Variation in Water Supply Leads to Different Responses of Tree Growth to Warming

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1 **Variation in water supply leads to different responses of tree**
2 **growth to warming**

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14 **Abstract:**

15 **Background:** Global climate change, which includes changes in precipitation,
16 prolonged growing seasons, and drought stress caused by overall climate warming, is
17 putting increased pressure on forest ecosystems globally. Understanding the impact of
18 climate change on drought-prone forests is a key objective in assessing forest
19 responses to climate change.

20 **Results:** In this study, we assessed tree growth trends and changes in physiological
21 activity under climate change based on patterns in tree rings and stable isotopes.

22 Additionally, structural equation models were used to analyze the climate drivers
23 influencing tree growth, with several key results. (1) The climate in the study area
24 showed a trend of warming and drying, with the growth of tree section areas
25 decreasing first and then increasing, while the water use efficiency showed a steady
26 increase. (2) The effects of climate warming on tree growth in the study area have
27 transitioned from negative to positive. The gradual advance of the growing season and
28 the supply of snowmelt water in the early critical period of the growing season are the
29 key factors underlying the reversal of the sensitivity of trees to climate. (3) Variation
30 in water supply has led to different responses of tree growth to warming, and the
31 growth response of *Pinus tabuliformis* to temperature rise was closely related to
32 increased water availability.

33 **Conclusions:** Our study indicates that warming is not the cause of forest decline, and
34 instead, drought caused by warming is the main factor causing this change. If
35 adequate water is available during critical periods of the growing season, boreal
36 forests may be better able to withstand rising temperatures and even exhibit increased
37 growth during periods of rising temperatures, forming stronger carbon sinks. However,
38 in semi-arid regions, where water supply is limited, continued warming could lead to
39 reduced forest growth and even death, which would dramatically reduce carbon sinks
40 in arid ecosystems.

41 **Keywords:** Climate change, drought stress, tree rings, stable isotope, snowmelt,
42 forest- prairie.

1. Introduction

Global climate change is putting increasing pressure on forest ecosystems on a global scale (Adams et al., 2009; Devi et al., 2020; Williams et al., 2010). Forest productivity depends on various interacting climatic and non-climatic factors, with the main climatic factors including solar radiation, available water, temperature, atmospheric CO₂ concentration, and nitrogen deposition, among others (Berner et al., 2013; Ciais et al., 2005; Siyum et al., 2019). It has been widely shown that higher temperatures lead to longer growing seasons (Berner et al., 2013; Piao et al., 2007; Poulter et al., 2013) while warmer conditions and CO₂ fertilization effects stimulate both photosynthesis and productivity (Ichii et al., 2013; Magnani et al., 2007; Tumajer et al., 2017), which in turn stimulate forest growth in areas where there are no other limiting factors. However, a growing number of studies have found that rising temperatures have led to a loss of boreal forest productivity (Berner et al., 2013; Pellizzari et al., 2016), a reversal of the carbon balance and even mass dieback events (Klos et al., 2009; McDowell et al., 2008; McDowell et al., 2011).

The observed decline in productivity was inferred to be mainly related to high temperature and drought stress (Berner et al., 2013; Dulamsuren et al., 2013; McDowell, 2011). Diverse studies, ranging from those based on greenhouse experiments (Adams et al., 2009) and forest-climate logic modeling (Williams et al., 2013; Williams et al., 2010) to region-scale forest health monitoring (Littell et al., 2008; Williams et al., 2013) and global forest reviews of patterns of mortality (Allen

64 et al., 2010; Tognetti et al., 2019), have suggested that warming is causing an increase
65 in the demand for atmospheric water in semi-arid forests (Buermann et al., 2014;
66 Duthom et al., 2016). Additionally, increased atmospheric water demand may lead to
67 water scarcity and higher tree mortality (Shvidenko and Schepaschenko, 2013;
68 Steinkamp and Hickler, 2015). For example, Kharuk et al. (2013) found that soil
69 water stress was a major contributor to forest mortality in the Trans-Baikal Lake
70 region.

71 Parts of inland Asia have warmed relatively rapidly over recent decades, and
72 increasingly frequent and severe drought events have also been observed in central
73 and eastern Asia (Guo et al., 2018; Spinoni et al., 2014; Stephenson et al., 2018).
74 Warmer air and altered precipitation can cause changes in tree growth rates (Clark et
75 al., 2012; Clark et al., 2014; Konar et al., 2010; Zolkos et al., 2015). Importantly,
76 increased temperature increases precipitation in winter and thus snow cover in
77 northern Eurasia (Berkelhammer et al., 2020; Christensen et al., 2021; Ye et al., 2008),
78 which both increases soil insulation as well as subsequent snowmelt, which also
79 increases soil water availability for plants, thus potentially delaying and reducing
80 drought caused by climate warming (Albert et al., 2018; Cooper et al., 2020; Zhang et
81 al., 2019). However, little is known about the response of forests in many regions to
82 climate change (Littell et al., 2008; Repo et al., 2021; Sanmiguel-Vallelado et al.,
83 2019), and variability in this vast area of the world is represented by relatively few
84 dendroclimatological studies (Liu et al., 2013; Shestakova et al., 2017; Zhang et al.,

2019). It remains unclear whether accelerated warming will increase or decrease radial growth of dominant trees in many regions (Huang et al., 2010; Schaphoff et al., 2016). Accordingly, in the context of climate change, a better understanding of the interactions between warming, the water cycle, and forest growth is crucial.

