Recent rising temperatures drive younger and southern Korean pine growth decline

Xiaochun Wang [a,b,*], Neil Pederson [b], Zhenju Chen [c], Kathryn Lawton [d], Chen Zhu [a,e], Shijie Han [f,g]

[a] School of Forestry, Northeast Forestry University, Harbin 150040, China
[b] Harvard Forest, Harvard University, Petersham, MA 01366, USA
[c] Tree-ring Laboratory, Forestry College/Research Station of Liaohe-River Plain Forest Ecosystem CFERN, Shenyang Agricultural University, Shenyang 110866, China
[d] Independent Scholar, Buffalo, NY, USA
[e] School of Ecological and Environmental Science, East China Normal University, Shanghai 200241, China
[f] School of Life Sciences, Henan University, Kaifeng 475004, China
[g] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China

HIGHLIGHTS

- Young Korean pine, but not older trees, showed a growth decline in response to climate warming.
- Trees in the southern region are more likely to decline, depending on age.
- Drought caused by climate warming is the main cause of young tree decline.

GRAPHICAL ABSTRACT
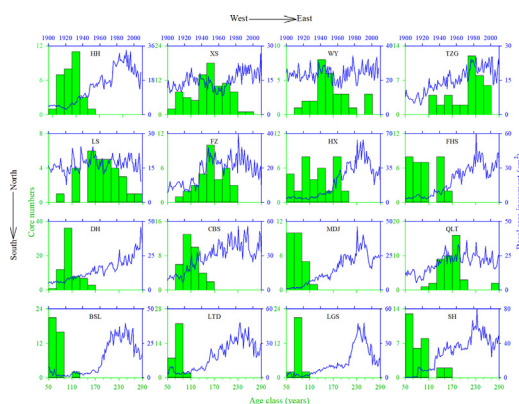
ABSTRACT

The Earth has experienced an unequivocal warming, with the warmest period of the past 150 years occurring in the last three decades. Korean pine (*Pinus koraiensis*), a key tree species in northeast Asia, is predicted to be particularly vulnerable to climate change. Here, we use dendrochronological methods to test whether the observed growth decline of Korean pine in northeast China is related to climate warming and whether climate-growth responses varied with age. A total of 628 cores from 401 trees across 16 sites were sampled over the entire distribution area of Korean pine in China. Samples were divided into three age classes: younger (50–130 years), middle (131–210 years), and older trees (>210 years), and measured by the ring-width index and basal area increment (BAI). Results showed a significant decline in BAI in most sites coinciding with an increase of temperature in the growing season and a decrease in precipitation since the 1980s. Meanwhile, we found that temperature-induced growth decline was significantly related to tree age. The BAI of younger trees decreased significantly and sharply (0.44 cm^2 year^{-1}, $P < 0.0001$), while old trees either decreased slightly or stabilized (0.04 cm^2 year^{-1}, $P = 0.33$). Tree growth in the southernmost locations was more likely to decline, what was most likely a result of forest-stand age. The age-related growth decline induced by climate warming might be explained by tree species traits, differences in growth rates between age classes and their relation to stress, changes

* Corresponding author at: Center for Ecological Research, School of Forestry, Northeast Forestry University, Harbin 150040, China.
E-mail address: wangx@nefu.edu.cn (X. Wang).

in root system, competition/stand structure or physiological mechanisms. Our results might also predict that early stand process-thinning is exacerbated by warming and drying. This research informs that the age effect of growth response to rising temperature should be considered in forest management under climate change, and particularly models of future carbon cycle patterns and forest dynamics.

1. Introduction

The Earth has experienced an unequivocal warming in its climate system during the last 150 years and impacts on forested ecosystems have become apparent. Notably, the 1983–2012 period has been successively warmer at the Earth's surface than any preceding decades of the past 800 years (IPCC, 2014). The increase in temperature is projected to be the greatest at high latitudes of the Northern Hemisphere (IPCC, 2014). Under a warming climate, changes in tree growth (Charney et al., 2016; Madrigal-González et al., 2018; Pompa-García et al., 2017; Shestakova et al., 2016), species distribution (Schelhaas et al., 2015), and structural or functional ecosystem response (Zhou et al., 2014) are expected. Since tree growth is important to the economy of timber production and ecosystem services (e.g., global carbon sink) (Binkley et al., 2002), we urgently need to understand the effect of warming on growth to predict changes in future forest productivity and the carbon cycle.

The impact of climate warming on tree growth varies over space and forest types. Recent tree growth decline induced by climatic variability has prevailed in most forest biomes (Silva and Anand, 2013). Drought or water stress during anomalously warm periods is generally considered to be the main cause for tree growth decline (Barber et al., 2000; Housset et al., 2015; Liang et al., 2016; H. Liu et al., 2013; Restaino et al., 2016; Wu et al., 2012; Zhou et al., 2014; Zimmermann et al., 2015), even though an increase in the concentration of carbon dioxide in these periods has also led to enhanced water use efficiency (Brito et al., 2016; Peñuelas et al., 2008; Silva et al., 2010). In northeast China, temperature has risen by ca. 1.75 °C over the last 50 years (1961–2010, 0.35 °C per decade) (Zhao et al., 2013), accompanied by a slight decrease in total precipitation. As a result of both trends, the potential for water stress is predicted to increase over a large part of forested China. The factors driving tree growth are various, and additional factors likely influence growth declines, for example, between-tree competition (Linares et al., 2010; Madrigal-González and Zavala, 2014) and ontogeny (Binkley et al., 2002; Foster et al., 2014; Madrigal-González and Zavala, 2014; Rozas et al., 2009). Conversely, growth enhancement (Camarero et al., 2015; Koutavas, 2008), no growth stimulation (van der Sleen et al., 2015), and synchronized regional growth (Shestakova et al., 2016) in response to increased temperature or atmospheric CO_2 concentration have been reported as well (Soulé and Knapp, 2006). From these results, it is apparent that investigations must be made over a range of locations, sites, and forest types.

