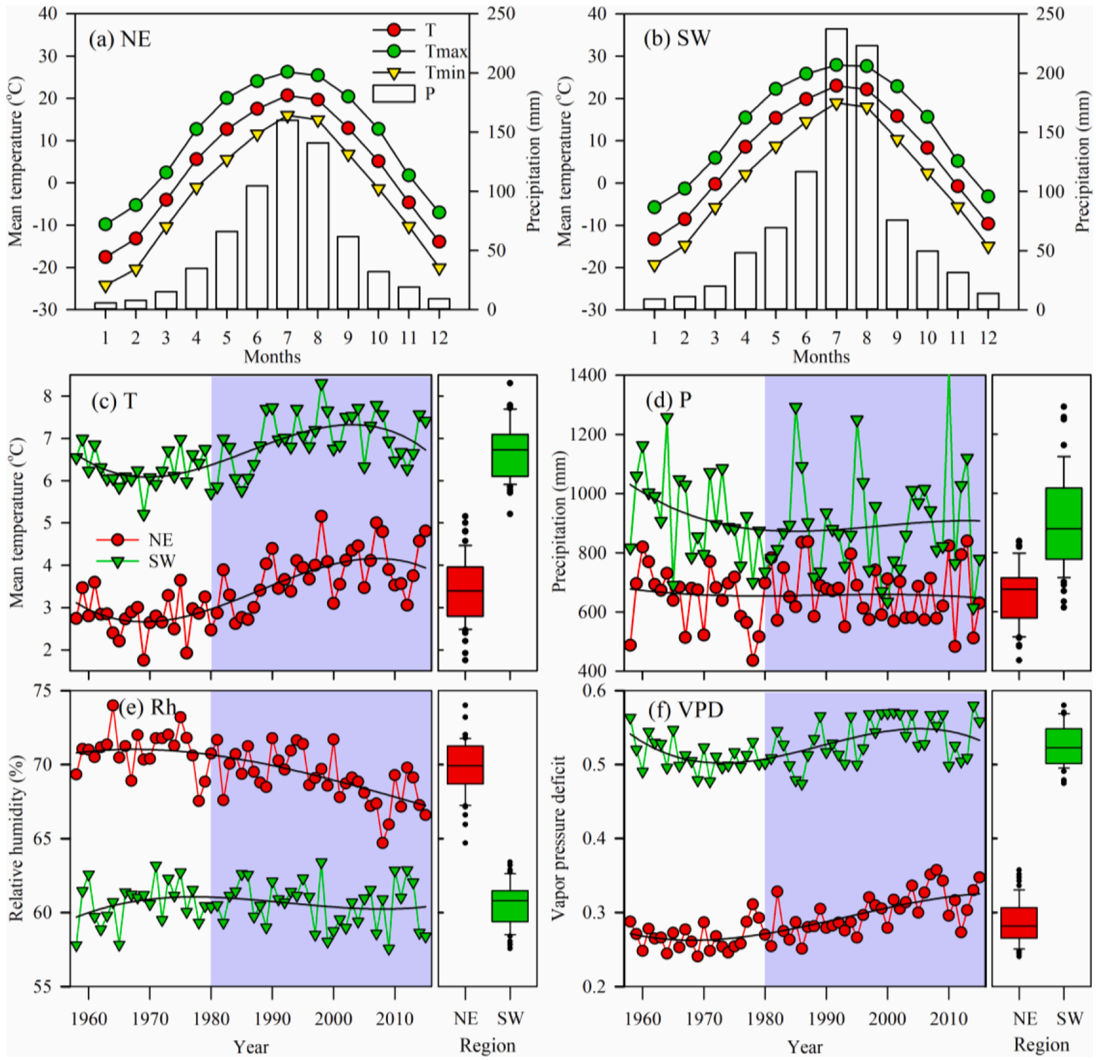

Fig. 2. (a-b) Climatic diagrams for the southwest (SW) and northeast (NE) areas of the Changbai Mountains and the variations in (c) mean temperature, (d) precipitation, (e) relative humidity, and (f) vapor pressure deficit from 1958-2015. Each climate factor (c-f) is fitted with a cubic function to highlight the low-frequency trend. There are significant differences between the SW and NE areas for all climate factors (c-f). T: mean temperature, T_{min}: minimum temperature, T_{max}: maximum temperature, Rh: relative humidity, P: total precipitation, VPD: vapor pressure deficit.

Table 1
Site information and sample characteristics for *F. mandshurica* in northeast China.