The study of stable carbon isotopes in tree rings has been widely used in research on forest degradation, global environmental change, and tree physiology (Beaulne et al., 2021; Jucker et al., 2017). In the present study, we assessed tree growth trends and changes in physiological activity under climate change based on patterns in tree rings and stable isotopes. We sought to determine how drought and climate warming have affected tree growth and to identify the climate drivers that control tree growth. We assume that climate warming causes a relative decrease in tree growth in the region, and we had the following specific goals: (1) to study the characteristics of regional climate change [temperature, precipitation, and standardized precipitation evapotranspiration index (SPEI)] and the reflection of climate change on tree traits (ring width, carbon isotope) of a coniferous species typical to the region; (2) to assess tree growth trends (basal area increment, BAI) and how warming and drought stress affect tree physiological activity [evapotranspiration and intrinsic water use efficiency (iWUE)]; (3) to analyze the climate drivers controlling tree growth and assess changes in forest productivity in the context of future climate change.

2. Materials and methods

2.1 Description of sampling points

The study area is located on Jundu Mountain northwest of the Haihe River Basin, which is within a forest-prairie transition zone and has a warm temperate continental monsoon climate. The sampling site is located in the largest natural *Pinus tabuliformis* forest in North China, with mature tree ranging from 80 to 360 years of age. In order to describe the climatic conditions in the study area, we selected the nearest meteorological stations, in Yanqing (115.58°E, 40.27°N, 487.9 m a.s.l.) and Huailai (115.3°E, 40.25°N, 570.9 m a.s.l.), which are 13 and 25 km away from the study area, respectively. According to meteorological data, the average annual temperature in the study area is about 9.6°C, the average annual precipitation is about 391.9 mm, and the annual frost-free period is 175 days. The main tree species found at the sampling points are *Pinus tabuliformis*, *Betula platyphylla*, and *Juglans mandshurica*. We selected *Pinus tabuliformis* as the study tree species because its tree rings are clearer and wider than those of the other dominant tree species.

Fig. 1. Location map and sampling site of the study area

2.2 Tree ring collection and processing

Studies assessing tree ring $\delta^{13}\text{C}$ isotopes show that four trees and four cores collected from a single sampling site can accurately represent the absolute $\delta^{13}\text{C}$ content and temporal trend of a sampling site (Gessler et al., 2014; Lu et al., 2019). In this study, 10 sample plots (20 m $\times$ 20 m) were selected to uniformly cover the study area, and a total of 40 mature trees (average age, 94 years) in good growth condition were selected. A total of 80 tree cores with a diameter of 5.15 mm were drilled at a height of 1.3 meters in May 2017. In order to prevent carbon source pollution, all samples were stored in glass tubes. Owing to improper operation of the collection process or peculiarities of the trees themselves, some tree cores were of poor quality, and the rings were thus difficult to identify. We selected 38 samples with clear tree rings and fewer missing rings for cross-dating and $\delta^{13}\text{C}$ analysis.

After the standard treatment of the tree core samples, including natural drying, fixing, grinding, etc., we used the LINTAB 5 measuring system (Rinntech, Heidelberg, Germany) to measure the tree-ring width (measuring accuracy, 0.001 mm). Additionally, all samples were visually cross-dated to avoid issues with missing or false rings. We used the COFECHA procedure for cross-dating the tree core samples and the RCSigFree procedure for inferring the chronology to mitigate the problem of trend distortion (Melvin and Briffa, 2008). Finally, we separated the standard tree ring samples according to the tree ring chronology, and samples from the same sample site

were combined into a single sample for each year for subsequent carbon isotope analysis.