When studying climate-induced growth response, ontogeny must be considered as a driving factor (Rozas et al., 2009). Ontogeny is a critical factor for growth responses since trees undergo age-related physiological changes and adapt to changing environmental conditions (Martínez-Vilalta et al., 2007). Disparate age-related sensitivities of tree growth to climate have been reported, ranging from no age-effect (Esper et al., 2008), to higher sensitivity in older trees (Prior and Bowman, 2014), to higher sensitivity in younger trees (Vieira et al., 2009). Young *Pinus cembra* and *Larix decidua* (<100 yr) were weakly influenced by climate, whereas the climate signal was higher in older trees (Carrer and Urbinati, 2004). Higher climatic sensitivity in older trees has been attributed to increased hydraulic resistance (Carrer and Urbinati, 2004; Foster et al., 2014), decreased carbon gains under high temperature (Mencuccini et al., 2005), or reduced duration of xylem differentiation (Rossi et al., 2008). Therefore, larger negative effects of climate warming on older trees may change the global carbon sink pattern (Luyssaert et al., 2008; Stephenson et al., 2014). On the contrary, larger effects of climate on younger trees may have been caused by a longer growing season (Rossi et al., 2008) and faster response to changing environmental conditions (Villalba and Veblen, 1994). Pompa-García and Hadad (2017) reported that warming winter maximum temperatures would decrease radial growth of *Pinus cooperi* and stronger in younger trees. Climate induced mortality was found to be significantly higher in young forests, most probably driven by regional warming and drought (Luo and Chen, 2013). Larger sensitivities to climate in young trees might become a limiting factor in terms of forest persistence and adaptation of forest structure and function to a warming climate (Luo and Chen, 2013). How tree growth changes with age under climate stress is critical to models of forest yield and carbon dynamics (Camarero et al., 2015). In addition, climate could induce non-linear effects on growth (Lloyd et al., 2013) by coupling with additional factors such as sites, ages, etc. Consequently, it is crucial to understand the age-related growth response to climate warming for predicting forest stand composition changes and likely future impacts on the carbon cycle (Ruiz-Benito et al., 2015).

Korean pine (*Pinus koraiensis*) is one of the dominant tree species in northeast Asia (Fig. 1) and is particularly sensitive to climate change (Lyu et al., 2017; Yu et al., 2013). Within the context of climatic change and forest productivity, we investigate Korean pine across its entire distribution area in China. Specifically, for this study, we examined the age-related growth response of Korean pine to rising air temperature in recent decades (since the 1980s). We hypothesize that: (i) an overall growth decline in recent decades has been caused by rising temperature and decreasing precipitation; (ii) the growth decline in older trees is higher than in younger trees. We test these hypotheses by identifying the variations of tree-ring index (TRI), tree-ring widths (TRW), and basal area increment (BAI), examining the climate-growth relationships, and discussing the results in light of forest ecosystem management under climate change.

2. Materials and methods

2.1. Study area

The study area covered almost the whole broadleaved-Korean pine forest distribution area within China (40.75–49.82° N, 124.75–135° E, Fig. 1a). The broadleaved-Korean pine forest is the zonal vegetation type found in the northern temperate subzone in northeast China. The forest is comprised mainly of *Pinus koraiensis* and various broad-leaved tree species, such as *Fraxinus mandshurica*, *Phellodendron amurense*, *Juglans mandshurica*, *Tilia amurensis*, *Tilia mandshurica*, *Betula costata*, *Quercus mongolica*, and *Ulmus japonica*.

