



Snowmelt and early to mid-growing season water availability augment tree growth during rapid warming in southern Asian boreal forests

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Abstract

Boreal forests are facing profound changes in their growth environment, including warming-induced water deficits, extended growing seasons, accelerated snowmelt, and permafrost thaw. The influence of warming on trees varies regionally, but in most boreal forests studied to date, tree growth has been found to be negatively affected by increasing temperatures. Here, we used a network of *Pinus sylvestris* tree-ring collections spanning a wide climate gradient the southern end of the boreal forest in Asia to assess their response to climate change for the period 1958–2014. Contrary to findings in other boreal regions, we found that previously negative effects of temperature on tree growth turned positive in the northern portion of the study network after the onset of rapid warming. Trees in the drier portion did not show this reversal in their climatic response during the period of rapid warming. Abundant water availability during the growing season, particularly in the early to mid-growing season (May–July), is key to the reversal of tree sensitivity to climate. Advancement in the onset of growth appears to allow trees to take advantage of snowmelt water, such that tree growth increases with increasing temperatures during the rapidly warming period. The region's monsoonal climate delivers limited precipitation during the early growing season, and thus snowmelt likely covers the water deficit so trees are less stressed from the onset of earlier growth. Our results indicate that the growth response of *P. sylvestris* to increasing temperatures strongly related to increased early season water availability. Hence, boreal forests with sufficient water available during crucial parts of the growing season might be more able to withstand or even increase growth during periods of rising temperatures. We suspect that other regions of the boreal forest may be affected by similar dynamics.

KEYWORDS

boreal forest, permafrost, rapid warming, Scots pine, snowmelt, tree rings

1 | INTRODUCTION

Among all forest biomes, boreal forests have experienced the strongest increase in temperature (Stocker, 2014). Temperature can impact tree growth in boreal forests in several ways: promoting warming-induced water deficits (Adams et al., 2009; Allen et al., 2010; Restaino, Peterson, & Littell, 2016; Van Mantgem et al., 2009), extending growing seasons (McMahon, Parker, & Miller, 2010), accelerating snowmelt (Barnett, Adam, & Lettenmaier, 2005), and increasing permafrost thawing (Schuur & Abbott, 2011). Water deficits are exacerbated by increased warming, and they are one of the most proximal climate threats to boreal forests (Allen et al., 2010; Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). Recent hot droughts have accelerated widespread growth declines and forest mortality in boreal forests of northwestern North America (Peng et al., 2011), Western Europe (Ciais et al., 2005), and northwestern Russia (Schaphoff, Reyer, Schepaschenko, Gerten, & Shvidenko, 2016). If such trends continue, it is even possible that large portions of the boreal forest may shift into a woodland biome, under extreme scenarios (Gauthier et al., 2015; Scheffer, Hirota, Holmgren, Van Nes, & Chapin, 2012).

Despite the expected overall negative impact of climate change on boreal systems, warming can also have local positive effects in certain regions. In the boreal forests of northeastern North America, for example, abundant precipitation might help these ecosystems to better cope with future warming (D'Orangeville, 2016). The alleviation of low temperature stress can also increase plant productivity as shown for northern Siberian boreal forests (Schaphoff et al., 2016), and longer growing seasons associated with warming have been reported to increase tree growth in high-latitude forests (Peñuelas & Filella, 2009; Piao, Friedlingstein, Ciais, Viovy, & Demarty, 2007). Unlike other forest biomes, water from snowmelt and permafrost thawing is important to boreal forests. The interaction of permafrost thawing, snowmelt, and temperature increase could influence tree growth more than climatically driven drought stress in the permafrost region of boreal forests (Saurer, Kirilyanov, Prokushkin, Rinne, & Siegwolf, 2016; Sniderhan & Baltzer, 2016; Sugimoto, Yanagisawa, Naito, Fujita, & Maximov, 2002; Zhang, Bai, Chang, & Chen, 2016; Zhang, Bai, Hou, Chen, & Manzanedo, 2019). Hence, the potential impact of warming on boreal forests is complex and likely to require consideration for both local and broad-scale factors.

Northeastern China's boreal forests reside in the drier sector of Asian boreal forest climate space. In numerous xeric forest-grassland ecotones of Inner Asia, rapid warming has led to a decline in tree growth (Liu et al., 2013). Increased birch mortality has also been linked to rapid warming in the boreal forests of southern Siberia (Kharuk, Ranson, Oskorbin, Im, & Dvinskaya, 2013). Yet, limited studies have been conducted to reveal how rapid warming affects the boreal forests in northeast (NE) China, which have large areas of continuous permafrost and long snow-covered periods.

Pinus sylvestris is one of the most widely distributed tree species worldwide and contributes a large proportion of the biomass of Eurasian

boreal forests. Its growth has been documented to have declined due to climate warming across large parts of Europe (Bigler, Bräker, Bugmann, Dobbertin, & Rigling, 2006; Reich & Oleksyn, 2008). Similar growth responses across the vast *P. sylvestris* boreal forests in Asia would have major consequences for the region, and even at the global scale.

