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# Warming aggravates physiological drought in *Betula platyphylla* during the winter–spring transitional period in Greater Khingan Mountains

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ABSTRACT

Tree growth is highly susceptible to hydrothermal changes during winter-spring transition, particularly in cold-temperate regions while short-term climatic fluctuations could play a primary role in inter-annual growth dynamics. To unravel this mechanism, we focused on *Betula platyphylla*, a key companion and pioneer species in *Larix–Betula* forests in the Greater Khingan Mountains. Using dendrochronology methods, we investigated warming impacts on its radial growth during winter-spring transition (February–April) based on short-term 10-day climate data. Here, we showed warming exacerbated physiological drought by intensifying snowmelt and soil freeze-thaw cycles, disrupting water balance and therefore suppressing tree growth. The temperature threshold (~4.0°C) for triggering tree growth advanced by 0.4 days/year since 1990, which in turn intensified pre-monsoon drought stress. Although freeze-thaw water dominated pre-monsoon growth, the tree growth was threatened by warming-induced soil hydrological changes. Our study highlights that winter-spring warming may constrain boreal forest carbon sequestration through intensified water stress, urging attention to non-growing season climatic controls on tree growth.

## 1. Introduction

Climate change has substantially increased the risks to ecosystem functions in terrestrial environments, such as causing biome shifts, and more pronounced changes are projected in the coming decades (IPCC, 2022). In particular, warming and drying climates pose serious threats to forests growing in high latitudes and cold regions in the context of global climate change (Allen et al., 2015; Williams et al., 2014; Zhang et al., 2017; Harrison et al., 2020). Increased mortality and even irreversible damage to forest trees are ubiquitous and often attributed to increased temperatures or reduced water availability during growing season (Allen et al., 2015; Zhang et al., 2017). Although studies on tree-growth responses to climate change have primarily focused on the growing season (Zhang et al., 2019), climate conditions during both dormant season and early vegetative phases could also exert substantial influences on tree growth dynamics. For instance, extended winter chilling delayed spring phenological development, which shortened the duration of active growth period and diminished annual biomass production (Liu et al., 2023). Increased growing season length due to warmer springs was not necessarily beneficial to tree growth because it could increase the risk of frost for trees and lead to soil moisture depletion (Liu et al., 2018; Lian et al., 2020). When spring snow melts too early, it provides less water from melting snow throughout the season. This leads to severe water shortages, making it harder to meet the high water needs during the hottest summer months (Qin et al., 2020).

Winters are warming much faster than other seasons, especially during the early growing season in middle to high latitudes due to global warming (Yang et al., 2020).Temperature and precipitation / snowfall changes in winter can affect tree growth and forest distribution either

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individually or in combination (Harvey et al., 2020; Sanmiguel-Vallelado et al., 2021; Girardin et al., 2022). Temperature-controlled spring phenological fluctuations in trees at high latitudes are affected by climate change (Huang et al., 2018; Geng et al., 2020). The metabolism of dormant trees is extremely weak or even ceases in boreal forests with limited water availability and greater energy loss in winter (Zhang et al., 2019; Nilsson, 2022). The transitional period between winter and spring (generally in the late non-growing season) is a critical period where weather conditions determine the beginning and duration of annual tree growth and affect growth capacity of trees. In water-limited regions, the inhibitory effects of winter-spring warming (and its cumulative impacts) on tree growth may outweigh the beneficial effects of temperature increases during the growing season (Gao et al., 2022).

Tree growth relied on water availability from March to April in the northern latitudes of the temperate zone (Zheng et al., 2022). However, rising temperatures during this period may exacerbate water deficits, thereby impairing tree survival and reproductive success (Williams et al., 2014). This temperature-driven moisture constraint exhibits pronounced regional variability. For instance, on the Changbai Mountains, elevated temperatures have triggered acute water stress in *Picea jezoensis* var. microsperma and *Pinus koraiensis* (Li et al., 2011; Yu et al., 2013; Bao et al., 2019). A parallel phenomenon is observed in the Lesser Khingan Mountains, where temperature variability has driven growth declines in *Pinus koraiensis* and *Picea koraiensis* (Yuan et al., 2020). Importantly, employing finer temporal resolutions (e.g., 10-day scales) rather than traditional monthly analyses can more precisely reveal climate-growth relationships during critical seasonal windows (Sano et al., 2009; Qi et al., 2022).

Temperate coniferous forests on the Greater Khingan Mountains of the northern China grow predominantly on permafrost (He et al., 2009), and these forests are susceptible to changes in winter climates (Wang et al., 2011; Li et al., 2017; Bai et al., 2019). The permafrost environment complicates the response and adaptation of these forests to climate change. For example, warmer winters result in earlier and excessive permafrost melting. In addition, warming leads to an earlier onset of snowmelt and snowmelt runoff (Dang et al., 2021; Zhang et al., 2021), in which alters surface hydrological environment (Schuur et al., 2015) and affects vegetation recovery (Wang and Liu, 2021). Various factors may cause or exacerbate water shortages during non-growing season on the Greater Khingan Mountains (Zheng et al., 2022), making permafrost ecosystems more sensitive and vulnerable to climate change than terrestrial ecosystems. It is reasonable to surmise that indigenous trees growing in frigid northernmost China have prevalently intrinsic attributes in growth and growth–climate responses that are deserving of further understanding. *Betula platyphylla* serves as both a companion and pioneer tree species on the Greater Khingan Mountains and often co-occurs with *Populus davidiana*, *Larix gmelinii*, and other tree species. The growth of *B. platyphylla* is highly vulnerable to variations in water and heat conditions and has been investigated using dendrochronology (Gradel et al., 2017). Previous research has shown that the radial growth of birch trees is hindered by climatic changes during non-growing season, particularly during the winter–spring transitional period. For example, drought conditions caused a decline and dieback of *B. platyphylla* in the Lake Baikal region of Siberia (Kharuk et al., 2013), and the growth of *B. utilis* exhibited a negative correlation with spring temperatures in Nepal (Dawadi et al., 2013). However, we lack an information on fine-scale responses of birch trees to climate change over non-growing season, particularly in cold areas of temperate zones experiencing severe winters lasting more than half a year. Therefore, studying the growth response of *B. platyphylla* to climate change during non-growing season at a finer temporal resolution in the Greater Khingan Mountains region may provide a holistic understanding of the intra-annual growth of boreal broadleaf trees.