Korean pine is a long-lived, shallow-rooted heliophile occurring from 500 m to 1300 m above sea level (a.s.l.) in northeast China. In juvenile ages, Korean pine is shade tolerant (Thomas and Farjon, 2013; Wu and Raven, 1999). Korean pine is sensitive to soil moisture and grows well (or poor) when the relative humidity is above 70% (or below 50%) (Flora of China Editorial Committee, 1999). Korean pine generally prefers temperate and relatively higher humidity climates as well as deep, fertile and well-drained acid brown forest soil (Wu and Raven, 1999).
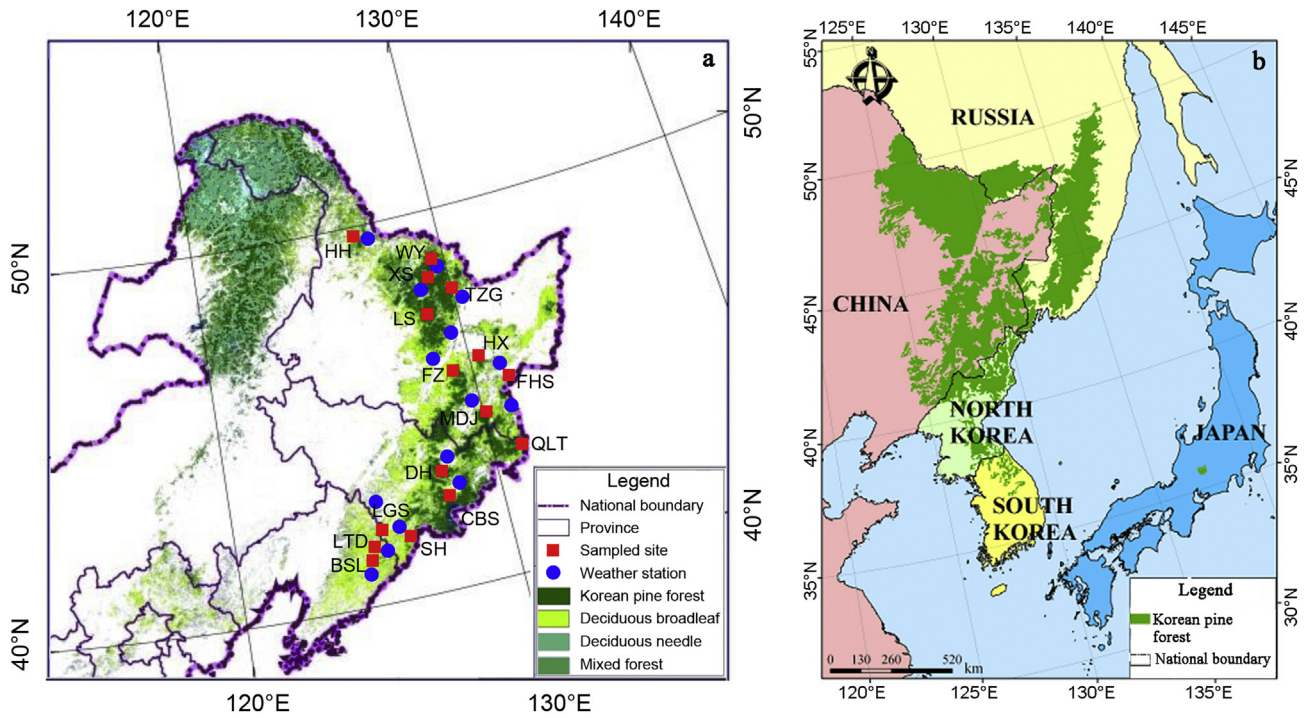
Fig. 1. Distribution maps of the broadleaved Korean pine forest in China (a) and Northeast Asia (b) edited from Zhang et al. (2015b). The sampling sites and weather station are represented by red squares and blue circles, respectively. The sampling site code is the same as in Table 1.

Our study area is located in the temperate continental monsoon climate, which is dominated by chilly winters and hot summers. Mean annual temperatures range from −1.6 °C to 7.0 °C. The annual total precipitation is 537–1108 mm, with *ca.* 80% received from May to September (Table 1). The soil in this region is dark-brown forest soil. Soil formation is generated by accumulation, leaching by weakly acidic solutions, and the clayification process of weak acidic humus in temperate moist forests.

2.2. Core sampling and chronology development

In springs of 2009 and 2014, we chose 16 strictly protected natural distribution areas of Korean pine (ten National Natural Reserves and six National Forest Parks) to take tree-ring cores (Table 2). Smaller trees, like <50 years old, was not collected because they may suffer more competition or other ecological factors affecting. One or two cores per tree were collected from healthy appearing living individuals at breast height (~1.3 m) using a 5.15 mm increment borer. A total of 653 cores from 415 trees were sampled in 16 forest stands in northeast China. Cores were fixed, air-dried and progressively sanded until each ring was clearly visible. Then, each ring was cross-dated to identify possible absent or false rings and assign an accurate calendar year using a skeleton-plot method under a microscope (Stokes and Smiley, 1968). Subsequently, ring width was measured to an accuracy of 0.001 mm using a Velmex tree-ring measurement system (Velmex Inc.). Measurements and dating accuracy were checked using the COFECHA program (Grissino-Mayer, 2001).

To remove the non-climatic signals related to tree age and minimize trend distortion, the "signal-free" approach was used to develop the chronology (Melvin and Briffa, 2008). Tree-ring index was calculated as a ratio of observed to expected growth, which was obtained by fitting the measured values with negative exponential curves or linear straight

Table 1
Information of the 15 weather stations nearest to sampling sites.

Weather station	Sampling site	Latitude (°N)	Longitude (°E)	Elevation (m)	MAT (°C)	MAP (mm)	Distance (km)	Time span
Sunwu	HH	49.433	127.350	235	−1.0	550	39	1954–2014
Wuying	WY	48.100	129.233	288	−0.1	617	16	1958–2011
Yichun	XS	47.733	128.917	241	0.9	639	39	1956–2014
Hegang	TZG	47.333	130.267	228	0.4	619	39	1956–2008
Yichun	LS	47.733	128.917	241	1.4	661	39	1956–2014
Yilan	HX	45.967	128.733	100	3.6	556	43	1959–2013
Tonghe	FZ	46.300	129.583	109	2.6	592	43	1953–2013
Jixi	FHS	45.300	130.933	281	4.0	537	47	1951–2013
Mudanjiang	MDJ	44.567	129.600	241	3.9	550	35	1951–2014
Suifenhe	QLT	44.383	131.167	591	2.7	574	141	1953–2013
Dunhua	DH	43.367	128.200	525	3.2	624	67	1953–2014
Baihe	CBS	42.533	128.250	467	2.8	679	39	1958–2013
Tonghua	LGS	42.100	124.917	237	6.9	861	68	1953–2013
Qingyuan	SH	41.683	125.900	403	5.4	888	45	1951–2013
Huanren	LTD	41.283	125.350	246	6.7	853	38	1953–2013
Kuandian	BSL	40.717	124.783	260	7.0	1108	22	1954–2013

Note: MAT-mean annual temperature, MAP-mean annual precipitation. Distance-the distance between the sampling site and the weather station.