	Site code	Long. (°E)	Lat. (°N)	Alt. (m)	C/T	MRW (mm)	Age (a)	Period (n≥3)
NE	LBS	128.041	44.076	908	62/41	1.32±0.46	168±36	1837-2015
	DHY	127.694	43.884	1180	37/20	0.96±0.40	135±37	1883-2010
	DHJ	127.84	42.942	1095	38/20	1.24±0.46	145±21	1849-2010
	DHX	127.858	42.847	935	38/19	0.80±0.50	149±66	1853-2010
	HS	127.534	42.683	704	39/20	1.22±0.31	208±9	1799-2014
	LSH	127.795	42.517	853	43/22	1.23±0.30	237±16	1771-2014
	CBS	128.117	42.417	718	38/22	1.31±0.28	237±8	1779-2013
SW	LGS	125.432	41.626	875	34/18	2.43±0.60	71±7	1943-2013
	SH	126.192	41.411	908	35/19	2.69±0.57	69±7	1944-2013
	XB	124.445	41.601	504	23/23	3.26±0.74	66±15	1938-2015
	LTD	124.908	41.328	795	37/19	2.10±0.73	86±15	1919-2013
	JC	124.736	41.241	895	25/25	2.13±0.93	80±4	1935-2015
	QS	125.040	41.094	547	25/25	2.42±1.02	61±4	1953-2015
	BSL	124.790	40.913	810	32/17	2.09±0.81	96±7	1914-2013

Notes: C/T-cores/trees, MRW-mean ring width.

features into three categories base on the difference among nine growth features (Fig. 4 and 5) and their response patterns to the main climatic factors (e.g., Fig. S1 and S2). They are RW (characterizing carbon sequestration capacity); PC, VD, and Ks (xylem features related to vessel density, more representation of hydraulic safety); and other xylem features (MVA, VN, Dh, and Kh, more representation of hydraulic efficiency). The correlation between the regional seasonal climate and the growth characteristics of three categories in each area (SW and NE) was

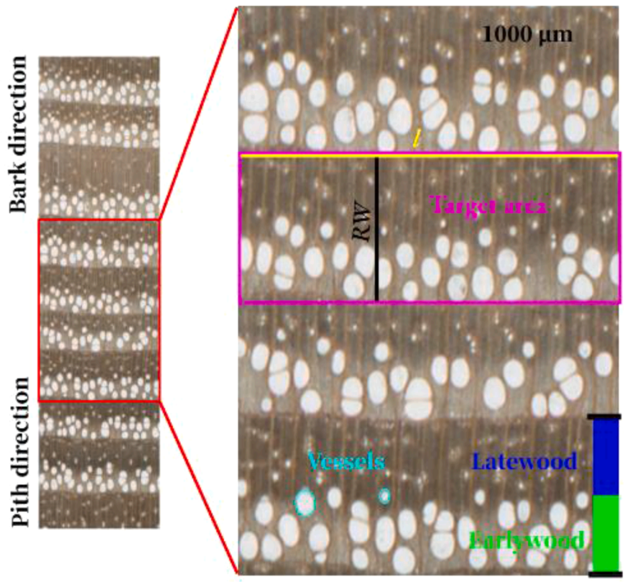

Fig. 3. Schematic illustration of xylem anatomy in tree rings of *F. mandshurica*. The ring width (RW), length of rectangle (l), vessel area (A), and the number of vessels (n) were measured and counted in the target area of each ring (purple rectangle or parallelogram: $RW \times l$). The vessel diameter (d) was calculated based on the perimeter, assuming a circular lumen shape. Only vessels with $A \geq 5000\ \mu m^2$ were measured in this study. For each ring, mean vessel area (MVA), vessel number (VN), total vessel lumen area (TVA), percentage of vessel area per ring (PC), vessel density (VD), hydraulic diameter (Dh), tree-ring theoretical hydraulic conductivity (Kh), and xylem-specific theoretical hydraulic conductivity (Ks) were calculated (See methods section for details). The l varied with different rings or samples. VN, TVA, and Ks depend on the l and they were normalized to a fixed frame with a tangential width of 1000 μm.

also analyzed. Finally, the temporal variation of the relationship between xylem anatomical features (three categories) and main climatic factors in the SW and NE areas of the Changbai Mountains were evaluated by using the moving correlation analysis (using a 20-year moving window).

3. Results

3.1. Ring width, xylem anatomical and hydraulic features among sites and their relationships

There were significant differences in RW, EWV, and hydraulic features between the SW and NE of Changbai Mountains. The RW, MVA, VN, TVA, Dh, and Kh in the SW area were significantly higher than those in the NE area, while PC, VD, and Ks were significantly lower than those in the NE area (Fig. 4). Trees in the SW area tend to produce more, larger, and lower density EWV (high VN and MVA, but low PC and VD) than those in the NE area. Trees in the SW area had higher hydraulic efficiency (high TVA, Dh, and Kh), and faster growth rates than those in the NE area (Fig. 4).

Almost the same correlation pattern was observed between RW, EWV, and hydraulic characteristics of *F. mandshurica* in the SW and NE areas (Fig. 5). RW in both areas was significantly positively correlated with VN, TVA, and Kh, and was negatively correlated with PC, VD, and Ks (Fig. 5) . VD was significantly negatively correlated with MVA, Dh, VN, TVA, and Kh (Fig. 5).

3.2. Effects of climate on ring width, xylem anatomical, and hydraulic features

The minimum temperature, especially in the growing season, was the main limiting factor affecting the radial growth, EWV formation, and hydraulic features of *F. mandshurica*. It showed significant and positive influence in SW and NE areas. Interestingly, xylem features associated with vessel density (PC, VD, and Ks) showed opposite signals in these two areas, positive climatic signals in the SW area and negative signals in the NE area (Fig. 6g-i). VPD had strong negative and positive effects on xylem features related to vessel density of *F. mandshurica* in the SW area and in the NE area, respectively (Fig. 6g-i). The Rh in the previous non-growing season (PNG) had a significant negative effect on the PC, VD, and Ks of *F. mandshurica* in the SW area, but had a positive effect in the NE area (Fig. 6g-i).