Here, we investigated the climate-growth response of 23 *P. sylvestris* populations that span most of the species' natural distribution in northeastern China. Temperature increased rapidly after the 1980s in this region (Zhang et al., 2016). We compared growth trends for 777 trees from a period of stable mean temperatures (1956–1986) to a period of rapid warming in the region (1987–2014) to assess their response to recent warming. Based on that reported for other boreal forests, we hypothesized that *P. sylvestris* trees in the relatively dry region of NE China would respond positively to temperature in the non-warming period (1956–1986) and then negatively in the rapidly warming period (1987–2014) due to drought stress. Alternatively, if increased temperature alleviates low temperature stress, and thereby extends the growing season, we hypothesized that the temperature response of tree growth across the study region would be increasingly positive throughout the entire record and, in particular, during the period of rapid warming. Finally, we hypothesized that water in all forms, such as snowmelt and growing season precipitation, became a key constraint to tree growth during rapid warming periods, given that snowmelt water is a key water resource for tree growth in boreal forests (Grippa et al., 2005; Vaganov, Hughes, Kirilyanov, Schweingruber, & Silkin, 1999).

2 | MATERIALS AND METHODS

2.1 | Study region

Pinus sylvestris is widely distributed across the boreal forests and occupies large regions in NE China, where it has its southeastern distribution boundary (Figure 1a). *Pinus sylvestris* is mainly distributed in the northern region of northeastern China, but there are some relic populations in more southerly areas (Figure 1b). The region has a monsoonal climate (Figure S1). The high-altitude areas in the center of our study region are the coldest, followed by the northern and the relatively mild southern regions. In terms of aridity, the western and southern portions are subarid, while the eastern and northern portions of the study region are subhumid (Figure S2). The mean summer temperature is lower than 20°C, and winter temperature is around –30°C (Figure S1). Precipitation is normally distributed with a peak in summer through this region. Drought is more prevalent in this region than in Europe (Figure 1a; Figure S3).

Twenty-three sites were sampled from old-growth *P. sylvestris* forests, covering most of the natural distribution of the species in northeastern China (Table S1). Sites were located far from residential areas and we know of no notable fire history that could have disturbed our target trees. Two or three cores were taken from each tree at breast height (1.3 m) using an increment borer. At least 20 trees were cored in each site, with the exception of Jinhe2, where we cored only four trees due to the limited number of trees. In total,