Table 2
Site description and statistical characteristic for the 16 Korean pine (*Pinus koraiensis*) chronologies used in this study.

Site	Latitude (°N)	Longitude (°E)	Elevation (m)	MRW (mm)	Time span	Age ± SD	SNR	MS	AC1	EPS	RBAR	No. T/C
HH	49.460	126.760	510	1.59 ± 0.59	1847–2008	127 ± 21	8.64	0.12	0.34	0.9	0.45	31/31
WY	48.120	129.230	351	1.57 ± 0.68	1738–2008	184 ± 43	11.25	0.18	0.47	0.92	0.38	29/29
XS	47.908	129.022	346	1.47 ± 0.48	1775–2014	176 ± 45	8.17	0.18	0.68	0.89	0.39	50/84
TZG	47.598	129.924	381	1.16 ± 0.31	1743–2013	227 ± 44	6.43	0.16	0.69	0.87	0.38	20/40
LS	47.180	128.890	427	1.57 ± 0.53	1724–2008	204 ± 45	8.24	0.15	0.40	0.89	0.35	30/30
HX	45.672	130.295	582	1.52 ± 0.91	1802–2013	145 ± 45	14.71	0.18	0.84	0.94	0.46	21/39
FZ	45.661	129.081	350	1.24 ± 0.56	1763–2013	184 ± 38	6.22	0.21	0.74	0.86	0.40	19/34
FHS	44.894	131.084	585	1.67 ± 0.94	1839–2013	112 ± 37	7.36	0.19	0.79	0.88	0.49	20/36
MDJ	44.400	129.790	611	2.01 ± 0.86	1880–2009	92 ± 19	17.42	0.18	0.80	0.95	0.43	29/29
QLT	43.358	131.238	419	1.40 ± 0.43	1775–2013	190 ± 30	10.55	0.16	0.78	0.91	0.43	22/43
DH	42.942	127.840	905	1.88 ± 0.50	1845–2011	125 ± 20	11.35	0.14	0.62	0.92	0.36	42/67
CBS	42.400	128.100	718	2.12 ± 0.70	1842–2013	131 ± 21	6.36	0.17	0.64	0.86	0.41	18/35
LGS	41.626	125.432	875	1.82 ± 1.06	1886–2013	102 ± 10	17.82	0.25	0.82	0.95	0.59	13/25
SH	41.356	126.211	930	1.76 ± 1.40	1825–2013	103 ± 32	7.64	0.19	0.92	0.88	0.51	20/34
LTD	41.304	124.897	882	2.01 ± 0.77	1859–2013	99 ± 10	7.44	0.21	0.71	0.88	0.45	16/32
BSL	40.913	124.790	1030	2.31 ± 0.61	1869–2013	94 ± 16	17.58	0.23	0.72	0.89	0.50	21/40

Notes: MRW-mean ring width, SNR-signal-noise ratio, MS-mean sensitivity, AC1-first-order autocorrelation, EPS-expressed population signal, RBAR-mean interseries correlation, No. T/C-tree/core numbers.

lines with any slope (Cook, 1985). Variance caused by changes in sample number was stabilized by using an additional 67% series length smoothing spline. All tree-ring index series in one site were merged into a tree-ring chronology using Tukey's biweight robust mean. Then, producing signal-free chronologies involves repeatedly dividing the raw ring widths by the detrended chronology until the variance is minimized (Melvin and Briffa, 2008). The iteration of this process was depended on replication (e.g. the 2–6 times of core numbers). A total of 16 chronologies were developed from 628 cores from 401 trees (Table 2). The correlation matrix among all chronologies during the period 1886–2008 can be found in the Appendix (Table S1). The correlation coefficient between chronologies slightly decreased with the increase of the distance between sampled sites, but the trend was not significant (Fig. S1).

2.3. Basal area increment (BAI) measurements

As trees increase in size, ring widths typically decline, causing characteristic age trends in the ring-widths series. The conversion of ring width into BAI provides a more accurate approximation of tree growth as the conversion minimizes age-related trends (Peñuelas et al., 2008; Phipps and Whiton, 1988). In healthy mature trees, BAI may continue to increase (Peñuelas et al., 2008) or stabilize, but it will not exhibit a decreasing trend until trees begin to senesce (Duchesne et al., 2003; LeBlanc, 1990). Therefore, a negative trend in BAI is a strong indication of a true decline in tree growth (Jump et al., 2006; LeBlanc, 1990; Peñuelas et al., 2008). The BAI of each series was computed by the Program Biaplt_XP. In cores without pith, the number of years missing to pith was estimated by a geometrical method. This method considers the mean growth rate of the innermost rings in complete samples (Camarero et al., 2015; Norton et al., 1987). The BAI series has biological noise due to an increased radius with time, each BAI series can be standardized to remove this growth trend. However, for this study, we are interested in these growth trends. Consequently, an unstandardized BAI was averaged over all individual cores at each site (Jump et al., 2006). A regional mean BAI was calculated by averaging all BAI series from 16 sampling sites during the common period 1886–2008.