We homogenized the resulting samples using a ball mill (Retsch, Haan, Germany) and then extracted the α -cellulose according to the method described by Ferrio and Voltas (2005) for stable carbon isotopic analysis. We placed 0.4–0.6 mg of α -cellulose samples per year in tin capsules, and then, an Elemental Analyzer (Flash EA 1112, Thermo Finnigan, Germany) and a Stable isotope ratio mass spectrometer (DELTAplusXP, Thermo Finnigan, Germany) were used to measure the $\delta^{13}\text{C}$ value with a systematic error of less than 0.2‰. The isotope ratios ($^{13}\text{C}/^{12}\text{C}$), indicating with the δ symbol, are presented relative to the Vienna Pee Dee Belemnite standard (for carbon). In order to focus on the effects of climate change on tree growth, we corrected the effect of tree-ring isotopes on changes in atmospheric $\delta^{13}\text{C}$ values based on the method described by McCarroll and Loader (2004). The atmospheric background $\delta^{13}\text{C}$ in the correction process was derived from the data published by Shestakova et al. (2017).

2.3 Data acquisition and calculation

Data on monthly temperature, precipitation, atmospheric pressure, and relative humidity (water vapor pressure, relative humidity, etc.) were obtained from the China Meteorological Data Sharing Service System (<http://data.cma.cn/>). We selected the Yanqing and Huailai meteorological stations for data representative of the study area and used the Kendall method and double mass curve (DMC) analysis to test the

homogeneity of the meteorological data. Thus, the meteorological data for these sites were determined to be reliable and without aberrations and thus well represent climate change occurring in the local area. Temperature anomalies and annual precipitation were used to represent climate changes in the study area (Fig. 2), where Temperature Anomalies represent the difference between the annual average Temperature and the multi-year average Temperature. The snowmelt water data were estimated from temperature and winter precipitation data, according to a simple formula (Zhang et al., 2019):

$$M = C_m (T_a - T_b). \quad (1)$$

Here, M is the potential snowmelt, in mm/day; C_m is the degree-day coefficient, in mm/degree-day; T_a is the average daily air temperature ($^{\circ}\text{C}$); T_b is the base temperature ($^{\circ}\text{C}$). In the calculations used, C_m was usually set at 2.74, and T_b was set at 0°C .

We set up soil temperature and soil volumetric water content measurement probes (Decagon 5TE) at different soil depths (0–20 cm, 20–40 cm, 40–60 cm) in the sample plot, together with an EM50 data collector, to monitor long-term soil temperature and soil volumetric water content since 2018.

To quantify the severity of the drought, we used station climate data to estimate standardized precipitation evapotranspiration indices (SPEIs) and saturated vapor pressure difference (VPD) (Li et al., 2021; Vicente-Serrano et al., 2010). SPEI is a multi-scalar drought index that determines the occurrence and duration of regional

droughts. We used monthly temperature, monthly rainfall, and weather station latitudes to calculate the study area SPEI change from 1957 to 2016 in R, with regional SPEI data (downloaded from https://spei.csic.es/spei_database) used to validate the SPEI calculations. We used air temperature (T_a) and relative humidity (RH) to estimate changes in VPD within the study area from 1957 to 2016 and used the measured water vapor pressure data from meteorological stations for verification by applying the following equation:

$$VPD = 0.61078 \times \exp\left(\frac{17.27 \times T_a}{T_a + 237.3}\right) \times (1 - RH). \quad (2)$$

We used daily temperature data to calculate the start and end of the growing season. The beginning of the growing season is defined as a period of five consecutive days with daily temperatures above 5°C, based on the typical value for the onset of wood generation (Maxwell et al., 2020; Rossi et al., 2008), while the end of the growing season is determined using a daily temperature threshold below 0°C.

In order to describe the absolute radial growth trend of trees, we converted tree-ring width measurements into basal area increment (BAI) values. BAI represents an accurate indicator of changes in tree vigor and growth over time, as it explains the changes caused by increasing round trunk volume (Biondi and Qeadan, 2008; Lepley et al., 2020; Mina et al., 2016). We calculated BAI based on a series of tree ring width sequences for intersecting dates:

$$BAI = \pi(R_t^2 - R_{t-1}^2). \quad (3)$$

Here, R is the radius of the tree and t is the year in which the tree rings were formed.

Finally, we calculated the mean BAI chronology for each location (Fig. 3b). The trend of BAI across two consecutive periods (1957–1987 and 1988–2016) was independently assessed by linear regression.

We estimated intrinsic water use efficiency (iWUE) using the quantitative relationship between $\delta^{13}\text{C}$ and iWUE determined (Sun et al., 2018; Zadworny et al., 2019):

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C}{1 + \delta^{13}C_a} \quad (4)$$

$$iWUE = \frac{C_a \times (b - \Delta)}{1.6 \times (b - a)} \quad (5)$$

Here, $\delta^{13}\text{C}$ is the stable carbon isotope value of tree-ring cellulose; $\delta^{13}C_a$ is the stable carbon isotope value in atmospheric CO_2 ; Δ is the ^{13}C discriminant value referring to the difference in isotope levels during photosynthesis between the tree leaf and air; C_a represents the concentration of atmospheric CO_2 ; a represents the stomatal fractionation coefficient in the diffusion process, which is about 4.4‰; and b represents the fractionation coefficient in the carboxylation process of Rubisco and PEP carboxylase, which is about 27‰. Additionally, the coefficient 1.6 represents the ratio of the diffusivity of water vapor to CO_2 in the air. The C_a values are from NOAA's Earth System Research Laboratory (<http://www.esrl.noaa.gov/>).