## 2. Materials and methods

### 2.1. Study area

The study area (51.06–51.59°N, 120.75–121.79°E) is located in the northern region of the Greater Khingan Mountains with an average elevation of 792 m a.s.l. (Fig. 1a). The sampling area consists of two ecosystems with abundant vegetation: permafrost and cold temperate forests. The ecosystems are characterized by a cold temperate continental monsoon climate, with a large diurnal temperature variation and an average annual temperature ranging from −7 to 4 °C (Fig. 1b). Winters are harsh and snowy, with the lowest temperature reaching −52 °C. The average annual temperature is < 0 °C for approximately half the year (Fig. 1c). Summers are short and rainy, with annual precipitation of approximately 450 mm. The precipitation peaks in July–September accounting for 80 % of the total annual precipitation(Fig. 1d).Birch budburst occurs in late April to early May and goes dormant in late September to early October (Du and Fang, 2014; Xu et al., 2021).

### 2.2. Tree-ring sampling and chronology development

We visited six sampling sites (JMB1,JLB1,JHB1,JHB2,NEB1,MEB2) to sample tree cores of *B. platyphylla* in September 2019 (Fig. 1a). At each sample site, we selected more than 20 trees and sampled two increment cores from different directions for each tree, totaling 134 *B. platyphylla* trees, 268 cores were selected for this study (Table 2). Samples were taken to laboratory and preprocessed, including drying, mounting, surfacing, and cross-dating, using conventional (standard) dendrochronological methods (Stokes and Smiley, 1968; Fritts, 1976). Each tree-ring width was measured with a precision of 0.01 mm and assigned a calendar year. We then used the COFECHA program (Holmes, 1983; 1986) to ensure cross-dating quality.

To remove the influence of disturbing factors from the tree-ring width data and to retain climatic signals, *B. platyphylla* tree-ring width series were detrended and normalized in the Arstan program (Cook and Holmes, 1986) using negative exponential or linear functions. For samples that could not be fitted by the above function, a spline function with a length greater than two-thirds of the total sequence length was used. Finally, we obtained six standardized chronologies (STDs) for the six sample sites.

Due to close proximity of sampling sites and sharing similar natural climatic conditions, the six STDs are positively correlated ($p < 0.01$, Table 1). Thus, we combined all six chronologies into one regional chronology (i.e., DXB6, Fig. 2) to investigate the commonality of radial growth and its response to climatic factors in the northern region of the Greater Khingan Mountains (Table 3).

### 2.3. Meteorological data and methods

Daily meteorological data, including daily air temperature (Tmax, Tmin and Tmean)

and daily precipitation, were obtained from the nearest Tulihe meteorological station in the study area of the China Meteorological Science Data Center (http://data.cma.cn). The standardized precipitation evapotranspiration index (1-month SPEI,CRU TS v4.05), a drought index (Vicente-Serrano et al., 2010), was used to investigate the impact of moisture abundance or deficit on tree radial growth. SPEI, monthly temperature and precipitation, and saturation vapor pressure (VP) data were downloaded from the KNMI Climate Explorer (http://climexp.knmi.nl). Vapor pressure deficit (VPD) data were calculated based on the monthly mean temperature (T) and VP using the following equation (Allan et al., 1998):

$$\mathrm{VPD} = 6.10695 * 10^{\frac{7.59271*\mathrm{T}}{\mathrm{T}+240.72709}} - \mathrm{VP}$$