The responses of ring width and other xylem features (MVA, VN, TVA, Dh, and Ks) to climate had similar correlation patterns (Fig. 6a-f). The positive effects of temperature on RW, VN, TVA, and Kh in the NE area were greater than those in the SW area (Fig. 6a-f). The positive effects of VPD on RW, VN, TVA, and Kh were greater in the NE area than those in the SW area. The negative effect of Rh in the PNG on RW, VN, TVA, and Kh was stronger in the NE area than those in the SW area (Fig. 6a-f). Climate responses were consistent with the monthly climate-growth response patterns of *F. mandshurica* in both areas (e.g., T_{min} and Rh in Fig. S1 and Fig. S2). The different response patterns of xylem features (three categories) in the two areas were consistent with the results of principal component analysis (Fig. S3).

3.3. Temporal variations of relationship between xylem features and climate

A clear shift of growth-climate relationships occured around the 1980s (rapid warming). After 1980, the climate responses of most of the measured parameters became more significant (Fig. 7). In these two areas, xylem features related to tree radial growth (RW) and vessel density (PC, VD, and Ks) responded inversely to temperature and VPD (Fig. 7). The responses of other xylem features (MVA, VN, TVA, Dh, and Ks) to temperature and VPD became significantly positive correlation in the two areas after 1980 (Fig. 7a). The climate response (temperature and VPD) of tree radial growth in the NE area became significantly positive correlation, while the change in the SW area was not significant. The relationship between most xylem features and temperature in PNG changed from positive to negative after 1980, just opposite to the growth-temperature relationships in PGS (Fig. 7b). For both PGS and PNG, the relationship between Rh and xylem features of *F. mandshurica* in the NE area became significantly negative correlation after 1980s, but this change was not reflected in the SW area.

4. Discussion

4.1. Differences in xylem anatomical features of trees under different environmental conditions

Xylem features may vary significantly with site conditions (Balzano et al., 2020; Castagneri et al., 2020; Zhu et al., 2020). In our study, there are significant differences in xylem features of *F. mandshurica* between the SW and NE areas, which indicates that xylem adapts/acclimates to these areas. Vessel size generally increases with the cambium age and decreases from base to top (Carrer et al., 2015; Rosell et al., 2017). The overall trees in the SW area are younger (Fig. S4) and shorter (data not shown) than those in the NE area. The difference of tree height/age between the two areas showed that the average vessel area of trees growing in the SW area was higher than those in the NE area. Therefore, differences in vessel size or other xylem features between the two areas may not be caused by tree height or tree age. In the SW (warm-dry) area, trees tend to form wider rings with more, larger, and lower density EWV (PC and VD), and are accompanied by higher Dh and Kh. On the contrary, trees growing under cold-wet conditions (NE) tend to form narrow rings with fewer, smaller, and higher density EWV, and have lower Dh and Kh (Fig. 8). This means that trees growing in warm-dry area fix more carbon and have higher hydraulic conductivity than trees in cold-wet