We estimated transpiration in the study area from 1957 to 2016 based on annual carbon sequestration and tree iWUE. The annual carbon sequestration estimate was adopted from the biomass model and allometric growth model for *Pinus tabulaeformis*

in the study area established by Yang et al. (2021).

2.4 Statistical analysis

We determined the time-dependent relationships between tree growth and climate by using Pearson correlation analysis and Kalman filters. We used a sliding window correlation analysis to assess the change in the correlation coefficient between climate factors and site chronology, and we also calculated the correlation between the temperature of each month during the growing season (March to November) and the growth of trees. The climate is generally considered to be the average of meteorological conditions, e.g., temperature and rainfall, over a 30-year period, as this length of time is considered sufficient to understand the trend in climate change. Accordingly, for our sliding window analyses, we used a fixed window of 30 years, starting with 1957–1986 and ending with 1979–2008, and repeating iterations in one-year increments (Biondi and Waikul, 2004). We also calculated the correlation between tree growth and seasonal (spring, summer, winter) mean climatic variables, as this is more representative of climatic conditions than data from any single month.

In order to explore the potential interaction between the water cycle and temperature, we calculated the correlations of temperature with precipitation, evapotranspiration, saturated water pressure difference, and water use efficiency (Littell et al., 2008; Poulter et al., 2013; Repo et al., 2021). We also examined how the interaction between precipitation and growth temperature correlations changed, by

using an 11-year time window to assess their consistency over the study period.

Structural equation models (SEM) can be used to assess the effects of multiple climate variables on tree growth and reveal the relative importance of various climate variables on radial growth by inferring covariance among the variables (Elliott et al., 2015; Grace et al., 2010). We used the AMOSV25 (IBM Corp., Armonk, NY, USA) to build structural equation models for two time periods, 1957–1986 and 1987–2016, because the correlation between temperature and water cycle shifted between these two periods. We also examined the relative importance of variables that may affect tree growth using the average BAI of tree rings in the study area, as well as temperature, which was divided into three variables (TEM₃₋₄, TEM₅₋₇, and TEM₈₋₁₀). We tested models with different variables, recorded their comparative fit index (CFI), normed fit index (NFI), χ^2 , Akaike information criterion (AIC), and root mean square error approximation (RMSEA) values, and used the final model with the with the optimized values (NFI > 0.9, CFI > 0.9, P > 0.05, and minimized χ^2 , AIC and RMSEA).

3. Results

3.1 Changes in climate and tree growth in the study area

The region has experienced a period of rapid warming since 1957, and the rate of warming has been increasing (Fig. 2). The average temperature from 1978 to 2019 was more than 1°C higher than the average temperature from 1957 to 1977. Although

the precipitation accumulation is also increasing, the standardized precipitation evapotranspiration index in the study area shows an obvious downward trend, likely owing to climate warming. The SPEI in the study area changed from positive to negative from 1957 to 2017, and the monthly mean SPEI changed from 0.31 in 1957–1977 to -0.61 in 1997–2017. Thus, the climate in the study area is facing a trend of warming and drying.

Fig. 2. Change in air temperature anomalies (a), annual precipitation (b), and standardized precipitation evapotranspiration index (c) in the study area in 1957–2018.

The black line represents the annual observed values, the solid red line represents the moving average over the 5-year window period, and the dashed purple line represents the trend based on the best fit line ($P < 0.01$).

Many studies have suggested that global warming is prone to induce physiological drought, which has a negative effect on tree growth. However, these studies ignore the impact of water supply in the early growing season on tree growth, especially in areas where water is limited. Snowmelt caused by warming has become an important source of water for tree growth in such areas. We analyzed the changes in the growth of tree ring width and sectional area of 10 sample points in this region from 1957 to 2016 and found that the growth of tree ring width and sectional area in this region first increased and then decreased. The inflection point was determined to occur in roughly 1988 by using a Kalman filter approach (Fig. 2). Before 1988, the growth rate of average tree-ring sectional area decreased by $0.799 \text{ cm}^2/10\text{a}$ ($R = 0.66$, $P < 0.01$). After 1988, the average tree-ring sectional area increased at a rate of $1.799 \text{ cm}^2/10\text{a}$ ($R = 0.43$, $P < 0.01$). This suggests that the response of trees to climate change in this region may have changed around 1988.