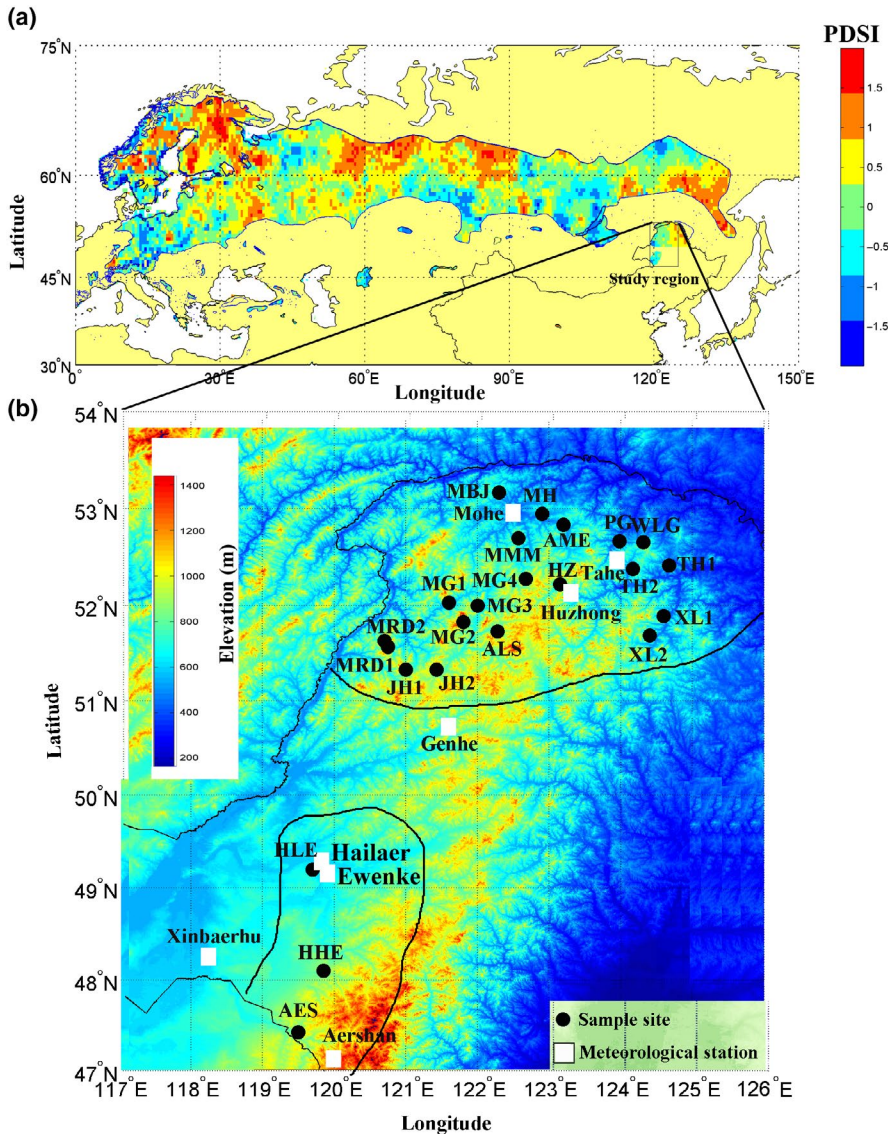


FIGURE 1 The moisture availability over the distribution of *Pinus sylvestris* (a) and the locations of the 23 sites sampled in northeast (NE) China (b). (a) The drought conditions (PDSI from 1957 to 2014) across the distribution of *P. sylvestris*. The boreal forest of NE China is located at a drier site than that in Europe. The species range was modified from the EUFORGEN distribution map (<http://www.euforgen.org/species/pinus-sylvestriswileyonlinelibrary.com>). (b) The sample sites and meteorological stations in NE China. The network of sample sites covered most of the natural distribution of *P. sylvestris* in NE China. No *P. sylvestris* trees are distributed in the center part of the study region. Black lines delineate the natural distribution boundaries of *P. sylvestris* in NE China [Colour figure can be viewed at wileyonlinelibrary.com]

1,504 cores from 777 trees were collected (Table S1). The sampled trees were selected using a random sampling design to maximize their climatic signal (Nehrbass-Ahles et al., 2014).

All samples were dried and glued to wooden mounts and sanded until growth rings were clearly visible. Rings on all cores were visually cross-dated and then measured to the nearest 0.001 mm using the LINTAB5 measuring system. The measured ring widths were verified using COFECHA (Holmes, 1983). Site chronologies were developed using the program ARSTAN (Cook & Holmes, 1984). In each site, trees were detrended using a linear or negative exponential function. The standard (STD) chronologies created in ARSTAN were used for subsequent analyses (Figure S4). Chronology statistics are provided in Table S1. The expressed population signal statistic (Wigley, Briffa, & Jones, 1984) was used to evaluate whether a chronology is representative of the sampled populations with a commonly used threshold of 0.85 (Wigley et al., 1984). All our site chronologies were representative of the sampled populations over the common period of 1950–2014.

2.2 | Climate data

Monthly climate data were obtained from the Chinese Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/>). The longest and most continuous climate records from these stations ranged from 1957 to 2014. These data were used for correlation analysis with the site chronologies to identify significant climate–growth relationships. Since only eight weather stations are located in or near the study region, we also included high-resolution precipitation data from the Asian Precipitation–Highly Resolved Observational Data Integration Towards the Evaluation of Water Resources–Monsoon Asia (APHRODITE-MA; Yatagai et al., 2009). The climate data have a high resolution ($0.25^\circ \times 0.25^\circ$ grid), which allows us to compare precipitation values between sites. The monthly station data and the APHRODITE-MA data were highly correlated with each other ($R^2 > .82$; $p < .001$).

The vapor pressure deficit (VPD) and the standardized precipitation evapotranspiration index (SPEI) are widely used to reflect

drought conditions. VPD was calculated based on monthly maximum temperature, minimum temperature, and relative humidity (Anderson, 1936). SPEI is a multi-scalar drought index based on climatic data to reflect the effects of temperature and water balance, and the anomalies in the difference between precipitation and potential evapotranspiration (Vicente-Serrano, Beguería, & López-Moreno, 2010). It was used to determine the onset, duration, and magnitude of drought conditions with respect to normal conditions in forest systems. Regional SPEI values (47°–54°N, 119°–124°E) for the period 1957–2014 were downloaded from <http://spei.csic.es/index.html>.

Daily temperature data were obtained from the Chinese Meteorological Administration and used to calculate the start and end of the growing season. The start of growing season was determined as the time when daily temperature was above 5°C for five continuous days which is based on typical values for the onset of xylogenesis (Rossi et al., 2008), while the end of growing season was calculated using a daily temperature threshold of below 0°C.

Regional snow cover fraction (Estilow, Young, & Robinson, 2015) (47°–54°N, 119°–124°E) for the period 1957–2014 was downloaded from the website <https://climate.rutgers.edu/snowcover/index.php>. In situ gravimetric soil moisture data from Huma station (51.72°N, 126.65°E) in the Global Soil Moisture Data Bank (Robock et al., 2000) was downloaded from the website http://climate.envsci.rutgers.edu/soil_moisture. To avoid the bias of soil moisture data from single station, high-resolution satellite-observed soil moisture data for the region (47°–54°N, 119°–124°E) were also used to evaluate the soil moisture patterns across the study region (Dorigo et al., 2017). The snowmelt water was calculated from temperature and winter precipitation data according to a simple formula: $M = C_m(T_a - T_b)$ (Vaganov et al., 1999), where M is snowmelt in mm/day; C_m is the degree-day coefficient in mm/degree-day; T_a is the mean daily air temperature (°C); T_b is base temperature; C_m is often set as 2.74 (USDA, SCS, 2004); and T_b is set as 0°C. The total snowmelt water was estimated by winter precipitation.

2.3 | Methods

We calculated the correlations between each STD chronology and climate (monthly mean temperature and monthly total precipitation) from the nearest climate station using a Pearson correlation. Climate–growth correlations were calculated for every month during the growing season (April–September). We also calculated the correlation of growth with seasonally averaged climatic variables, as this can be more representative of climatic conditions than single months (Cook, Meko, Stahle, & Cleaveland, 1999). Time-dependent tree growth and climate relationships were estimated using a Kalman filter (Allen et al., 2018; Deusen, 1990; Visser & Molenaar, 1988, 1990). The variations of correlation coefficients between climate factors and site chronologies were assessed using a moving window correlation analysis. We used a fixed window of 30 years, and iterations were repeated in 1 year increments. The long-term trend of tree growth was detected using the ensemble empirical

mode decomposition method (Wu & Huang, 2009) to identify the switch in tree growth.