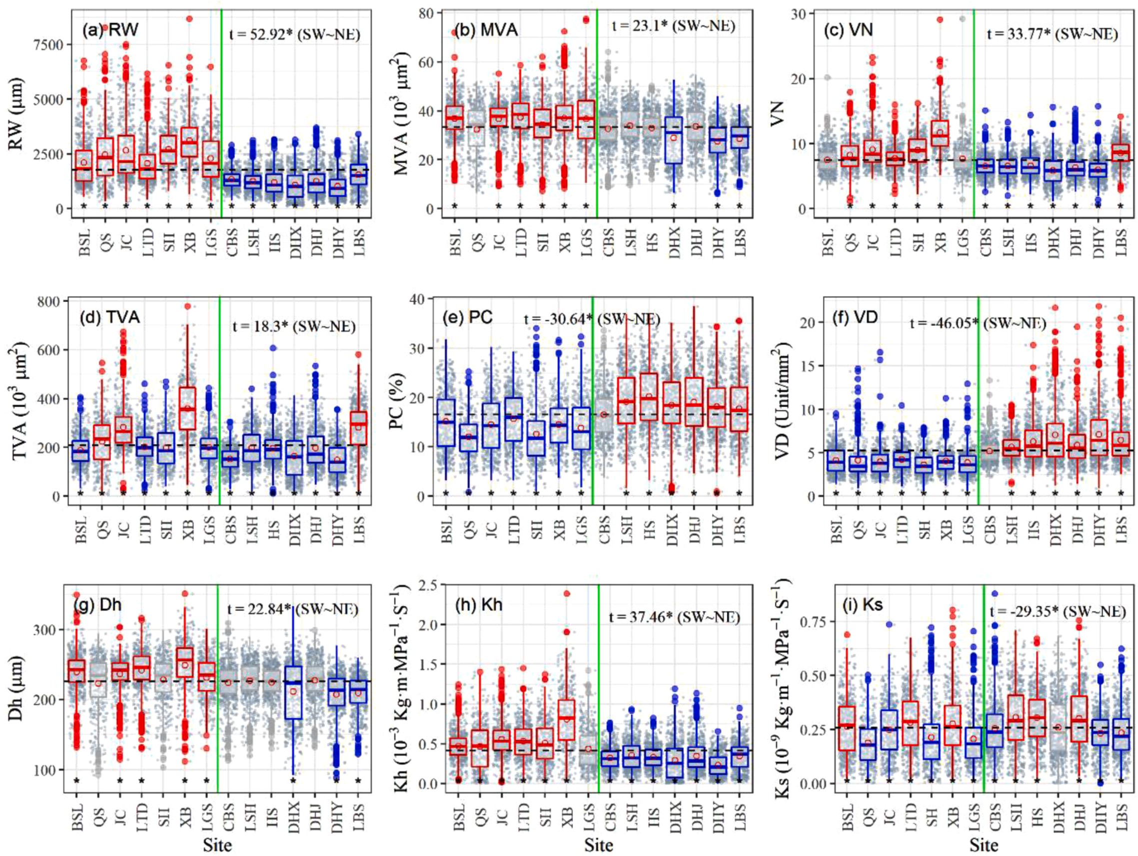

Fig. 4. Boxplots for characteristics of pooled RW, EWV, and xylem hydraulic features of *F. mandshurica* among sites. (a) ring width (RW), (b) mean vessel area (MVA), (c) vessel number (VN), (d) total vessel area (TVA), (e) percentage of vessel area (PC), (f) vessel density (VD), (g) hydraulic diameter (Dh), (h) tree-ring theoretical hydraulic conductivity (Kh), (i) xylem-specific theoretical hydraulic conductivity (Ks). The green line separates sites in the two areas and highlights the *t*-test results between the SW and NE areas. The red, blue, and gray boxes show differences that are significantly above, significantly below, and not significant the average (black dashed line), respectively. * = $p < 0.05$.

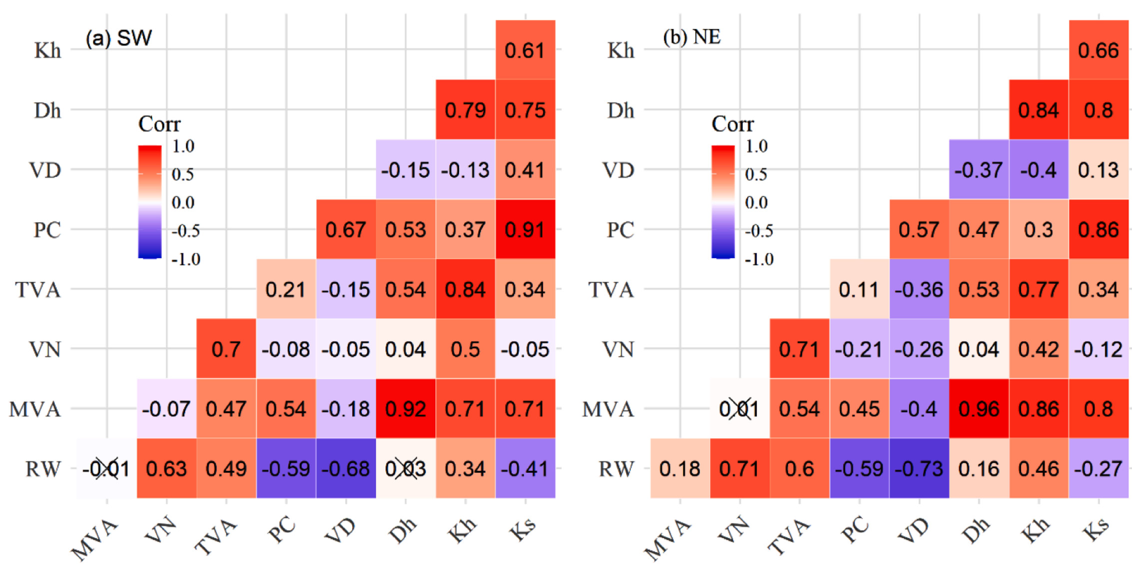

Fig. 5. Correlation relationships between RW, EWV, and xylem hydraulic traits of *F. mandshurica* in the (a) SW and (b) NE areas. In each graph, numbers that have been crossed out indicate non-significance ($p > 0.05$). RW = ring width, MVA = mean vessel area, VN = number of vessels, TVA = total vessel area, PC = percentage of vessel area, VD = vessel density, Dh = hydraulic diameter, Kh = tree-ring theoretical hydraulic conductivity, Ks = xylem-specific theoretical hydraulic conductivity.