We found that there was no significant trend in stable carbon isotopes in tree rings in the study area, but the iWUE of *Pinus tabulaeformis* showed a significant increasing trend (Fig. 2c), increasing by $6.68 \mu\text{mol}\cdot\text{mol}^{-1}/10\text{a}$. The iWUE from 2007 to 2017 was 35.7% higher than the average iWUE from 1957 to 1967. In particular, the increasing trend was obviously increased after 1988, reaching 10.29

$\mu\text{mol}\cdot\text{mol}^{-1}/10\text{a}$, and this year was consistent with the turning point of the tree growth trend. To some extent, iWUE reflects the degree to which trees are subject to water stress, and higher WUE values indicate more serious water stress. Thus, the growth rate of trees appeared to be faster after 1988. However, owing to the influence of climate warming and drying, the water stress of trees was gradually intensified, leading to a rapid increase in WUE.

Fig. 3. Trends in tree ring width (a), growth of tree sectional area (b), $\delta^{13}\text{C}$ content of tree rings, and intrinsic water use efficiency (c) during 1957–2017. The black solid line represents the measured tree ring data at each sample point, the red

solid line represents the average tree rings and BAI variation trend across 10 sample points, and the blue broken line represents the average $\delta^{13}\text{C}$ of tree rings across sites.

3.2 Impact of climate warming on tree growth

We found that the correlation between tree growth and temperature in the study area changed from negative to positive during 1957–2017 (Fig. 4). The correlation between temperature and tree growth was negative during 1956–1988 (mean, -0.34; median, -0.35; standard deviation, 0.1). However, it changed to positive values (mean, 0.11; median, 0.11; standard deviation, 0.04) from 1989 to 2017.

Fig. 4. Relationship between tree growth and temperature in different periods

organized by month (a and b) as well as season and year (c and d) (with 30-year

window periods also indicated). The vertical line represents the mean Pearson correlation coefficient for each 30-year period, with the different colors representing the different 30-year periods from 1957 to 2017.

This change over time was more obvious in the relationship between tree ring growth and seasonal temperature. The correlation between tree ring growth and temperature changed in spring, summer, and autumn (Fig. 4c and 4d), showing a positive response to temperature. However, for some months, there was also a change in the relationship between tree growth and monthly temperature, while a negative effect of temperature on tree growth was always observed in May, June, and July. The difference in water supply among months may be the main factor underlying this change.

3.3 Effects of water supply on tree growth throughout the growing season

Warmer temperatures may lead to an earlier arrival of the growing season, with the start of the growing season being 1.5 d/10a earlier since 1957(Fig. 5b). We also found that the end of the growing season began to be delayed at a rate of 1d/10a (Fig. 5a), but this change was not significant. Compared with the starting date of the average growing season from 1957 to 1967, the starting date of the average growing season from 2007 to 2017 was 10 days earlier. The starting date of the growing season has advanced from late April up to early April, and the corresponding growing season has been extended by 15 days.

Despite the observed warming climate, historical meteorological records show

that snowmelt usually begins in late March, with precipitation mainly occurring in the form of snowfall in early March, while snowpack generally disappears in early April (Fig. 5c). The time series of snow cover in the region shows that March is the main time in which snowmelt occurs, and there is little snowpack after April.

Fig. 5. Change in the end (a) and start (b) of the growing season and change in snowmelt amount in March and April in the study area (c). The solid black line represents the observed value, the dashed purple line represents the trend based on the best fit line ($P < 0.01$), and the bar chart shows the change in snowmelt water in

March and April from 1956 to 2017.

Soil moisture records show a clear rise in soil moisture from March to April. The replenishment of soil water by snowmelt water may be the main factor underlying this increase, because the soil temperature also changed from negative to positive during the same period (Fig. 6). In the early stage of tree growth, the physiological activities of trees begin to increase their demand for water, and trees are then particularly vulnerable to water stress. We found that the previously observed negative effect of temperature on tree growth in March and April has been reversed since 2000 (Fig. 4), which may be related to the earlier growing season being caused by warming. The beginning of the growing season shifted earlier to late March in 2000, and the soil moisture content has been significantly increased by the supply of snowmelt water. From this, we can hypothesize that warming caused the growing season to move earlier to the end of March, with snowmelt occurring early in the growing season, and this earlier snowmelt water thus alleviated the water limitation previously occurring early in the growing season.

Fig. 6. Changes in soil temperature and moisture across different soil layers from 2019 to 2020.

As the influence of temperature on tree growth did not change in the middle of the growing season, we also analyzed the trend in saturated vapor pressure difference (VPD) and evapotranspiration (E_T) in the study area from 1957 to 2017 (Fig. 7). We found that the VPD and E_T in the study area increased over time, with VPD increasing by 0.18 hPa/10a and E_T by 17.68 mm/10a. All these factors reflect that the climate in the study area is gradually becoming arid, and the water stress on trees is thus gradually becoming intensified.