The correlation between total precipitation and the growth–temperature correlation during May–July across sites was calculated to investigate the potential interactive effects of precipitation on growth–temperature dependencies. We also investigated how the interactions between precipitation and the growth–temperature correlation might have changed using a 30-year window to assess their consistency during the study period.

Structural equation modeling (SEM) was used to address the effects of multiple climate variables on radial growth and reveal the relative importance of various climate variables on radial growth by partitioning covariance among variables (Elliott, Miniati, Pederson, & Laseter, 2015). Variables were selected from those significantly correlated with radial growth. The SEM with observed variables was used to test our hypothesis using the program Amos v25 (IBM company). We tested the relative importance of variables that may influence tree growth between the period 1958–1986 and the period 1987–2014. Variables used in the models were mean tree-ring chronology for the northern 20 sites (radial growth); April snowmelt (Snowmelt₄); May–July mean temperature (TEM₅₇); August mean temperature (TEM₈); May–August total precipitation (PRE₅₈); May–August SPEI (SPEI₅₈). Mean temperature was separated into two variables (e.g., TEM₅₇ and TEM₈) because only the effect of TEM₅₇ on tree growth reversed between the two periods. April snowmelt was included in the SEM to assess the influence of snowmelt on tree growth. Models with different variables were tested and the final model with the best fitness indices was used (χ^2 , p value, Normed Fit Index [NFI], Comparative Fit Index [CFI], and root mean square error of approximation [RMSEA], with NFI > 0.9, CFI > 0.9, p > .05 and, lower χ^2 and RMSEA indicate satisfactory fit).

3 | RESULTS

There was no long-term increasing trend in April–September temperature from 1958 to 1986. Starting in 1987, the region experienced a period of rapid warming (Figure S5a). Mean temperature from 1987 to 2014 was about 1°C higher than that from 1958 to 1986. Despite this warming, neither precipitation nor SPEI had a long-term trend (Figure S5b,c). In parallel with changes in mean temperature around 1987, tree growth also showed an increasing trend after 1987, while tree growth declined slightly before that year (Figure S6). The relationship between tree growth and May temperature changed from negative to positive around 1987. This date was determined using a Kalman filter (Figure S7). In addition, temperature–growth relations were negative in the period 1956–1986 but switched to positive in the period 1987–2014 (Figure 2; Figure S8). Tree growth was negatively correlated with monthly temperatures from April to July in 21 of our 23 sites in the period 1958–1986. However, after 1987, all 20 northernmost sites have reversed their climate response, showing a positive influence of temperatures in April, May, and July (Figure 2).