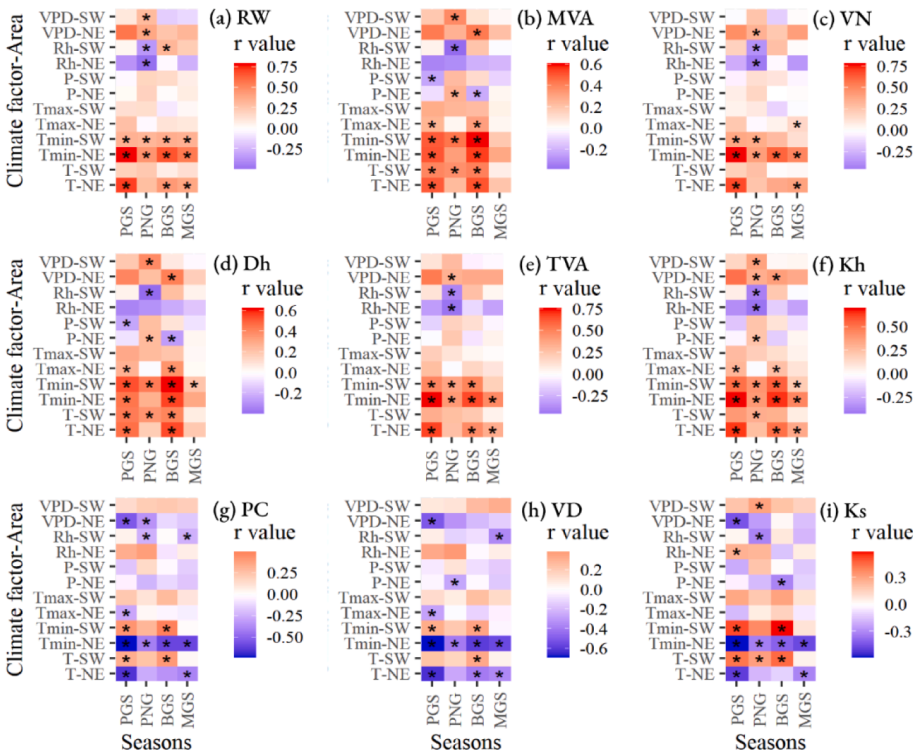

Fig. 6. Correlation relationships between seasonal climate factors and regional mean radial growth, EWV formation, and hydraulic features of *F. mandshurica* in the SW and NE areas during the period 1958-2013. (a) ring width (RW), (b) mean vessel area (MVA), (c) vessel number (VN), (d) hydraulic diameter (Dh), (e) total vessel area (TVA), (f) tree-ring theoretical hydraulic conductivity (Kh), (g) percentage of vessel area (PC), (h) vessel density (VD), (i) xylem-specific theoretical hydraulic conductivity (Ks). T = mean temperature, T_{min} = minimum temperature, T_{max} = maximum temperature, Rh = relative humidity, P = total precipitation, VPD = vapor pressure deficit. PGS = previous growing season (previous May to October), PNG = previous non-growing season (previous November to current April), BGS = beginning of the growing season (current May to June), MGS = middle of the growing season (current July to August). * = $p < 0.05$

conditions. According to the results of physiological study by Ji et al. (2005), the photosynthetic rate and water use efficiency of *F. mandshurica* growing under moderate drought stress was higher than that of the control. They pointed out that *F. mandshurica* can fully exert its photosynthetic potential under long-term moderate water stress, which is consistent with our results.

Trees can adapt to climate change by adjusting xylem features. Xylem is the result of the combined action of cell division rate and duration, which depends on specific regional environmental driving factors, local adaptations and individual plasticity (Arzac et al., 2016; Olano et al., 2017; Vaganov et al., 2006). In the SW area of the Changbai Mountains, the higher effective accumulated temperature (resulting from higher temperatures and longer growing seasons) ensures the strong assimilation capacity (Fritts, 1976; Zhu et al., 2018b). In order to take advantage of favorable conditions, trees need to have a stronger water transport capacity (Fritts, 1976; Vaganov et al., 2006), corresponding to significant increase in MVA, Dh, VN, TVA, and Kh (Fig. 4). Tree growth is less in the NE area, indicating a lower water demand than in the SW area. As a result, trees tend to form fewer and smaller vessels, resulting in reduced water transport capacity (Martinez-Sancho et al., 2017; Tumajer and Treml, 2016). Difference in vessel density and proportional vessel area coverage between the SW and NE areas suggest that trees in the NE area can compensate for small vessel with higher vessel density to maintain the required water transport. The tradeoff between vessel size and density indicates that the tradeoff between hydraulic efficiency and safety (Tyree and Zimmermann, 2002) and is between earlywood and latewood of xylem (Björklund et al., 2017; Souto-Herrero et al., 2018).

In both areas, RW is significantly positively correlated with VN, TVA, and Kh, and negatively correlated with PC, VD, and Ks. More EWV and higher TVA/Kh mean higher water transport capacity, which ensures the trees to maintain a higher photosynthetic efficiency and form a wide ring (Fonti et al., 2010; Fritts, 1976). Our results indicate that the xylem features related to density (PC, VD, and Ks) are different from other xylem features (Fig. 4 and Fig. 5). This may be related to the water use strategy of trees. It is generally believed that the size and density of vessels represent the water transport efficiency and hydraulic safety, respectively (Fonti et al., 2010; Tyree and Zimmermann, 2002). There is a significant negative correlations between MVA and VD in both the SW and NE areas (Fig. 5), which supports the hypothesis of tradeoff between hydraulic efficiency and safety (Tyree and Zimmermann, 2002). During drought, reducing vessel size to avoid cavitation may reduce the hydraulic efficiency of trees (Fonti et al., 2010). At the same time, trees usually increase vessel density to avoid hydraulic failure (Vaganov et al., 2006), such as the *F. mandshurica* in the NE area in this study and other species in tropical, temperate and Mediterranean forests (Hietz et al., 2017; Martinez-Sancho et al., 2017; Prislan et al., 2018). The significant positive correlation between RW (TVA) and VN is higher than that between RW (TVA) and MVA, indicating that the influence of RW and TVA on the number of vessels may be greater than that on the size of vessels. This is consistent with previous studies (Fonti and García-González, 2004; Zhu et al., 2020).