2.4. Climatic data and statistical analysis

Climatic data were collected from the weather station nearest to each sampling site (http://data.cma.cn/en; Table 1, Fig. 1). Climate variables included monthly mean temperature, total precipitation, and the standardized precipitation-evapotranspiration index

(SPEI), computed by software SPEI (Vicente-Serrano et al., 2010). The time interval of the SPEI calculation was one month. Two sampling sites (XS and LS) share the same climate data (Yichun weather station). Relationships between tree-ring chronologies and climate variables from previous June to current September at each site were tested using response function analysis (Biondi and Waikul, 2004).

Spatial correlations were made between the regional BAI and the growing season (May–September) CRU TS3.23 temperature and precipitation ($0.5° \times 0.5°$) during the period 1980–2010 as well as the mean June–August normalized difference vegetation index (NDVI) during the period 1982–2006. The NDVI used here was derived from the high quality GIMMS (Global Inventory Modeling and Mapping Studies). Spatial correlations were calculated using the KNMI climate explorer (van Oldenborgh et al., 2008). Maps with filled *P*-values >5% were masked out.

To investigate the potential for an age-related BAI trend in recent years (since 1983) and chronology-climate relationships, three age-classes were created for the BAI series and tree-ring chronologies: young (cambial age 50–130 years), middle (131–210 years), and old (>210). Ages used in this work are cambial ages at breast height (~1.3 m). The age loss from ground surface to sampling height was not considered because all trees were sampled at approximately the same height (Wu et al., 2013).

Statistical analyses, such as regression and correlation, were performed using the STATISTICA software package (StatSoft, Inc.).

3. Results

3.1. Climate change in recent decades

A warming trend of 0.04 °C year^{-1} in the growing season (May–September) from 1983 to 2013 was observed across the whole study area (Figs. 2a; S2a). The largest warming trend within our study region over the last three decades was found in Heihe (HH), which is the northernmost limit of Korean pine distribution. There, the warming trend was 0.795 °C per decade. The smallest warming trend was found at Laotuding (LTD), near the southern distribution of Korean pine. The warming trend at Laotuding was 0.129 °C per decade. Conversely, growing season precipitation decreased slightly at most sites. A mean rate of −5.03 mm precipitation per year was found across our study region (max. −7.93 mm year^{-1} at TZG, min. 0.89 mm year^{-1} at LTD) (Figs. 1b, S2b). Warming with a concurrent decrease in precipitation caused severe aridification in northeast China since 1983 (Figs. 1c; S2c).
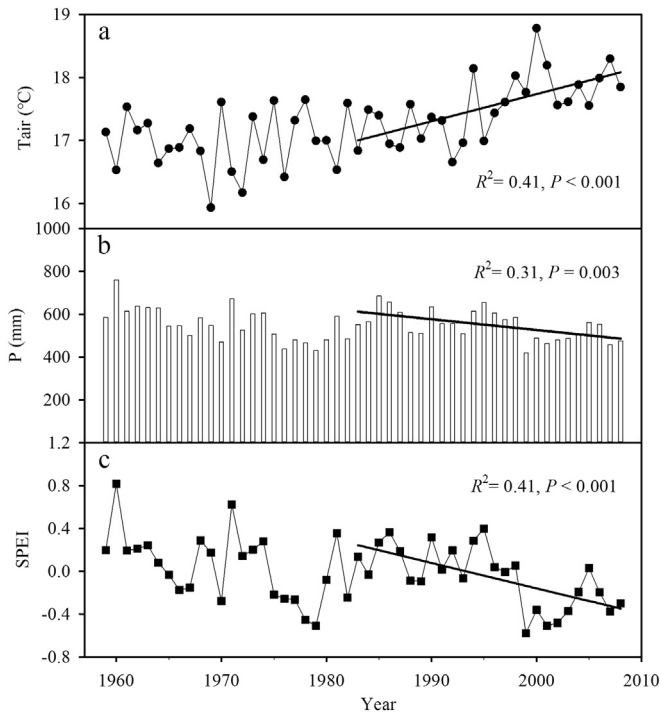
Fig. 2. Variations of (a) annual mean air temperature (T_{air}), (b) annual total precipitation (P) and (c) the standardized precipitation-evapotranspiration index (SPEI) averaged from 15 weather stations in northeast China from 1959 to 2008. Regression analysis (1983–2008): T_{air}: $y = 0.0432x - 68.69$, $R^2 = 0.41$, $P < 0.001$; P: $y = -5.0297x + 10,586.2$, $R^2 = 0.31$, $P = 0.003$; SPEI: $y = -0.0238x + 47.35$, $R^2 = 0.41$, $P < 0.001$.

3.2. Age-related growth trend

Since the 1980s a remarkable growth decline trend occurred in the regional mean tree-ring index, tree-ring width, and basal area increment (Fig. S3). The declining trend in BAI did not have consistent latitudinal or longitudinal patterns (Fig. 3). The decline in BAI at the four northern sites (XS, WY, TZG, and LS) was, however, not significant, while it was highly significant in the four southern sites (BSL, LTD, LGS, and SH) (Fig. 3).