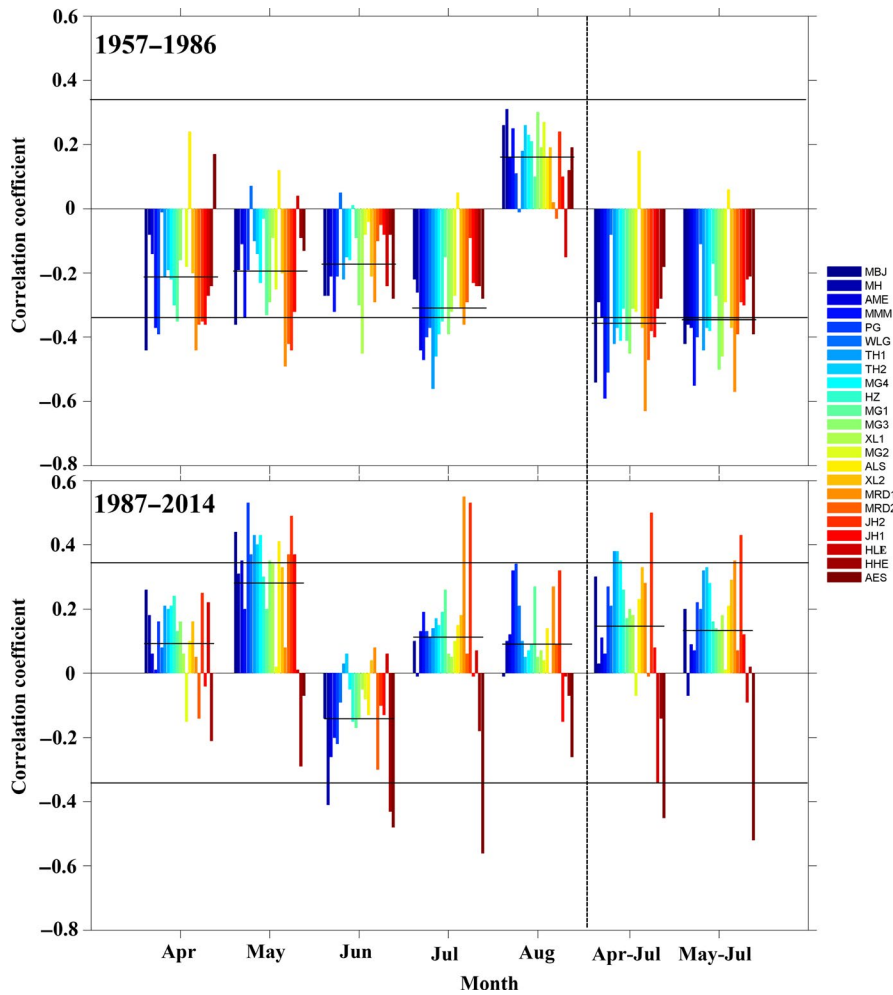


FIGURE 2 Monthly and seasonal correlation of *Pinus sylvestris* growth with temperature in the non-warming period (1957–1986) and in the warming period (1987–2014). Months include current growing season (April–September), and seasons include April to September (Apr–Sep) and May to September (May–Sep). The solid line in each group represents the mean correlation value of the group. The sites were listed from north to south according to their latitudes. The correlations between temperature and tree growth were largely reversed between the two periods. The horizontal lines indicate the significance level ($p = .05$) [Colour figure can be viewed at wileyonlinelibrary.com]

Correlation coefficients at the population level changed greatly, increasing from 0.29 to 0.71 (median = 0.55; $SD = 0.13$) in the northern sites between the two climate periods. At the same time, the mean basal area increment (BAI) of the 20 northern sites showed a significant positive trend ($r = .66, p < .01$) during the period of rapid warming (Figure 3). Growth increased by an average of $9.23 \text{ mm}^2 \text{ BAI/year}$ since 1987.

When examining the influence of drought on tree growth from April to August, both monthly precipitation and SPEI showed positive correlations with tree growth before 1987. These correlations strengthened slightly across all sites during the rapidly warming period (Figure S9).

Warmer temperatures likely triggered an early onset of the growing season (Figure 4). The start of the growing season advanced by 2 days per decade since 1959. Consequently, the growing season starts 10–12 days earlier in average by 2014, compared with 1959 (Figure 4). The growing season started around mid-May during the first 5 years of our study period, but, the onset of the growing season advanced to late-April by the last 5 years. We did not find a significant change in the end of the growing season date for the common period (Figure 4). We found no significant correlation between growing season length and tree growth in both the non-warming ($r = -.35-.1, p > .05, n = 28$) and warming periods

($r = .1-.35, p > .05, n = 28$), and no significant relationship was determined for the whole period as well. There was no significant correlation between permafrost thaw depth and tree growth ($r = -.27-.32, p > .05, n = 40$).

Despite the rapid warming since 1987, instrumental records from 1967 to 2014 indicate that the snowpack in our study area regularly lasted until April and historical weather records showed early-April precipitation mainly fell in the form of snow (Figure 4). While mean temperature in April is below 0°C , snowmelt began in late-April, and snowpack generally disappeared in early-May. The time series of snow cover fraction in the region indicates virtually no snow cover in May after 1979 (Figure 4b). Soil moisture records also showed reduced soil water content from May 15 to June 7 (Figure S10). Snowmelt water had become more available for tree growth during the warming period in the northern 18 sites (Figure S11). We also detected that negative effects of May VPD on tree growth reversed since 1987, when the start of tree growth appears to coincide with higher soil water content (Figure S12).

Based on the above results, we hypothesized that the shifting of the growing season to April during the period of rapid warming, the presence of snow cover during early growing season or just preceding the onset of the growing season, and a consequent alleviation of water limitation during the early growing season contribute to the

FIGURE 3 The basal area increment (BAI) for every site and mean across-site BAI trend. (a) The mean BAI for the 20 northern sites, and its trends before and after the year 1987. (b) The mean BAI for the three southern sites, and its trends for each period [Colour figure can be viewed at wileyonlinelibrary.com]