4.2. Response differences of xylem features to climate in different areas

Temperature higher than drought is the main climatic factor limiting/affecting the radial growth and xylem features of *F. mandshurica* in both areas. Temperature before or at the time of vessel formation is significantly positively correlated with all earlywood vessel features except for PC, VD, and Ks, which is consistent with some previous studies (Perez-de-Lis et al., 2016; Vaganov et al., 2006; Zhu et al., 2020). The significant correlation between xylem features and temperature ends in May or June (BGS, Fig. 6), which indicates that the end time of earlywood vessel formation is June or earlier. Studies on cambial activity and leaf phenology have confirmed that most EWV in ring-porous trees are formed before the photosynthetic capacity is fully restored, as in the case of *Castanea sativa* Mill. (Fonti and García-González, 2004) and *Quercus robur* L. (Tumajer and Treml, 2016). The formation of earlywood depends mainly on plant hormones and carbon accumulated in the previous year (Fritts, 1976; Guada et al., 2020; Lavric et al., 2017; Puchalka et al., 2017). Longer growing seasons are associated with higher temperatures, higher effective accumulated

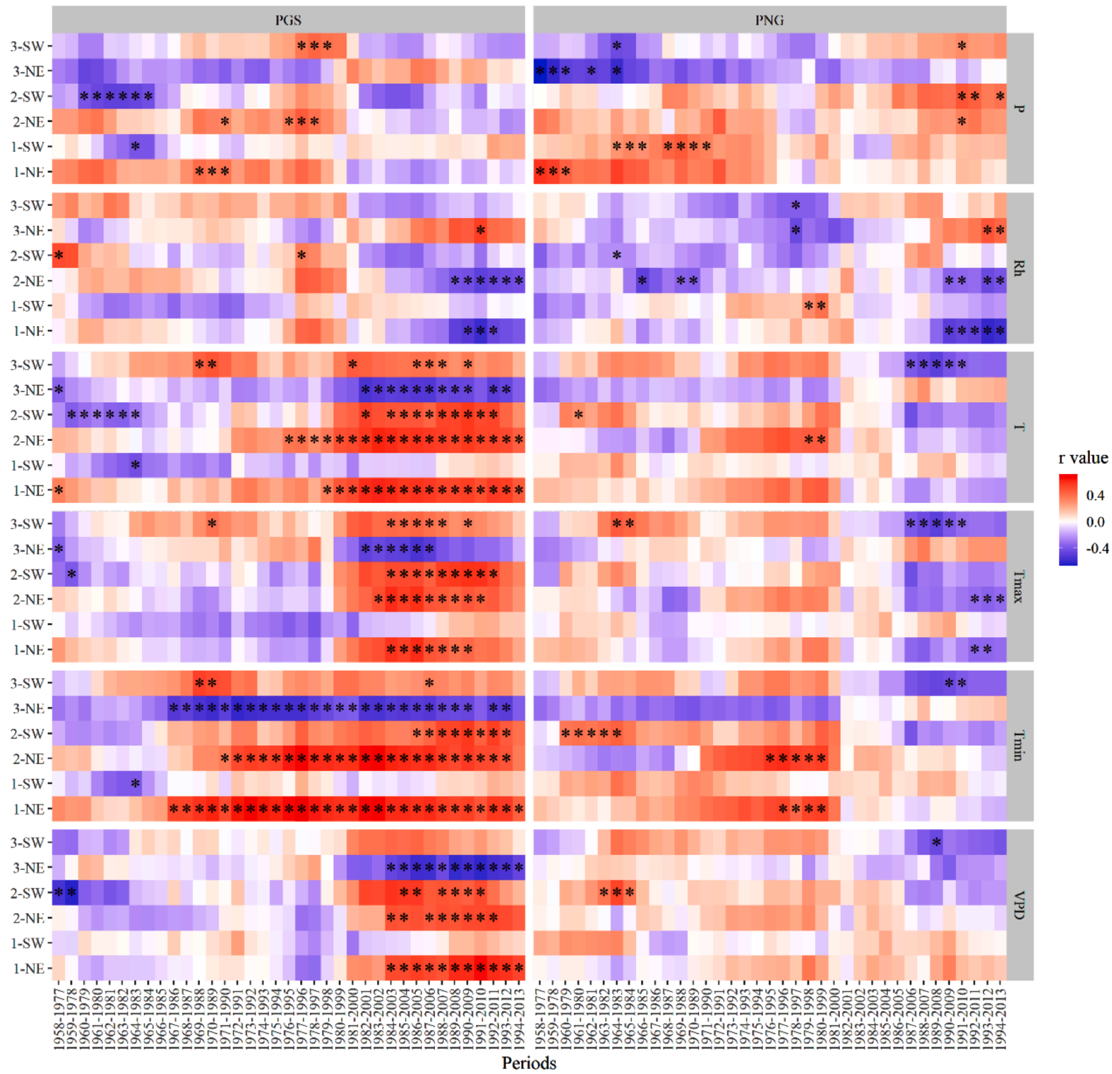

Fig. 7. The temporal variations between main climate factors in (a) the previous growing season (PGS) and (b) previous non-growing season (PNG) and the regional mean radial growth characteristics of *F. mandshurica* in the southwestern (SW) and northeastern (NE) areas. 1 = the ring width (RW). 2 = mean time series of the mean vessel area (MVA), vessel number (VN), total vessel area (TVA), hydraulic diameter (Dh), and tree-ring theoretical hydraulic conductivity (Kh). 3 = mean time series of the percentage of vessel area (PC), vessel density (VD), and xylem-specific theoretical hydraulic conductivity (Ks). T = mean temperature, T_{min} = minimum temperature, T_{max} = maximum temperature, Rh = relative humidity, P = total precipitation, VPD = vapor pressure deficit. * = $p < 0.05$.