We examined the growth–climate relationships between birch

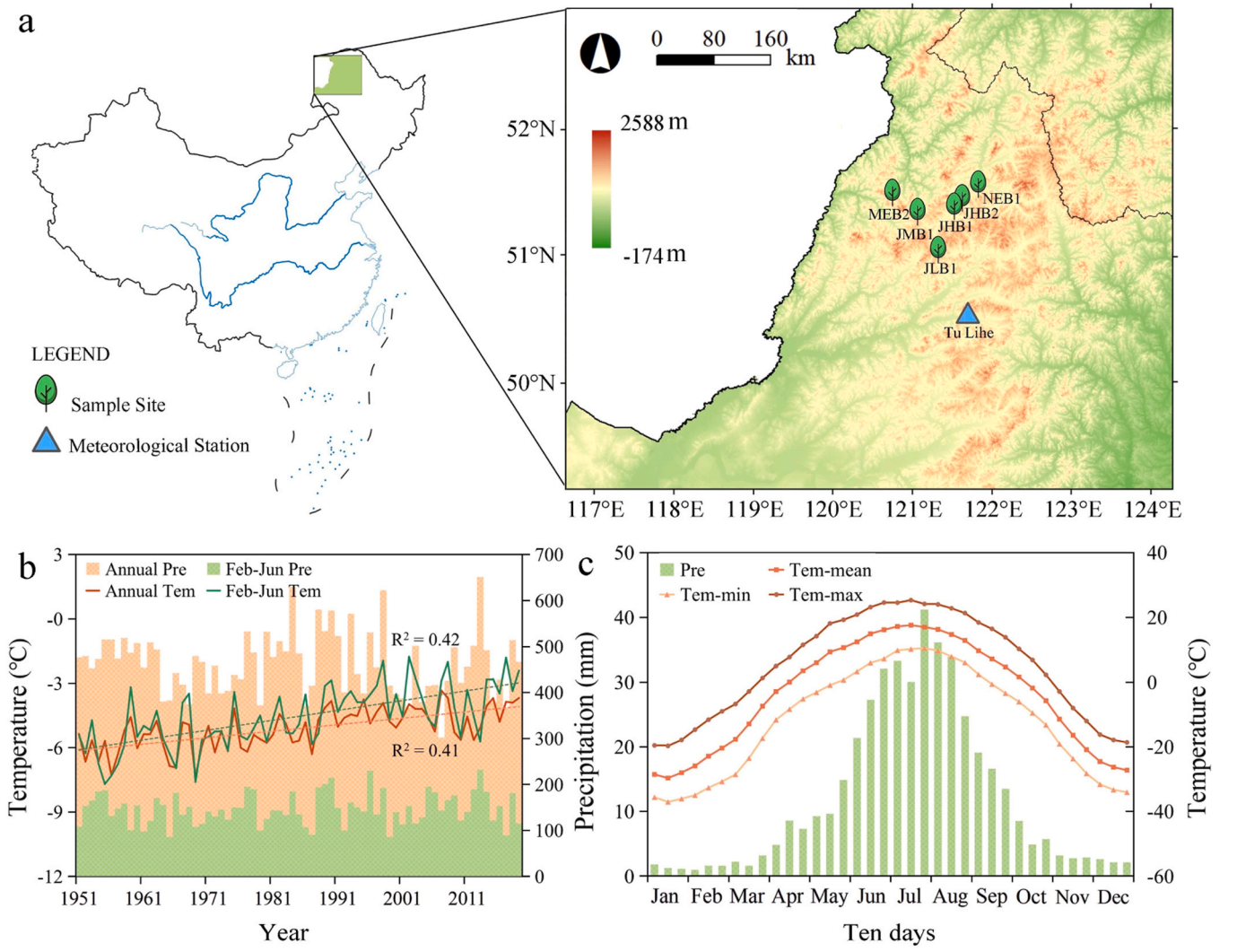


**Fig. 1.** A: location of sample sites and meteorological station.JMB1,JLB1,JHB1,JHB2,NEB1,MEB2is sample site and TuLihe is TuLihe meteorological station. B: annual mean temperatures (Annual Tem), annual total precipitation (Annual Pre), annual February–June mean temperatures (Feb–Jun Tem) and annual February–June total precipitation (Feb–Jun Pre) variations. C: 10-day variations of mean temperatures (Tem mean), total precipitation (Pre), mean minimum temperatures (Tem-min) and mean maximum temperatures (Tem-max).

**Table 1**
Correlations among the birch STDs at six sites during 1961–2019.

| | JLB1 | JMB1 | MEB2 | JHB1 | JHB2 |
|---|---|---|---|---|---|
| JMB1 | 0.161 | | | | |
| MEB2 | 0.386** | 0.648** | | | |
| JHB1 | 0.216 | 0.721** | 0.448** | | |
| JHB2 | 0.469** | 0.367** | 0.581** | 0.546** | |
| NEB1 | 0.248 | 0.639** | 0.508** | 0.643** | 0.502** |

Note: "**" and "*" indicate 99 and 95 % confidence levels, respectively.

growth and monthly climatic variables using Pearson's correlation during 1961–2019. We examined the temporal stability using a moving correlation with a 31-year window. We selected the months from November of previous year to October of current year as a growing year to study the intra-annual variation of growth–climate relationships. To minimize the autocorrelation effects, we used the first-order difference variables of STD chronologies and climate variables in the correlation analysis.

Given that climate data on a 10-day scale allow a more precise examination of the birch growth–climate relationship(Qi et al.,2022), we divided each month into three phases (I: the first 10 days of a month; II: the second 10 days of a month; and III: the remaining days of a month). The average temperature and total precipitation for three phases of a given month were calculated using daily climate data from 1990 to 2018. We calculated the correlation coefficients between birch growth and the climatic variables (mean, maximum, and minimum

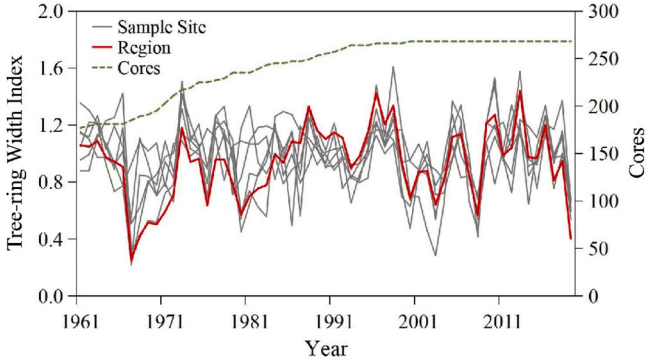


**Fig. 2.** Birch tree-ring width STDs and sample depths (cores) (1961–2019).

**Table 2**
Information on the 6 sampling sites of birch in the study area.

| Sampling site CODE | Elevation (m) | Longitude (°E) | Latitude (°N) | Number of trees | Number of cores |
|---|---|---|---|---|---|
| JLB1 | 1010 | 121.3 | 51.06 | 21 | 42 |
| JHB1 | 750 | 121.56 | 51.45 | 26 | 52 |
| JHB2 | 767 | 121.54 | 51.43 | 20 | 40 |
| JMB1 | 743 | 121.03 | 51.37 | 23 | 46 |
| NEB1 | 775 | 121.79 | 51.6 | 20 | 40 |
| MEB2 | 709 | 120.75 | 51.49 | 24 | 48 |

temperatures, and precipitation) on a 10-day scale. Based on 10-day scale correlation results (positive or negative) with temperatures (Tmax, Tmean, Tmin), we defined seasonal climate variables as following: Dormant Winter Phase (previous November to current February), Winter-Spring Transition, WST (current Late February to mid-April) and Ecological Spring Phase (current April to May). Principal component analysis (PCA) was used to investigate the effect of temperature on birch growth.