We further found that, on average, the BAI of the youngest age classes declined more since the 1980s than the older age classes (Fig. 4). The BAI in sites composed of younger trees (e.g., BSL, HH, LTD, LGS, and MDJ, except for DH, Fig. 3) decreased significantly and sharply (0.44 cm^2 year^{-1}, $P < 0.0001$, Fig. 4). Trees in the middle age class decreased significantly but not as sharply as the younger sites (0.13 cm^2 year^{-1}, $P = 0.02$, Fig. 4; e.g., CBS, FHS, FZ, HX, QLT, and SH, Fig. 3), while sites with older trees decreased slightly or stabilized (0.04 cm^2 year^{-1}, $P = 0.33$, Fig. 5; e.g., LS, TZG, WY, and XS, Fig. 3).

Overall, Korean pine growth for young and middle classes has recently suffered a marked decline. The rate of growth enhancement non-significantly decreased with tree aging (Fig. 5a), while the rate of growth decline significantly increased with tree aging (Fig. 5b). In addition, the BAI slope of Korean pine growth significantly increased with tree aging (Fig. 5c).

3.3. Growth-climate relationship

Pearson's correlations indicated a significantly negative effect of the growing season (May–September) temperature on the tree-ring index of Korean pine in most sites (Fig. 6a), while the growing season precipitation had positive effects on tree growth (Fig. 6b). Most important for growth were the current and previous June and September temperature (Fig. S4). This growth-climate relationship did not seem to obviously

vary over our study area (Figs. 6, 8 and S4). The BAI of Korean pine decreased significantly with the growing season temperature increase since 1983 in most sites, on the contrary, it increased at DH and WY sites (Figs. 7 and S5). The BAI also increased with the growing season SPEI, but this was not as significant as the effect of temperature. Therefore, climate warming accompanied by decreasing precipitation was found to be unfavorable for Korean pine growth.

Tree-ring indices of young, middle, and old Korean pine exhibited similar climate-growth relationships, but these relations became nonsignificant in the oldest class for most months except for June (Fig. 8).

The older trees were more sensitive to higher temperature and lower precipitation, while younger trees were more sensitive to lower temperature and higher precipitation (Fig. 9a). The slope of BAI trend from 1983 to 2013 obviously increased with the effect of temperature on tree growth from negative to positive, while the variation of BAI slope with the effect of precipitation on growth is not obvious (Fig. 9b).

4. Discussion

Our analysis of 16 populations of Korean pine across its distribution area in northeast China indicated that the increased warming since the 1980s caused a decline in growth. This finding supported our first hypothesis and confirmed the assumed growth decline across northeast China (Tang et al., 2010; Wang et al., 2017). While the reduction in annual precipitation seemed to be important as well, temperature appears to be the driving factor for growth decline. Unexpectedly and contrary to our second hypothesis, we found that the youngest trees showed the greatest decline in growth. The slope of growth decline significantly decreased with tree aging.

4.1. Climate warming and climate-growth relationships

The negative influence of June temperatures on pine growth followed previous studies that found the water availability at the beginning of growing season to be critical for growth (Wang et al., 2013; Wang et al., 2017). Some researchers found that February–April temperature was also an important limiting factor of Korean pine growth in China (Lyu et al., 2017; Zhu et al., 2009). Our findings differed, however, because February–April temperatures were significant only at a few sites. We also found that the negative effect of rising temperature masked the effect of precipitation. This result indicated that high temperature was a climate constraint to Korean pine growth. The intensity of growth decline may be exacerbated in the warmest areas of its range, which was supported by the largest decline occurring at the site with the highest temperature increase (HH). Elevated growing season (May–September) temperatures coupled with decreased precipitation can cause drought stress. These conditions can cause high evapotranspiration rates, which may reduce the levels of stored carbohydrates, resulting in lower ring-width growth (Fritts, 1976). September was another important month affecting Korean pine growth. In dry years, there was commonly no growth when cambial activity was close to zero during the dry summer, while the photoassimilates of some tree species (e.g. *Pinus brutia*, *Pinus sylvestris*) were still accumulated. These stored carbohydrates were used for late wood production in autumn when soil water availability permits growth (Gruber et al., 2012; Körner, 2003). Therefore, the variability of the growing season temperature was the main cause for growth changes of Korean pine in northeast China.

Rising growing season temperatures could negatively impact the vitality of Korean pine through several mechanisms. One plausible reason could be higher carbon losses due to increased maintenance respiration and reduced carbohydrate availability for growth (Lavigne and Ryan, 1997). Maintenance respiration is expressed as a function of temperature and increases with a rise in temperature in many experiments and ecosystem models (Girardin et al., 2014; Tang et al., 2014). The thermal stress caused by rising growing season temperatures could be