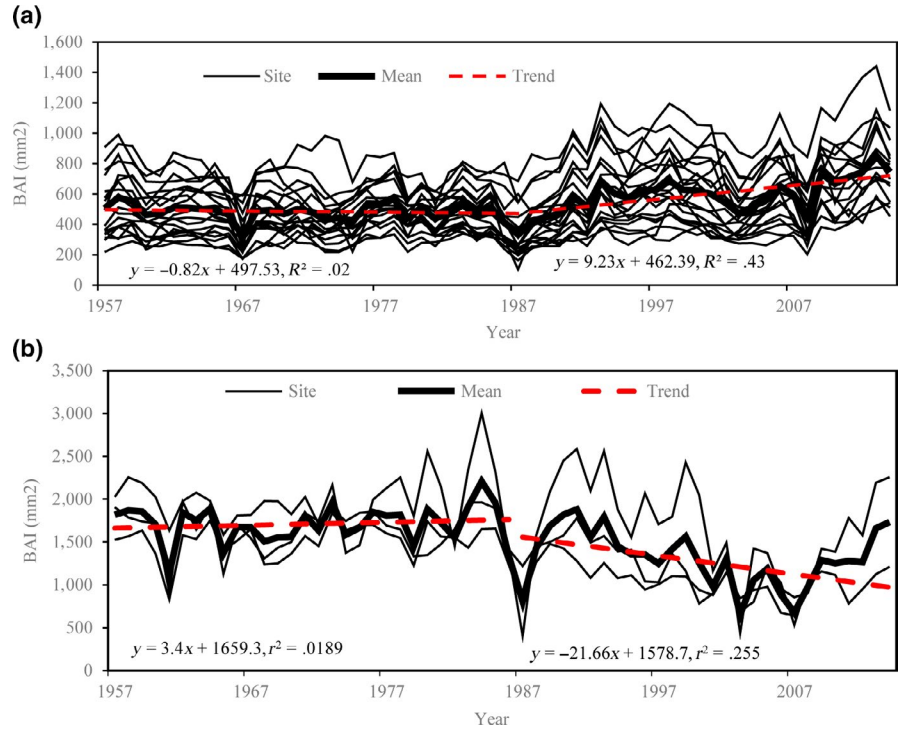
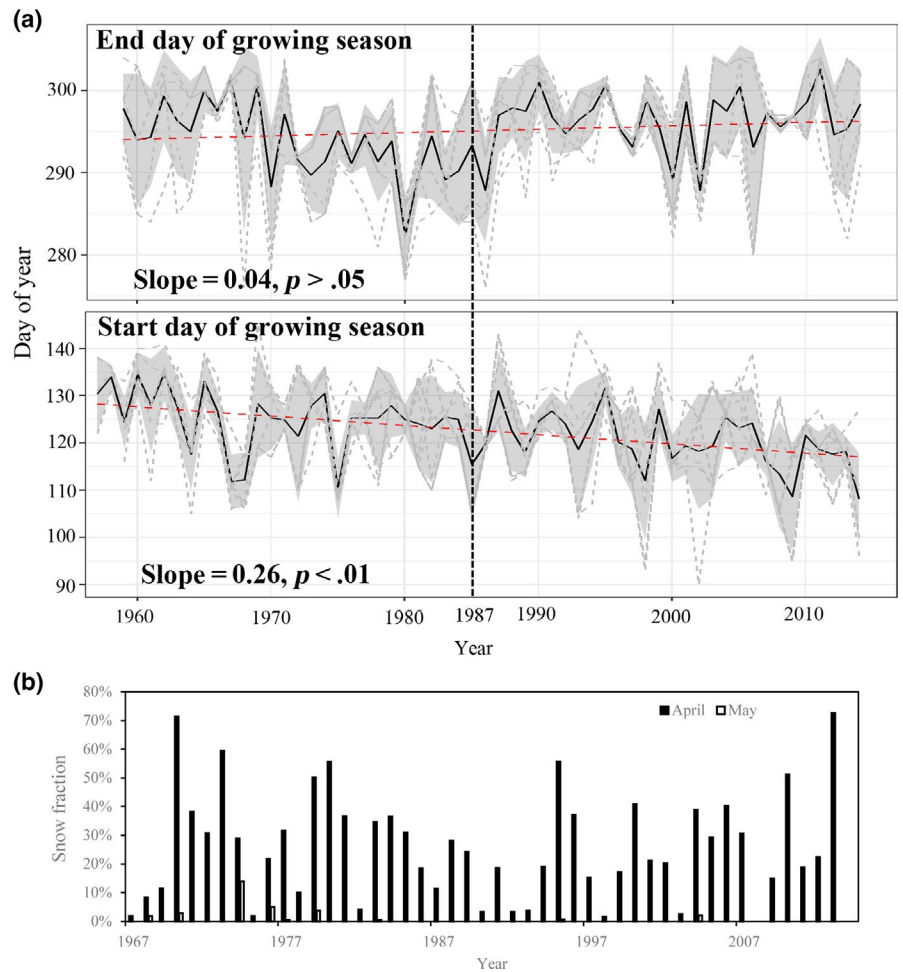


FIGURE 4 Changes in growing season length and snow cover fraction from 1967 to 2014. (a) Changes in the start day and end day of the growing season from 1960 to 2014. Dashed lines represent the climate stations, and solid lines represent the regional mean. Shaded areas represent the confidence interval. A significant trend was found for the beginning of the growing season, but not for the end of the growing season. (b) Changes in snow cover fraction from 1967 to 2014. Snow existed in April, but mostly disappeared by May [Colour figure can be viewed at wileyonlinelibrary.com]