A linear model was used to quantify the potential effects of thermal change on the growth–climate response during the early growing season, and to identify the threshold for the adaptability of birch populations under changing thermal conditions. We then used the temperature threshold on a daily scale to obtain the date of occurrence (day of the year, DOY) from 1990 to 2018. Correlation analysis and graphical tabulations were performed using R software packages (dplR, ggbiplot, vegan, tidyverse, and ggplot2).

## 3. Results and analysis

### 3.1. Correlation between ring width and climatic factors during winter-spring

Monthly temperatures (mean, maximum and minimum) have negative correlations with *B. platyphylla* tree-ring width during winter-spring, and the correlations in the previous December and current February–April were significant ($p < 0.05$, Fig. 3). Both precipitation and moisture indices (SPEI) showed positive correlations with tree growth from February to April where the correlation in April was significant ($p < 0.05$). The tree growth was negatively correlated with

**Table 3**
STD statistics for six site chronologies and the regional chronologies (DXB6).

| Sampling site CODE | Series intercorrelation | Mean sensitivity | Standard deviation | Time span (EPS > 0.85) | Expressed population signal | Signal-to-noise ratio |
|---|---|---|---|---|---|---|
| JLB1 | 0.586 | 0.393 | 0.503 | 1972–2019 | 0.931 | 13.531 |
| JHB1 | 0.639 | 0.355 | 0.497 | 1930–2019 | 0.970 | 31.874 |
| JHB2 | 0.641 | 0.377 | 0.522 | 1952–2019 | 0.965 | 27.461 |
| JMB1 | 0.614 | 0.364 | 0.464 | 1901–2019 | 0.964 | 26.445 |
| NEB1 | 0.616 | 0.316 | 0.497 | 1948–2019 | 0.912 | 10.356 |
| MEB2 | 0.628 | 0.337 | 0.473 | 1924–2019 | 0.966 | 28.418 |
| DXB6 | 0.518 | 0.355 | 0.488 | 1922–2019 | 0.990 | 97.040 |

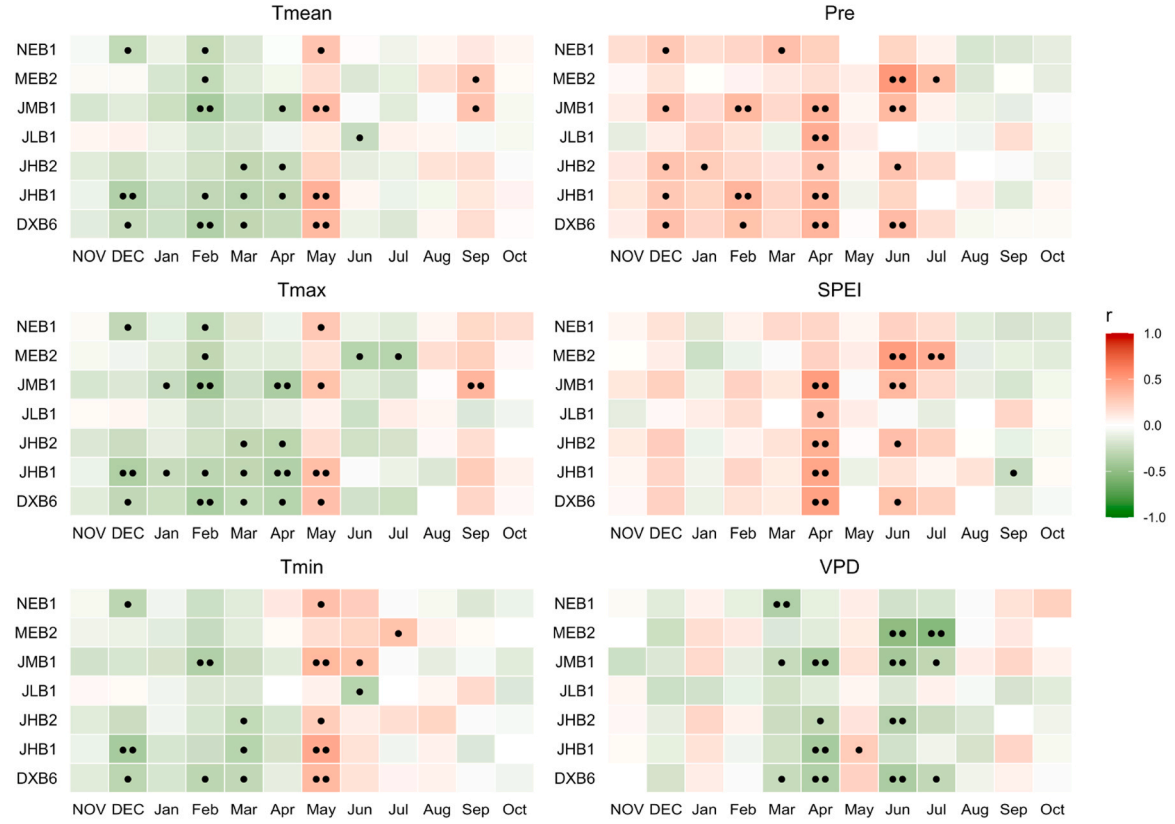


**Fig. 3.** Correlations between birch STDs and the primary monthly climatic variables in the study area during 1961–2019. "●●" and "●" indicates 99 % and 95 % confidence levels, respectively.

saturated VPD from February to April and reached significance in April ($p < 0.05$) (Fig. 3).