Fig. 7. The trend in saturated vapor pressure difference (a) and evapotranspiration (b) in the study area from 1956 to 2016. The solid black line represents the annual observed values, the solid red line represents the moving average of the 5-year window period, and the dashed purple line represents the trend of the fitting.

In order to study the relationship between warming and aridity in the study area, we analyzed the trend in Pearson correlation coefficients between temperature and water-related factors over time (i.e., precipitation, VPD, E_T , and iWUE) (Fig. 8).

Fig. 8. Trend in Pearson correlation coefficients between temperature and

water-related factors (i.e., precipitation, VPD, E_T , and iWUE) (using 11 years as the

window size). The blue and red lines indicate trends in the linear regression fit, where

the solid lines indicate significant correlations and the dashed lines indicate non-significant correlations. The purple horizontal line represents the average Pearson's correlation coefficient over the following three periods of time: 1962–1978, 1979–1995, and 1996–2012.

We found that the correlation between annual precipitation and temperature was weakly negative overall, with an average correlation coefficient of -0.1. In the warming period, the negative correlation between precipitation and temperature was slightly strengthened (Fig. 8a). There was a positive correlation between temperature and VPD (Fig. 7b), and the correlation increased during the warming period ($P < 0.01$). It can be understood that warming intensifies the water deficit of the atmosphere and to some extent intensifies the climate aridity. The correlation between temperature and E_T was also positive (Fig. 7c). However, during the warming period, this correlation weakened ($P < 0.01$) and gradually became non-significant. This indicates that the effect of temperature on E_T becomes weaker as the climate warms, and thus, water supply can gradually become the main factor influencing E_T . There was also a positive correlation between temperature and iWUE (Fig. 7d), but the positive correlation gradually weakened ($P < 0.01$) and even became a negative correlation after 2000.

We also found that in the warming period, the correlations between precipitation and saturated water pressure difference, evapotranspiration water use efficiency, and temperature all experienced their own turning points within the study period. The

negative effect of temperature on precipitation became reversed around 1978, and it seems that the positive effect of temperature on VPD was also reversed at that time. Similarly, the positive influence of temperature on E_T was reversed around 1986, and the positive correlation between temperature and WUE became very low and gradually turned into a negative correlation. Therefore, the correlation over different periods of warming between temperature and water-related factors varied. Thus, we can divide climate warming from 1957 to 2017 into two distinct phases and analyze the mechanisms of climate change affecting tree growth based on the different responses of tree growth and other factors to warming between these two different periods.

3.4 Impacts of climate change on tree growth over time

Based on these results, we hypothesize that climate warming has caused the beginning of the tree growing season to move forward to the end of March, thus coinciding with the snowmelt season. Snowmelt water alleviates the water limitation historically occurring in the early part of the growing season, thus reversing the negative effects of temperature on tree growth in March and April. However, drought was not effectively alleviated during the whole growing season. Instead, warming exacerbated the drought limitation of the growing season. The climate in the study area exhibited a gradual warming and drying trend (Fig. 2 and 7). Water stress on tree growth gradually intensified (Fig. 3c), and warming may be the main underlying factor. Thus, between May and July, the negative effects of warming on tree growth

were not mitigated, and water supply may be the main factor determining the impact of warming on tree growth.

To evaluate this hypothesis, we established structural equation models (SEMs) with standard path coefficients for 1957–1986 (Fig. 9a) and 1987–2016 (Fig. 9b), respectively.

Fig. 9. SEM structural equation model for climate variables and radial growth of trees during two different periods (1956–1986 and 1987–2016) with standard path coefficients. Model variables include the snowmelt amount, average temperature from March to April (TEM₃₋₄), average temperature from May to July (TEM₅₋₇), precipitation from May to July (PRE₅₋₇), standardized precipitation evapotranspiration index from May to July (SPEI₅₋₇), average temperature from August to October (TEM₈₋₁₀), and basal area increment of trees (BAI). The model fit parameters were as follows for the two periods: 1957–1986, $\chi^2 = 3.413$, $p = 0.066$, NFI = 0.948, CFI = 0.946, RMSEA = 0.016; 1987–2016, $\chi^2 = 3.461$, $p = 0.054$, NFI = 0.937, CFI = 0.919, RMSEA = 0.016. All the test results are in accordance with the criteria described in the Materials and methods section (i.e., NFI > 0.9, CFI > 0.9, $p > 0.05$). NFI, normed fit index; CFI, comparative fit index; RMSEA, root mean square error approximation.