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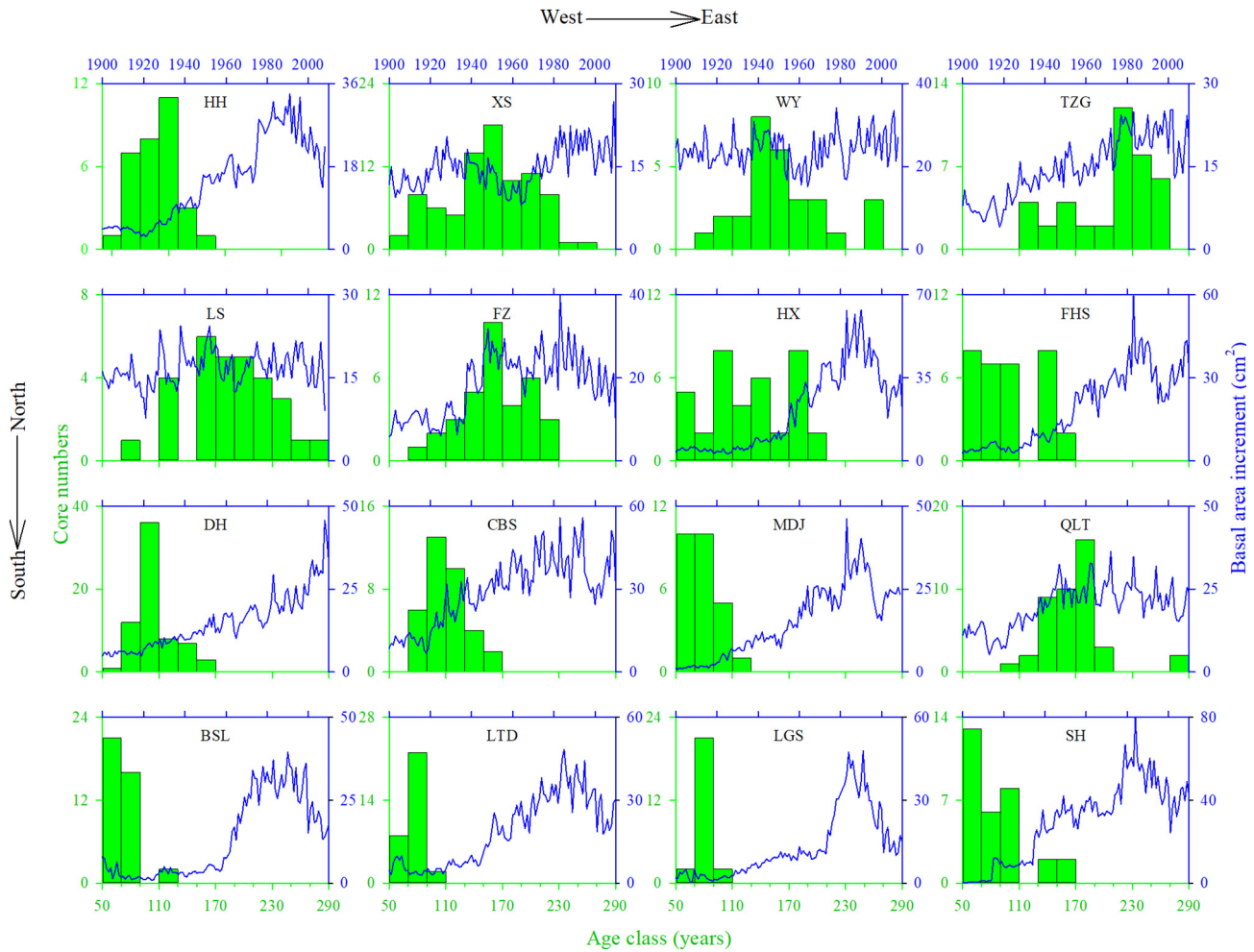
Fig. 3. Variations of the average annual basal area increment (BAI) during the period 1900–2010 (blue line) and the age structure at breast height in each sampling site (green bars). The sampling site code is the same as in Table 1.

reflected in the declines we observed in the tree-ring data. Rising growing season temperatures could also increase atmospheric demand for water vapor, which deteriorates the water status in leaf and stem tissues (Köcher et al., 2009). This diminishes tree growth because of the water availability constraints on photosynthesis caused by drought-induced stomatal closure (Adams et al., 2009; Brito et al., 2016; Way and Sage, 2008). In many cases, rising growing season temperatures and reduced precipitation interacted to limit tree growth