The 31-year moving correlations of February–April mean, maximum, and minimum temperature variables with the regional chronology changed from positive to significantly negative over time during 1969–2019 ($p < 0.01$). The positive correlations between the regional chronology and February–April precipitation and SPEI both increased gradually over time from 1969 to 2019 ($p < 0.01$) while the negative correlations with VPD showed a significant increase during 1969–2019 ($p < 0.01$) (Fig. 4).

With the increase in February–April mean temperatures, the moving correlations between regional chronology and February–April mean temperatures changed significantly from positive to significantly negative ($p < 0.01$) (Fig. 5), and the positive correlations with February–April precipitation increased significantly ($p < 0.01$) during 1969–2019.

The correlations between *B. platyphylla* tree-ring width and spring precipitation were also predominantly positive, especially in late April on a 10-day scale ($p < 0.05$) (Fig. 6). Negative correlations between tree-ring width and mean, maximum, and minimum temperatures were observed from late December of the previous year to mid-April of the current year, with a significant increase in negative correlations from late February to mid-April ($p < 0.05$). Positive correlations between tree-ring width and temperature variables existed from late April to early June, reaching a 0.05 significance level from late April to early May. The negative correlations between tree-ring width and mean and minimum temperatures from late February to mid-April were significant ($p < 0.05$), whereas the positive correlations were significant from late April to early June ($p < 0.05$) (Fig. 6).

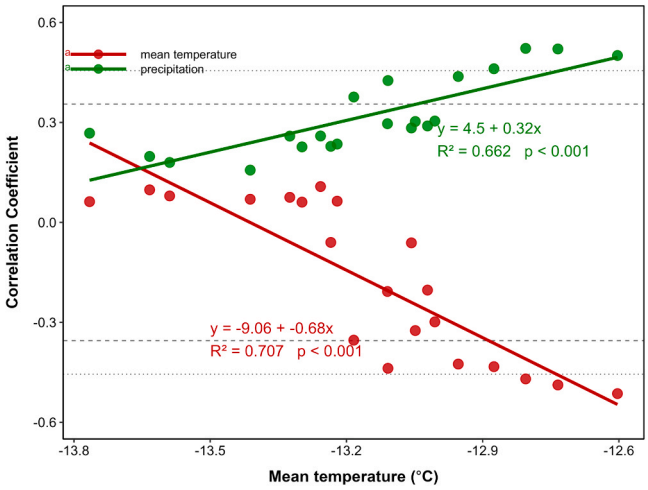


**Fig. 5.** The variation in the 31-year moving correlations between birch STDs and the February–April mean temperatures/precipitation along the temperature gradient in the study area. Dashed lines and dotted lines 99 % and 95 % confidence levels, respectively.

### 3.2. Response disparity

PC1, PC2, and PC3 of the correlation coefficients between the regional birch standard chronology and the 10-day mean temperatures during winter-spring (late February–early June) accounted for 58.0 %, 21.8 %, and 10.2 % of the total variance, respectively. The contribution of PC1 revealed two opposite patterns of birch radial growth response to temperatures during spring on a finer scale compared to data statistics