We found that during 1956–1986, the correlation between warming and summer precipitation was low ($R = -0.10$, $P = 0.166$), while during 1987–2016, there was a very significant negative correlation between temperature and summer precipitation ($R = -0.36$, $P < 0.001$) (Fig. 9). SEM analysis also indicated the importance of snowmelt water for tree growth during 1987–2016, as the correlation between average temperature in March and April and tree growth changed between the two periods owing to the influence of snowmelt water. Warming tends to exacerbate drought conditions, and the positive effect of precipitation on tree growth was weakened by the influence of temperature and the compensation effect of SPEI. We also found that the effect of autumn temperature on tree growth was reversed from negative to positive between the two periods, but there was no significant correlation between autumn precipitation and tree growth. Thus, the SEM analysis supports our previous hypothesis that, as a result of climate warming, the growing season of trees is beginning earlier each year in the study area. The growing season has advanced enough to overlap in time with periods of high soil moisture resulting from snowmelt. Thus, the increased supply of snowmelt water has reversed the negative effects of warming on tree growth in the early growing season. However, warming also intensifies drought, and water stress exacerbates the negative effects of warmer summers on tree growth.

4. Discussion

4.1 Different responses of tree growth to temperature

In this study, we found that the annual and seasonal correlations between temperature and tree growth changed from negative to positive as the climate warmed over the years. This is similar to the findings of Zhang et al. (2019), showing that increasing temperatures are often caused by a shift from negative to positive temperature–tree growth relationships, but in disagreement with the results of some other studies (Ciais et al., 2005; Peng et al., 2011; Schaphoff et al., 2016). Most relevant studies have suggested that rising temperatures over the years have caused a shift from positive to negative temperature–tree growth relationships. In the early stage of climate warming, temperature rises increase the photosynthetic carbon sequestration of trees, and the extension of growing seasons has also been linked to temperature rise (D'Orangeville et al., 2016; Penuelas et al., 2009). Collectively, these factors strengthen positive relationships between rising temperatures and tree growth in the early stages of warming. However, continued temperature increases exacerbate water deficits (which increases evapotranspiration), leading to drought stress during tree growth (Gradel et al., 2017; Restaino et al., 2016; van Mantgem et al., 2009), ultimately inducing trees to eventually close their stomata and stop growing altogether (Choat et al., 2012). Drought stress caused by warming leads to negative relationships between temperature rise and tree growth. In areas where the water supply is limited, insufficient water supply tends to result in hydraulic failure of trees, and thus, global warming is even thought to be the main driving force behind general increases in tree

mortality in arid regions (Berner et al., 2013; Liu et al., 2013; Jucker et al., 2017). In our study, a negative correlation between temperature and precipitation was also confirmed, indicating that long-term warming trends promoted the drying of the climate to some extent. Moreover, the reversal of the relationship between tree growth and temperature from positive to negative occurred mainly in the early and late growing season, while the negative effect of temperature on tree growth was always present in the middle of the growing season. Therefore, our results are indeed consistent with other studies on the physiological response of trees to warming (Shestakova et al., 2017; Shvidenko and Schepaschenko, 2013; Steinkamp and Hickler, 2015).

4.2 Effects of water supply in the early and middle stages of tree growing seasons

However, it is not immediately obvious why the shift in the temperature–tree growth relationship occurred in March and April. We hypothesize that it is related to the water supply in the early growth period of trees. The growth of *Pinus tabulaeformis* begins in early April (Rossi et al., 2008; Seo et al., 2011). However, the precipitation in our study area is very low in April, averaging only 15.5 mm. We also found that before 1986, the precipitation accumulation was very low in winter and mainly concentrated in summer. The average winter precipitation accumulation during 1956–1986 was only 9.1 mm. Combined with the early melting of snow, the water supply to support the growth of wood in the early part of the growing season may be limited (Bonanomi et al., 2020; Repo et al., 2021; Tognetti et al., 2019). In contrast, during 1987–2017, the average precipitation accumulation in winter was 26.7 mm, and the

warming temperature increased the proportion of precipitation falling in winter. However, some studies have found that warmer temperatures do not lead to earlier snowmelt, increased precipitation in winter leads to increased snow cover change, and deeper snowpack can require greater energy input to overcome cold content and liquid water holding capacity and initiate snowmelt (Martin et al., 2018; Mood and Smith, 2021; Musselman et al., 2017). The interaction between the lengthening of the growing season and the presence of snow in April makes snowmelt an important source of water supporting the growth of trees in the early growing season (Li et al., 2021; Reinmann et al., 2019; Vellend et al., 2017; Zhang et al., 2019). Higher soil water supply caused by snowmelt water can counterbalance the drought stress caused by warming and promote a positive relationship between temperature in the early growing season and tree growth. In turn, snowmelt has become an important water resource for trees in the early growing season of boreal forests (Littell et al., 2008; Martin et al., 2018; Repo et al., 2021), where carbohydrates produced and stored early in the growing season can then be used to overcome nutrient deficiencies, cold, or drought (Dietrich and Kahmen, 2019; Palacio et al., 2014).