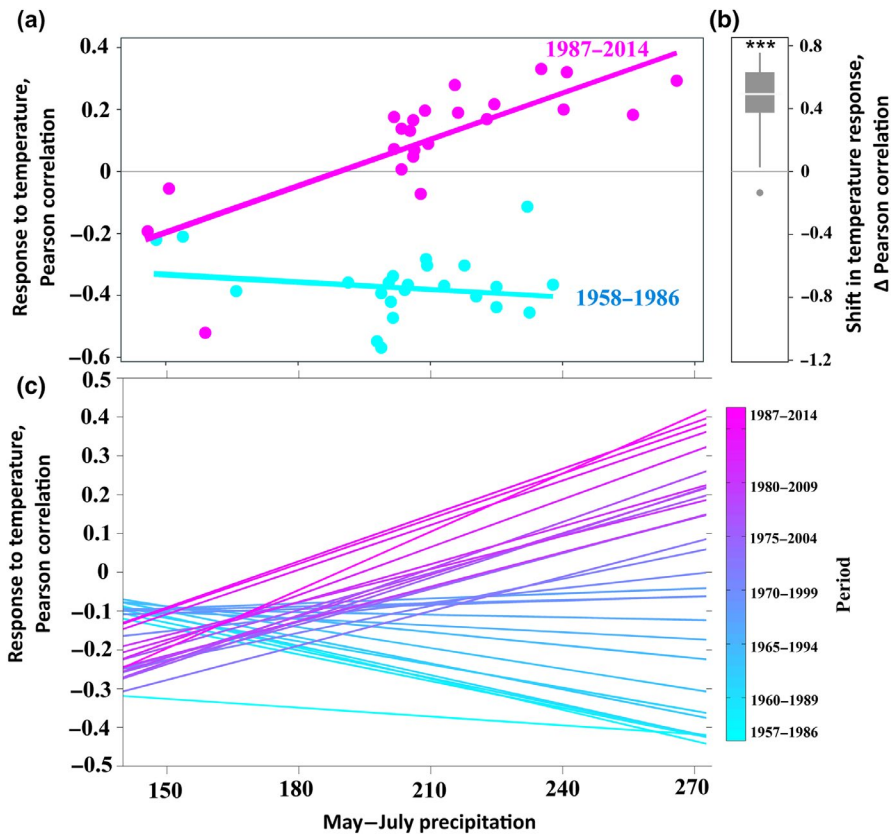


FIGURE 5 Relationship between the temperature-growth correlation of *Pinus sylvestris* and precipitation. (a) Correlation between May and July precipitation and the temperature-growth correlation. Blue dots represent the correlation in the period 1957–1986; red dots represent the correlation in the period 1987–2014. Temperature-growth correlation was calculated for May–July. A significant increase in the precipitation dependency of the temperature-growth relationship was found from the year 1986 in the study region. (b) Shift in growth response to temperature between the period 1958–1986 and the period 1987–2014. (c) Temporal changes in the relationship between precipitation and temperature-growth correlation moving with the 30-year window

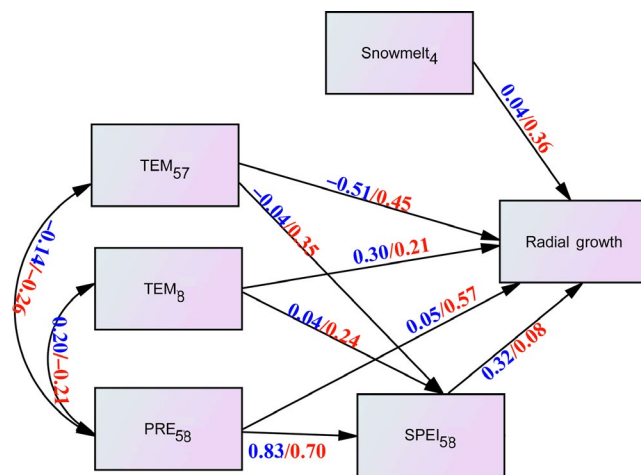


FIGURE 6 A structural equation model (SEM) with standardized path coefficients for climate variables and radial growth (standardized tree-ring width) during the 1958–1986 (blue) and 1987–2014 (red) periods. Variables used in the models were radial growth, as represented by the mean tree-ring chronology for the northern 20 sites. Snowmelt₄, April total snowmelt; TEM₅₇, May–July mean temperature; TEM₈, August mean temperature; PRE₅₈, May–August total precipitation; SPEI₅₈, May–August SPEI. TEM₅₇ and TEM₈ were separated into two variables because the effect of TEM₅₇ on tree growth reversed between two periods. The model fit was $\chi^2 = 3.022$, $df = 5$, $p = .697$, NFI = 0.935, CFI = 1.00, with RMSEA = 0.00 for the non-warming period and $\chi^2 = 4.855$, $df = 5$, $p = .434$, NFI = 0.918, CFI = 1.00, with RMSEA = 0.00 for the warming period. All diagnostics indicate satisfactory fit (i.e., NFI > 0.9, CFI > 0.9, and $p > .05$) [Colour figure can be viewed at wileyonlinelibrary.com]

reversed correlation between temperature and growth for April and May since 1987. If this is the case, early and mid-growing season precipitation ought to influence the correlation between temperature and growth. To test this hypothesis, we examined the relationship between early to mid-growing season (May–July) precipitation and temperature-growth correlation during the periods with no warming and rapid warming (Figure 5). We found no significant correlation between precipitation and temperature-growth correlation prior to the period with rapid warming ($r = .17$, $p > .05$), but an extremely strong and significant correlation with precipitation since 1987 ($r = .78$, $p < .001$). The relationship between total May–July precipitation and the growth response to temperature became increasingly positive since 1987 (Figure 5c).

We also tested this hypothesis using SEM, which indicated that snowmelt water and precipitation became more important for tree growth during the warming period (Figure 6). The SEM framework also indicates that temperature did exacerbate droughts, but that the influence of drought on tree growth decreased due to a compensating effect of a strengthening relationship between precipitation and radial growth. The effect of May–July temperature reversed from negative to positive between the two periods.

4 | DISCUSSION

While the growing season has been advancing progressively over the entire study period, a switch seems to have occurred around

1987 when the advancement of the growing season was sufficient to overlap temporally with high soil water availability from snowmelt. The combination of the progressive advancement of the growing season and the increased availability of snowmelt water during the critical early part of the growing season enabled the distinct response of growth to temperature between the early and late study period in the northern region.