temperatures, and higher photosynthetic rates. In short, these factors can increase carbohydrate assimilation (Fritts, 1976; Vaganov et al., 2006). This promotes earlywood formation of this year or the following year (Martinez-Sancho et al., 2017; Tumajer and Treml, 2016). Temperature during dormancy has a positive effect on xylem formation. Warm winters can protect trees from direct freezing injuries (Su and Lin, 2003; Vaganov et al., 2006; Zhu et al., 2015) and frost-induced cavitation (Gea-Izquierdo et al., 2013). In addition, winter moisture (VPD and Rh) has negative effects on MVA, VN, Dh, TVA, and Kh in both the SW and NE areas. This may be because higher humidity in winter makes trees more vulnerable to frost damage (Su and Lin, 2003; Zhu et al., 2015).

Interestingly, only xylem features associated with earlywood vessel density (PC, VD, and Ks) have different anatomical responses to interannual climate between different areas. These variables are more representative of hydraulic safety. The result indicates that there is a difference in the hydraulic strategy of *F. mandshurica* in the SW and NE areas (Fig. 8). In favorable years, trees in these two areas directly increase the efficiency of water transport by increasing the number and size of vessels (VN and MVA) to maximize hydraulic efficiency (TVA, Dh, and Kh). In addition, due to the high risk of hydraulic failure in the SW area, trees also use an adaptative strategy to ensure adequate water supply by increasing vessel density (PC, VD, and Ks), thereby improving hydraulic efficiency and safety (Martinez-Sancho et al., 2017). However, trees in the NE area have lower risk of hydraulic failure (smaller vessels) than those in the SW area, and they can afford to increase hydraulic efficiency at the cost of reducing hydraulic safety to a certain extent (Zhu, 2019; Zhu et al., 2020). Therefore, there is no compromise formula for increasing vessel density in trees in the NE area. The hydraulic strategy related to vessel density (VD, PC, and Ks) can be achieved by adjusting the ratio/allocation of earlywood and latewood of xylem (Fig. 8).

4.3. Xylem adjustment of F. mandshurica to rapid warming

The effect of non-growing season temperature on most xylem features became negative after the rapid warming in the 1980s, especially for trees in the SW area. Zhu et al. (2018a) obtained similar results on *Picea jezoensis* var. *microsperma* in the north of the study area. In the non-growing season, photosynthesis stops and there is no new source of photosynthetic products. High temperatures during dormancy can increase the respiration of trees and indirectly reduce the material and