4.3 Variation in water supply induces different responses of tree growth to warming

We found that from May to July, when the temperature–tree growth correlation did not change over the course of the historical data, rainfall showed a significant decreasing trend, while VPD showed a significant increasing trend. However, there

was no significant change in rainfall or VPD during the period of August to October, when the temperature–tree growth correlation did indeed change over time. Shestakova et al. (2017) also found a similar response to warming in tree growth under different rainfall conditions. They found that the growth of the Siberian cold-dry forest increased in areas with rainfall greater than 160 mm in May and decreased in drier areas of the study range. Similarly, Liu et al. (2013) found that in northeastern China, the BAI increment of trees decreased in areas with an average annual precipitation accumulation of 200–400 mm, while tree growth increased in areas with an average annual precipitation accumulation of 400–700 mm. Zhang et al (2019) also found that *Pinus sylvestris* populations subject to heavy rainfall (201 to 265 mm) from May to July responded more positively to temperature increases than the drier parts of the study area (145 to 160 mm absolute precipitation accumulation from May to July). Another analysis of long-term climatological data showed that climate warming in China caused an increase in actual annual evapotranspiration from 1960 to 2002 in arid regions, whereas this was not found in subhumid regions (Gao et al., 2007). All this suggests that drought stress caused by warming is the main cause of forest decline, and if the water availability is sufficient, future warming is likely to promote plant growth and forest expansion in such regions (Berner et al., 2013; Rotenberg and Yakir, 2010). In our study, owing to the earlier growing season, snowmelt water in the beginning of the growing season became an important water source supporting tree growth. The supply of melting snow presents trees with the

positive effects of climate warming, while in drier regions, climate warming has often led to widespread forest degradation (Restaino et al., 2016; Schaphoff et al., 2016; van Mantgem et al., 2009).

Our study suggests that warming is not directly the cause of forest decline, but that warming is instead the main cause of drought. Global warming increases the sensitivity of semi-arid forests to drought, which is manifested by decreased forest growth and tree mortality caused by warming (Peng et al., 2011; Williams et al., 2013; Williams et al., 2010). Global warming led to shorter periods of drought (18.7 weeks) and longer durations in inland Asia, and it was sufficient to promote widespread forest declines and tree mortality (Adams et al., 2009; Berkelhammer et al., 2020). Increasing precipitation can improve water stress to some extent, but on seasonal and longer time scales, increasing evaporation demand caused by warming may exceed precipitation input, leading to water stress in forest ecosystems (Adams et al., 2009; Williams et al., 2013; Desnoues et al., 2017). The intensification of drought caused by continued warming will not only lead to the decline or even death of forest growth in semi-arid regions, but also lead to the eventual degradation of forests into grasslands in semi-arid regions, which will significantly reduce the total available carbon sink of these altered ecosystems in arid regions.

5. Conclusion

In this study, we used tree-ring chronology and stable isotopes to assess the

response of tree growth to climate change. We found that the effects of climate warming on tree growth transitioned from negative to positive during the period of 1957–2017. Adequate water supply during the growing season, especially snowmelt water available in the early part of the growing season, appears to be the key to the reversal of the climate sensitivity of trees in this area. The beginning of the growing season continued to advance gradually throughout the study period. The gradual advance of the beginning of the growing season combined with the availability of snowmelt water early in the growing season resulted in a shift in the response of tree growth to temperature in the study area. Variation in water supply has led to different responses of tree growth to warming throughout the growing seasons. Our study suggests that warming per se is not the direct cause of forest decline, but is indeed the main cause of drought, which generally causes forest decline. SEM analysis also demonstrated that the growth response of *Pinus tabuliformis* to the observed temperature increase was closely related to the increase in water availability. As a result, boreal forests may be better able to withstand rising temperatures if they have sufficient water, with boosted growth even possible during periods of rising temperatures. However, in semi-arid regions where water supplies are limited, continued warming could lead to reduced forest growth or even death.

List of Abbreviations

Number	Abbreviations	Meaning
1	SPEI	standardized precipitation evapotranspiration index

2	BAI	basal area increment
3	iWUE	intrinsic water use efficiency
4	VPD	saturated vapor pressure difference
5	<i>RH</i>	relative humidity
6	<i>E_T</i>	evapotranspiration

593

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596 **Author contributions**

597 ZP, JG and YX planned and designed the research. ZP performed experiments
598 and conducted fieldwork with the help of WY. ZP analyzed the data and wrote the
599 manuscript under the guidance of JG and ZY. WD led the compilation of data
600 compilation and significantly contributed to the analysis of data and its interpretation
601 and rewrote the final version of manuscript.

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611 **Consent for publication**

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Competing interests

The authors declare that they have no competing interests.

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