Our findings contrast with those reported in other American and European boreal ecosystems, where increasing temperatures are often associated with a shift from positive to negative temperature–growth relations (Ciais et al., 2005; Peng et al., 2011; Schaphoff et al., 2016). In these studies, water deficits were exacerbated by increasing temperature, which have been suggested to be the main drivers of widespread increases in tree mortality (Adams et al., 2009; Allen et al., 2010; Restaino et al., 2016; Van Mantgem et al., 2009). The strengthened correlations of tree growth and precipitation in our populations during the period of warming suggest that, like in American and European boreal forests, there was an increase in demand for moisture with warming. Hence, there is consistency in our results versus other boreal systems with regard to the physiological response of boreal trees to warming.

Extended growing seasons in boreal systems are linked to increased temperatures (D'Orangeville et al., 2016; Peñuelas & Filella, 2009; Piao et al., 2007). Our findings are consistent with other studies indicating that an extended growing season is primarily driven by an advancement of spring (Chen, Hu, & Yu, 2005; Song, Linderholm, Chen, & Walther, 2010). However, there was limited direct influence of extended growing season on *P. sylvestris* growth during the period of study in our network; permafrost thaw depth showed little relevance, too. Therefore, the direct influence of growing season length and permafrost thaw depth on tree growth appear of little importance over the last few decades.

Most radial growth of *P. sylvestris* was produced during May–July (Rossi et al., 2008; Seo, Eckstein, Jalkanen, & Schmitt, 2011). May precipitation in our study region is low, ranging from 20 to 40 mm. The combination of high temperatures in May prior to 1986, the low amount of precipitation, and a small fraction of snow cover might have made trees water-limited at the start of the growing season. In contrast, as the start of the growing season moved progressively toward late-April, instrumental records indicate the potential for a greater amount of water in the form of snowpack. Mean snow cover fraction from 1987 to 2014 in April was 23% (range = 0%–73%, $SD = 0.18$) compared to 0% in May. Snowmelt is an important water resource for tree growth during the early growing season in boreal forests (Grippa et al., 2005; Kirilyanov, Hughes, Vaganov, Schweingruber, & Silkin, 2003; Vaganov et al., 1999). Counterintuitively, snowpack appears to melt at a lower rate in a warmer world because of the contraction of the snowmelt season to periods of lower available energy (Musselman, Clark, Liu, Ikeda, & Rasmussen, 2017). The interaction between the advancement of the growing season and the presence of snow cover in April gave trees access to more water than when the growing season generally commenced in mid-May. In some temperate and boreal forests, snow thaw circles occur around

the tree trunks, a phenomenon also observed in our study region. These snow thaw circles provide water for plant growth in the early growing season (Vellend, Young, Letendre, & Rivest, 2017). A resulting higher soil water content could offset the negative influences of VPD on turgor pressure (Rogiers et al., 2011), which is crucial for cell enlargement. In contrast, limited soil moisture leads to stomatal closure, which would exacerbate the effects of higher VPD, resulting in lower turgor pressure. Water is also an important source for the manufacturing of carbohydrates. Carbohydrates created and stored early during the growing season can be used to resist nutrient limitation, cold, or drought (Palacio, Hoch, Sala, Körner, & Millard, 2014; Puri, Hoch, & Körner, 2015).

We found a more positive growth response to temperature in populations where there is substantial precipitation from May to July (ranging from 201 to 265 mm) versus those in a drier portion of our network (May–July precipitation ranged from 145 to 160 mm). *Pinus sylvestris* in a cold-dry forest in Siberia near to our study region increased growth in areas where May–July precipitation was >160 mm, while growth declined at the same time in drier areas within that study (Shestakova, Voltas, Saurer, Siegwolf, & Kirilyanov, 2017). It might be that the *P. sylvestris* in northeastern China have a similar growth response to warming around the threshold observed in populations in nearby Siberia. Similarly, in the nearby dry regions, basal areal increment of trees decreased in regions where mean annual precipitation (MAP) is 200–400 mm, while tree growth increased in regions where MAP is 400–700 mm (Liu et al., 2013).

We have identified an interaction between rapid warming, shifting growing seasons, regional climate, and the growth response of trees in a boreal forest system. Access to snowmelt water with an earlier arrival of growing season conditions combined with sufficient precipitation allowed trees to benefit from rapid warming. However, unlike other boreal forest regions, the monsoonal climatology in our study region made snowmelt water a critical supply of water in the early growing season.

Widespread forest decline is being reported in western North America (Restaino et al., 2016; Van Mantgem et al., 2009), Europe (Bigler et al., 2006; Ciais et al., 2005), and Russia (Schaphoff et al., 2016). Although Europe is generally wetter than our study region, European Scots pine populations suffered from growth decline and high forest mortality associated with drought, except in the far north (Bigler et al., 2006; Reich & Oleksyn, 2008), indicating the species might shift its distribution northward in Europe. However, the boreal *P. sylvestris* populations in northeastern China is responding positively to climate warming, showing increased growth in recent years. Our results indicate that water availability at the beginning of the growing season might be critical in the adaptation of boreal *P. sylvestris* to rising temperatures in monsoonal Asia.

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CONFLICT OF INTEREST

The authors declare that no conflict of interests exists.

AUTHOR CONTRIBUTION

X.Z., N.P., and Z.C. conceived the idea. X.Z., Z.C., and X.B. collected tree cores. J.L., F.S., and F.Z. measured the tree-ring width. M.H. provided climate data and performed part of the analysis. X.Z. performed most the analysis and wrote the manuscript. N.P., R.D.M., L.D., T.T.R., and Z.C. provided valuable suggestions and co-wrote the manuscript.

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