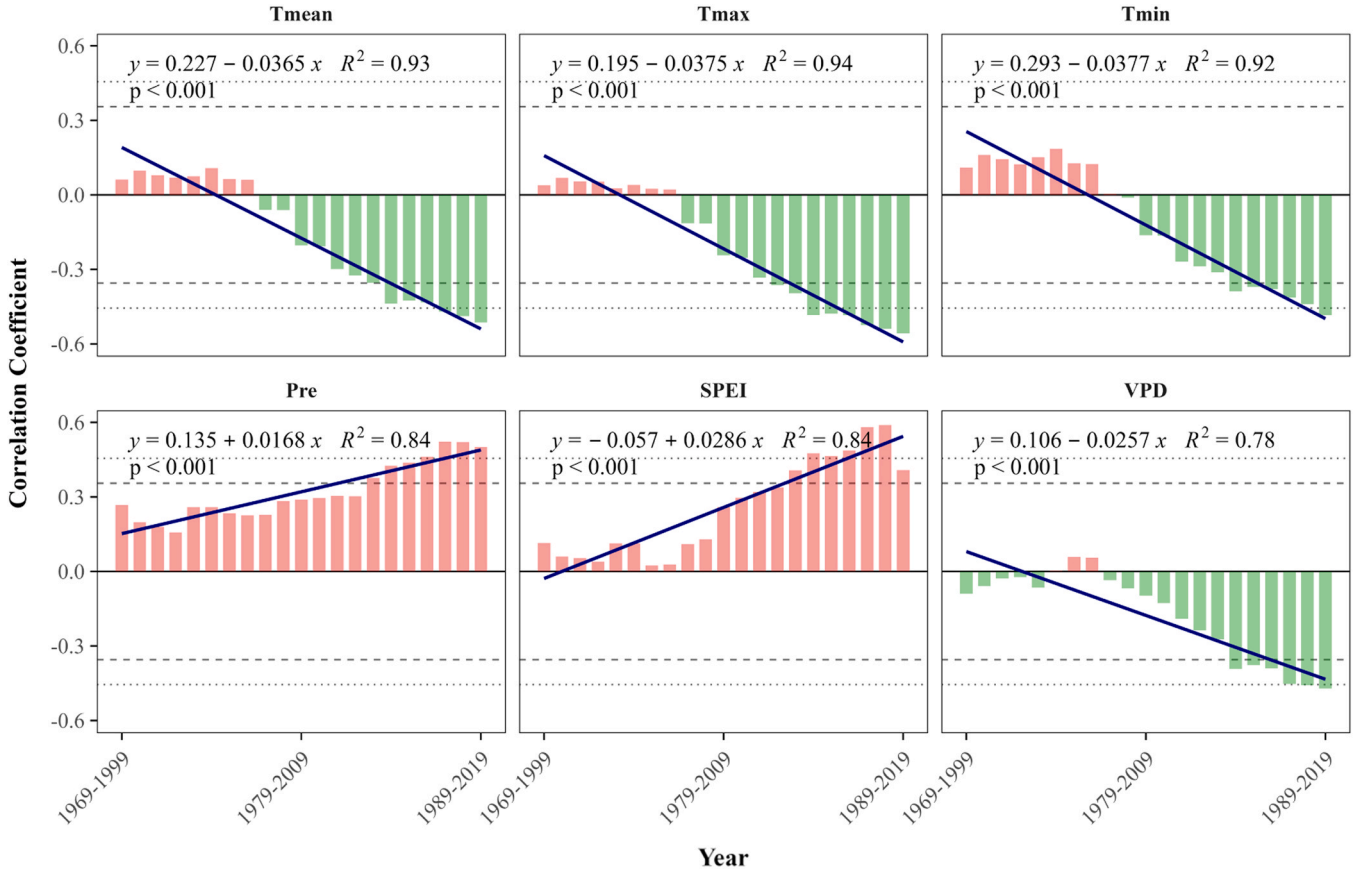


**Fig. 4.** The 31-year moving correlations with a 1-year step between birch regional chronology and February–April monthly climatic variables in the study area during 1961–2019. dashed lines and dotted lines 99 % and 95 % confidence levels, respectively.


**Fig. 6.** Correlations between six birch chronologies and a regional chronology (DXB6) with 10-day climatic variables in the study area (1961–2019). I: the first 10 days of a month; II: the second 10 days of a month; and III: the remaining days of a month. "●●" And "●" indicate 99 and 95 % confidence levels, respectively.

on a monthly scale: from early February to late April *versus* early May to early June. The variance explanation and contribution of the PC1 positive vector were both greatest in early and mid-April, and the variance explanation and degree of contribution of the PC1 negative vector were greatest in May. For PC2, the variance explanation and contribution in the positive vector were the greatest in late March, and the variance explanation and contribution in the negative vector were the greatest in late February and early March (Fig. 7).

### 3.3. Response threshold

The correlations between tree-ring width and mean temperatures over time shifted from negative to positive during spring and varied significantly ($p < 0.01$) at monthly, 10-day and daily scales, respectively (Fig. 8). Specifically, the daily data fit growth–climate response variations better and more reliably than the monthly and 10-day data because of the large amount of data. The growth–climate response threshold temperature shifted to 3.99 °C based on the daily data (Fig. 8). The threshold temperature occurrence date was significantly advanced by 12 days from 124 day in 1990 to 112 day in 2018 with an average of 0.4 days annually ($R^2 = 0.1501$, $p < 0.05$, Fig. 9).

## 4. Discussion

### 4.1. Physiological drought and soil-thaw influence

Water availability has a major influence on tree growth in cold-temperate forests with high temperature fluctuations (Phillips and Gentry, 1994; Luo and Chen, 2013; Zhang et al., 2014, 2017; Stocker et al., 2023). Physiological drought stress in trees occurs when water is physically present but inaccessible due to various environmental, soil, or biological factors.The study area is located in the cold-temperate zone and is warming significantly, with temperature changes particularly prominent in the non-growing and early growing seasons (Fig. 1). Deciduous trees enter their dormant stage during winter with slow physiological and metabolic activities and their early spring growth depends primarily on nutrient accumulation from previous year (Amico Roxas et al., 2021). When winter finishes and temperature increases, carbon and nutrients are remobilized from storage to resume tree growth (Piper, 2020). The metabolic reactivation for overcoming winter dormancy requires favorable climatic conditions and, thus, is susceptible to climatic variations (Piper and Fajardo, 2023). A warming climate can lead to excessive depletion of nutrients and water that accumulated prior to the growing season, which is detrimental to tree radial growth in the following growing season.

In the early growing season, birch radial growth is not only controlled by temperature but also by water supply (Fig. 6). During this time, *B. platyphylla* lacks new leaves and thus cannot photosynthesize

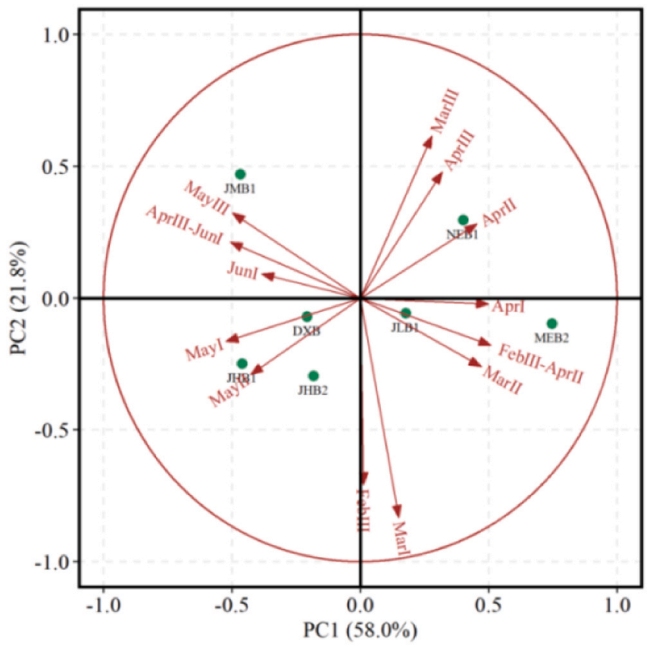


**Fig. 7.** PCA (PC1, and PC2) of correlation coefficients between the 10-day mean temperatures during winter-spring (late February–early June) and birch STDs in the study area . .