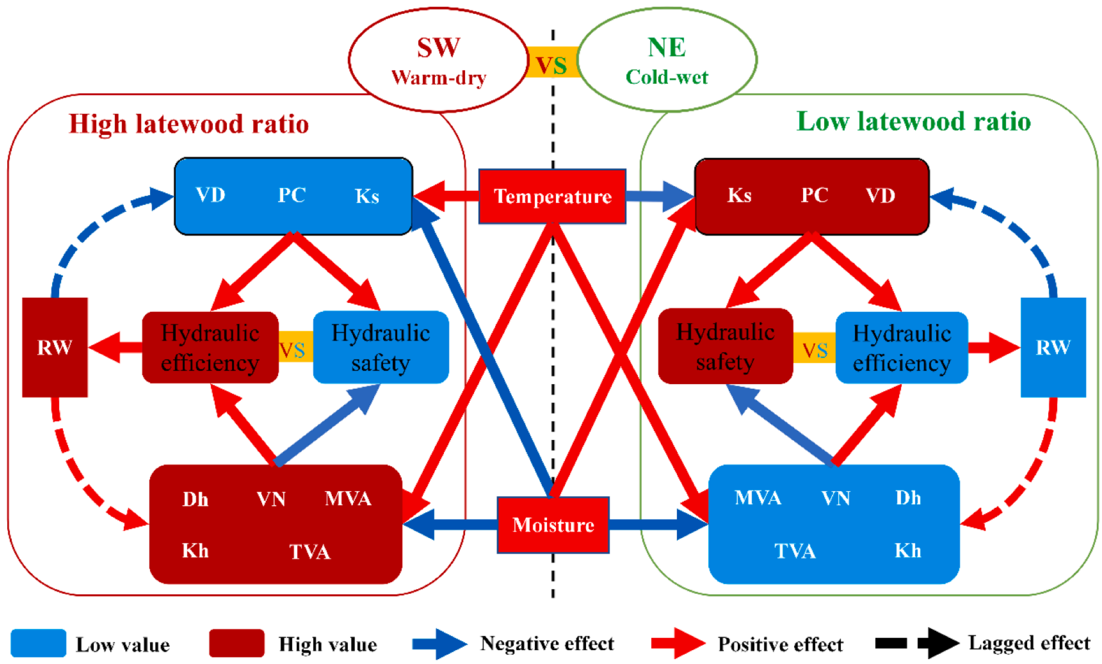

Fig. 8. Schematic illustration of the effect of main climate factors on xylem formation of *F. mandshurica* in the SW and NE areas. RW = ring width, MVA = mean vessel area, VN = vessel number, TVA = total vessel area, PC = percentage of vessel area, VD = vessel density, Dh = hydraulic diameter, Kh = tree-ring theoretical hydraulic conductivity, Ks = xylem-specific theoretical hydraulic conductivity.

energy available in the early stages of EWV formation in the following year (Fritts, 1976; Vaganov et al., 2006). In addition, higher temperatures exacerbate drought stress and increase the risk of drought-induced cavitation (Gea-Izquierdo et al., 2013).

The positive effects of PGS temperature on most xylem features (MVA, VN, Dh, TVA, and Kh) were significantly enhanced around 1980, indicating that rapid warming could significantly improve the hydraulic efficiency of xylem. Warming will increase the photosynthetic rate of trees, resulting in greater water demand than before (Ji et al., 2005). It requires trees to have higher water transport capacity or hydraulic efficiency after warming (Balzano et al., 2020; Gea-Izquierdo et al., 2013). This provides a reasonable physiological explanation for the dramatic and rapid growth of ring-porous tree species in temperate forests (e.g., *Phellodendron amurense* Rupr. and *Quercus mongolica* Fisch. ex Ledeb) around 1980 (Zhu, 2019; Zhu et al., 2018b). However, the increase of moisture (P, Rh, VPD) and temperature will hinder the accumulation of organic matter by photosynthesis (Fritts, 1976), thus indirectly reducing the material basis of EWV formation and tree growth in the next year. This is why PGS moisture (P, Rh, VPD) starts to have a negative influence on most xylem features around 1980. It is worth noting that although rapid warming is generally beneficial to ring-porous species, it also brings greater risk of hydraulic failure, especially for *F. mandshurica* in the SW area (Zhu et al., 2020). If climate warming continues, trees in the SW area of Changbai Mountains may decline due to hydraulic failure. More research is needed to reveal whether other species perform as well as *F. mandshurica*. Our results highlight that tree-ring anatomy has great potential in explaining the relationship between tree growth and climate.

5. Conclusion

F. mandshurica growing in warm-dry and cold-wet areas has the ability to adjust xylem features to adapt to different site conditions and climate warming. In the SW area (warm-dry), trees tend to form wide rings and high vessel numbers, as well as EWV with low densities and proportions. Therefore, trees growing in warm-dry areas have higher hydraulic efficiency. On the contrary, trees growing in the NE area (cold-wet) are just the opposite. The correlations between the xylem features of *F. mandshurica* growing in the two areas are basically the same. The xylem features related to density are different from other xylem features, which may be related to water use strategy of trees. RW is significantly positively correlated with VN, TVA, and Kh, and negatively correlated with PC, VD, and Ks. MVA and VD are significantly negatively correlated in both areas, which supports the hypothesis of tradeoff between hydraulic efficiency and safety.

The minimum temperature is the limiting factor of radial growth and xylem formation of *F. mandshurica* in warm-dry and cold-wet areas. RW, MVA, VN, Dh, TVA, and Kh are significantly positively correlated with temperature and negatively correlated with moisture in the non-growing season in both areas. At the same time, the response of PC, VD, and Ks to climatic factors in these two areas are completely opposite. *F. mandshurica* can adjust the vessel density or ratio of earlywood by changing the relative proportion of earlywood and latewood, to cope with climate change and balance hydraulic efficiency and safety. Rapid warming significantly improves the hydraulic efficiency of trees to maximize carbon fixation under conditions that temperature limits the growth of trees (i.e., there is enough water available). The increase in hydraulic efficiency can meet the demand for water transport caused by the increase in assimilation efficiency and the lengthened growing season caused by warming, providing a potential physiological mechanism for the growth increase and range expansion of ring-porous broad-leaved tree species in temperate forests. Our results highlight the importantce of xylem anatomical features in explaining the relationship between tree growth and climate. It is worth noting that *F. mandshurica* in warm-dry areas benefit more from the current climate warming, but the warming climate also increases their risk of hydraulic failure. Further research is needed to determine whether other tree species can perform the same as *F. mandshurica* under climate change. How climate change affects the extent of species distribution and genetical diversity of different tree species in the region is also worth studying.

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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Supplementary materials

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