and supply nutrients. In the aboveground, a higher temperature could trigger metabolic activities and increase respiration (Sun, 2019) while increasing temperatures also activate consumption of carbohydrates and water stored around the roots (Yan et al., 2020). These temperature-induced physiological activities in both above- and below-ground were not conducive to the growth of *B. platyphylla* in the coming seasons. During most of the pre-growing season, soil remained frozen and the roots of the trees remained dormant and could not provide water to the trees(Fig. 10). In addition, sunlight exposure (particularly in the late afternoon) can aggravate tree moisture loss, leading to an increased frostbite risk. Thus, temperature had a significantly limiting effect on *B. platyphylla* radial growth in the early-growing season with negative temperature-growth relationships and positive precipitation-growth relationships, particularly during the soil pre-thaw period (February–April).

Snow (precipitation) is more important in the tree-growth environment during winter and spring in the Greater Khingan Mountains than during early winter because of the low air humidity and high wind speed. The nudging effect of wind and snow sublimation affect the distribution and thickness of snow patching heat and the moisture environment of the soil (Zhang et al., 2008). However, warming-induced snowpack reduction can increase the risk of frost damage to stem bases or roots of trees during the winter–spring transitional season because snow cover insulates cold air (Gradel et al., 2017).

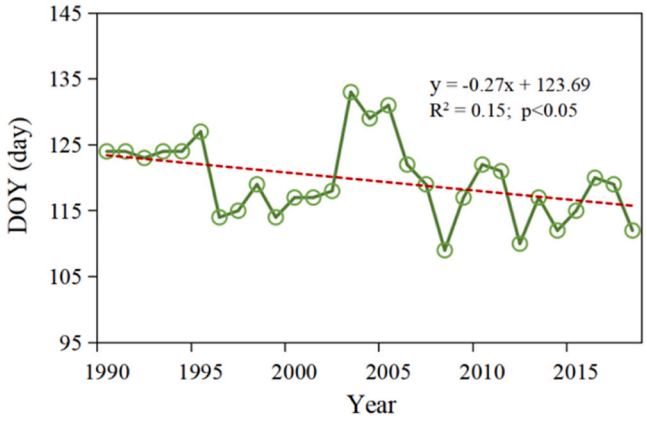


**Fig. 9.** Interannual variations of the occurrence dates (DOY) for temperature thresholds during 1990–2018.

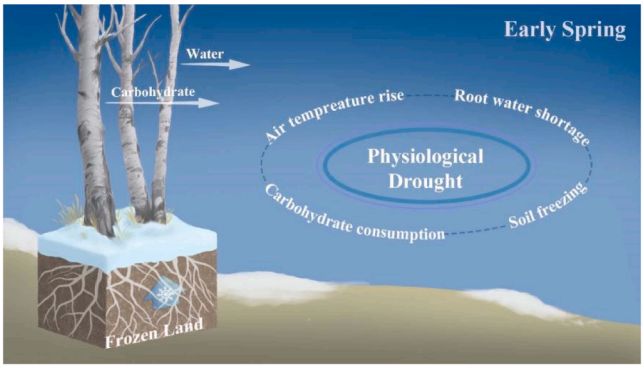


**Fig. 10.** Schematic diagram of physiological drought and carbohydrate loss in White birch from February to April.

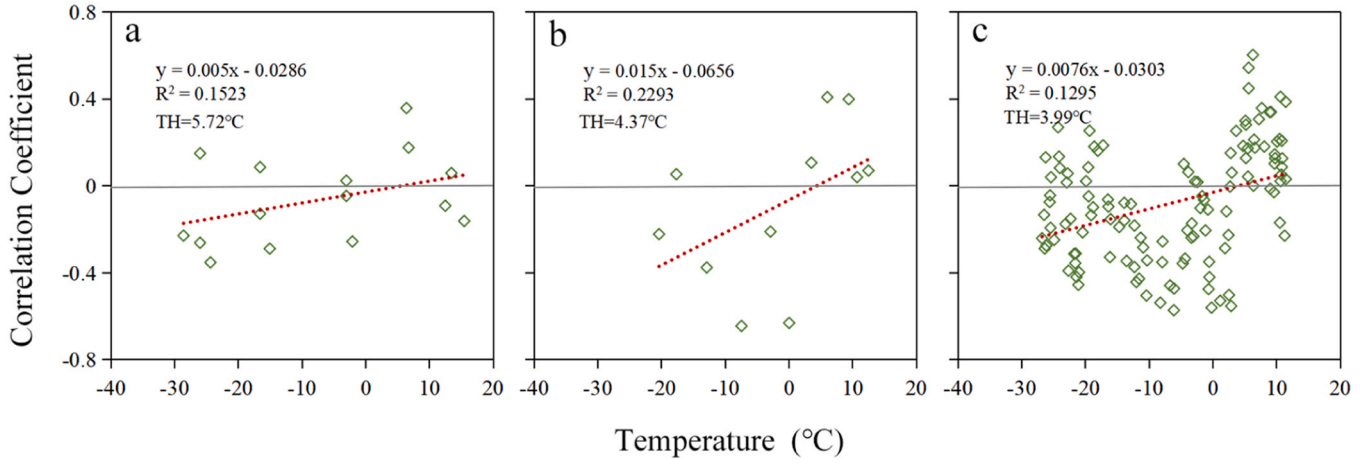


**Fig. 8.** Temperature thresholds for the correlation shift between birch STDs and mean temperatures in spring at (a) monthly scale, (b) 10-day scale, and (c) daily scale.

### 4.2. Increase in sensitivity and vulnerability of tree growth to climate

*B. platyphylla* radial growth was constrained by climate-induced drought during February–April, which is a typical winter–spring transitional period in cold temperate regions. The growth of a dominant conifer tree species, *Larix gmelinii* (Bai et al., 2019; Han et al., 2021) and another pioneer/companion species, *Populus davidiana* (Yun et al., 2021) was also inhibited by physiological drought during the winter–spring transitional period in the same region, so as *Pinus koraiensis* growing on Changbai Mountain (Bao et al., 2019). In the context of global warming, climatic factors fluctuate on annual and interannual scales, and thus, inevitably change the tree growth and growth–climate responses in the study area. The correlations among *B. platyphylla* tree-ring width and temperature, precipitation, and SPEI changed during the winter–spring transitional period (February–April). In addition, the gradually increasing temperature during early spring continuously advanced and lengthened the "opposite phase" of air and ground temperatures (Yun et al., 2021), resulting in a gradually increasing limitation on tree growth in the study area.

*B. platyphylla*, *L. gmelinii* and *P. davidiana* are all cold-resistant deciduous species and their growth and physiological activities are severely threatened by climate warming (Williams et al., 2014). This threat will continue to increase with gradually increasing temperatures in the future. For example, from February to April (late winter/early spring), the temperature varied drastically in the study area and showed a sharp diurnal temperature differences. Drastic temperature changes exacerbate the physical shrinkage and expansion of the tree body, resulting in adverse effects on normal dormancy during non-growing season and tree growth during growing season (Gao and Wang, 2008).

As discussed previously, annually increasing temperatures during late winter–early spring can exacerbate the physiological drought of trees prior to soil thaw, causing nutrient depletion in trees (Williams et al., 2014), resulting in reduced frost resistance and compromised spring growth. Warming also prolongs the duration of repeated freezing and thawing of groundwater, which may cause embolisms in tree xylems (Mayr et al., 2003). In addition, winter snow cover may affect the soil and the microclimate under the snow (Decker et al., 2003; Henry, 2008; Pauli et al., 2013). However, snow accumulation is gradually decreasing in snowpacks in the study area from year to year (1970–2020), thus increasing soils exposure to environmental extremes (Bale and Hayward, 2010; Brown and DeGaetano, 2011), which in turn exposed tree stems in warmer air and roots in colder soil (Groffman et al., 2001) causing physiological drought.

### 4.3. Temperature threshold and physiological drought

Breaking dormancy and resuming the physiological activity of tree cambia relies on temperature clue (Rossi et al., 2016; Begum et al., 2018; Huang et al., 2020) while tree species have preferred temperature ranges in different regions. Temperature thresholds for changes in physiological processes, growth states, and stages have specific physiological and phenological implications.During the winter-spring transition, the response of birch to temperature shifted from negative to positive. while precipitation-growth relationship was always positive. The increased temperature promotes snow- and ice-melt and earlier onset of ground thaw, resulting in an increased thawing soil depth and soil water availability. Freeze–thaw-induced soil water increases soil moisture availability and mitigates water stress on tree growth (Wang and Liu, 2021). As temperature increases, cell division and differentiation becomes active, and tree roots break dormancy to transport water (King et al., 2013; Huang et al., 2018).

The temperature threshold for the shift of correlations between *B. platyphylla* tree-ring width and temperatures is 4℃ in the study area, and the date of this temperature threshold has significantly advanced 12 days during late winter–early spring since 1990. Early snowmelt and permafrost degradation are related to interannual variations of this temperature threshold, showing positive effects on some tree species in a short term (Bao et al., 2019). Although the date of spring drought stress relief in trees is advancing, it is insufficient to mitigate the negative effects of winter–spring warming on *B. platyphylla* growth (Fig. 4). The earlier spring physiological drought stress and tree sprouting (Deslauriers et al., 2008; Wang and Liu, 2021; Qi et al., 2022) further separated the time of tree-growth initiation and the arrival of monsoonal rainy season (July–August). That is, tree radial growth would largely rely on an early spring rainless season with deteriorating water stress on trees in hot–dry June before monsoonal rainy season (Figs. 3 and 6). The environmental conditions are more complex in terms of intra-annual variations in water and heat background because the study area is located in the cold-temperate zone of China. As global temperatures increase, permafrost degradation is bound to increase further, and the water supply to the soil environment is prone to disruption. We also found similar studies on the response of tree growth to climate change in the non-growing season (Williams et al., 2014) and concluded that future plant growth and composition in the study area should consider local environmental characteristics and species phenological attributes.

## 5. Conclusions

This study provides critical insights into the physiological drought stress experienced by *B. platyphylla* in the Greater Khingan Mountains under a warming climate, particularly during the winter–spring transitional period. *B. platyphylla* radial growth is highly sensitive to water availability during pre-growing season (February–April) and a temperature threshold of ~4.0°C marks the transition from growth inhibition to promotion. Under warming climate, the influence of temperature on tree growth changed from positive to negative for the past 50 years while water availability exerted an increasingly dominant role on tree growth. This indicates that heat-induced drought stress will likely control the sensitivity of future forest productivity and functions in the Greater Khingan Mountains.

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## CRediT authorship contribution statement

**Xin Gao:** Writing – original draft. **Au TsunFung:** Writing – review & editing, Writing – original draft. **Zhenju Chen:** Writing – original draft. **Wenjun Sun:** Writing – original draft, Conceptualization. **Junxia Li:** Writing – original draft. **Feng Li:** Writing – original draft.

## 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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## Data availability

The data that support the findings of this study are available on request from the corresponding author, Zhenju Chen , upon reasonable request. E-mail address: chenzhenju@syau.edu.cn (Z. Chen).

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