(Way et al., 2013; Zimmermann et al., 2015). Our results show that although precipitation does not play an important direct role in controlling growth, it does have a significant and indirect role in influencing growth (Juday and Alix, 2012; Lyu et al., 2017). In addition, it is possible that higher temperatures could exceed the temperature threshold for photosynthesis and cause a reduction in CO_2 assimilation, thus overriding the potential CO_2 fertilizer effect (D'Arrigo et al., 2004; Peñuelas et al., 2011).
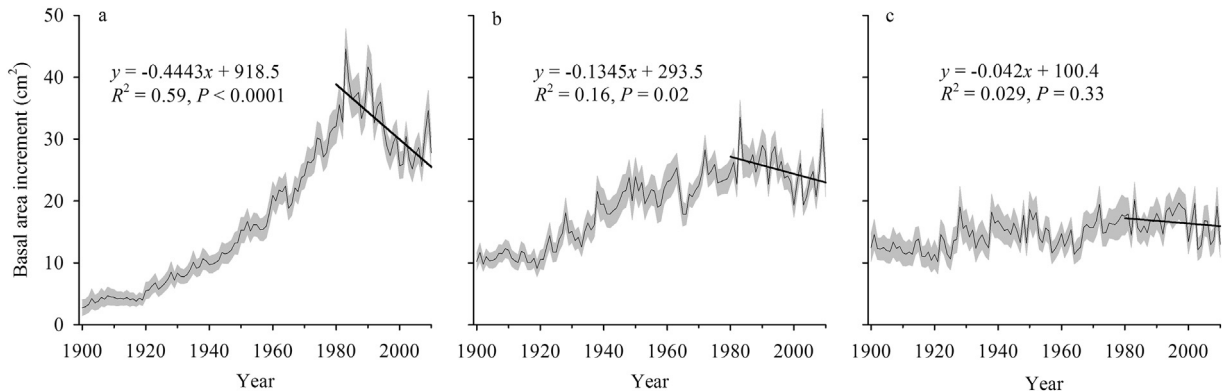
Fig. 4. Temporal variation of average basal area increment (BAI) for (a) young (50–130 year-old trees), (b) middle (131–210 year-old trees) and (c) old (>210 year-old trees) Korean pines. The shade area (gray) represents the 95% confidence limits for means.
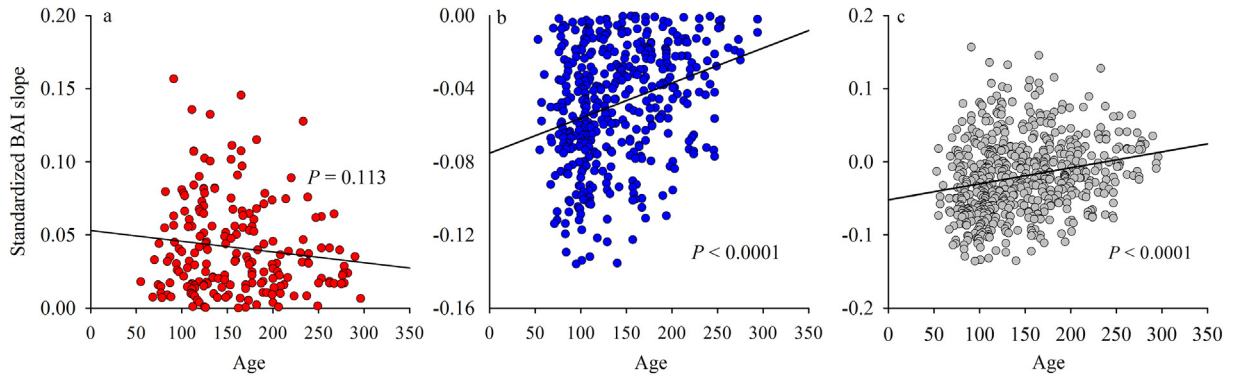
Fig. 5. Relationship between tree age at breast height and the slope of standardized BAI during 1983–2013 for slope (a) greater and (b) less than zero and (c) total. The straight line is the linear fitting between tree age and BAI slope, and the P-value is shown on the panel.

### 4.2. Recent unprecedented growth decline

We found a BAI decline in all but one site after a peak in growth around 1983. This deceleration of Korean pine growth rates during the last three decades was consistent with those found in many semi-arid forests around the globe (Brito et al., 2016; Liang et al., 2016; H. Liu et al., 2013; Restaino et al., 2016; Wu et al., 2013), as well as in high altitudinal and boreal forests (Barber et al., 2000; Girardin et al., 2014; Gómez-Guerrero et al., 2013; Housset et al., 2015; Wu et al., 2012). Some European temperate forests have also been experiencing growth declines (Jump et al., 2006; Linares et al., 2010; Peñuelas et al., 2008; Silva et al., 2010; Zimmermann et al., 2015). Our results were not consistent with previous evidence of growth enhancement at the elevational treeline (Camarero et al., 2015; Salzer et al., 2009) or recent steady growth found in tropical (van der Sleen et al., 2015) or subtropical forests (Silva et al., 2009).

While it appeared that the marked growth decline of Korean pine since the 1980s was related to higher growing season temperatures, it is possible that other factors were involved. Since the 1980s, for example, further variables including nitrogen deposition (X. Liu et al., 2013), air pollution (Rosenfeld et al., 2007), and land-use (Liu et al., 2014) significantly changed and might have partly accounted for pine-growth decline in northeast China. Determining the impact of other factors, however, was beyond the scope of our study here.

In addition, the chronologies of BAI were developed without considering any standardization technique, thus these chronologies have biological noise due to an increased radius with time. Therefore, the BAI for a specific year is not independent of the following year. For example, the BAI at DH site increased over time, and this may still be such biological noise effect.

4.3. Age effect

Younger Korean pines declined more than older trees. Our findings coincided with growth trends detected in Mediterranean conifers *Juniperus thurifera* (Rozas et al., 2009), *Pinus canariensis* (Brito et al., 2016), and *Pinus pinaster* (Vieira et al., 2009) as well as in *Picea schrenkiana* in northwest China (Wu et al., 2013). Similarly, a growth decline was more noticeable in younger *Pinus uncinata* during the second half of the 20th century than in older trees (Camarero et al., 2015). In Alberta and Saskatchewan, Canada, higher tree mortality in younger than in older trees among *Pinus banksiana*, *Picea mariana*, *Picea glauca*, *Populus tremuloides* and *Populus balsamifera* was associated with recent regional warming and decreased water availability (Luo and Chen, 2013). Similarly, younger *Nothofagus dombeyi* with high climatic sensitivity in northern Patagonia were more likely to die than older trees that also happened to be less sensitive to climate (Suarez et al., 2004). In contrast with our results, Zhou et al. (2013) reported that
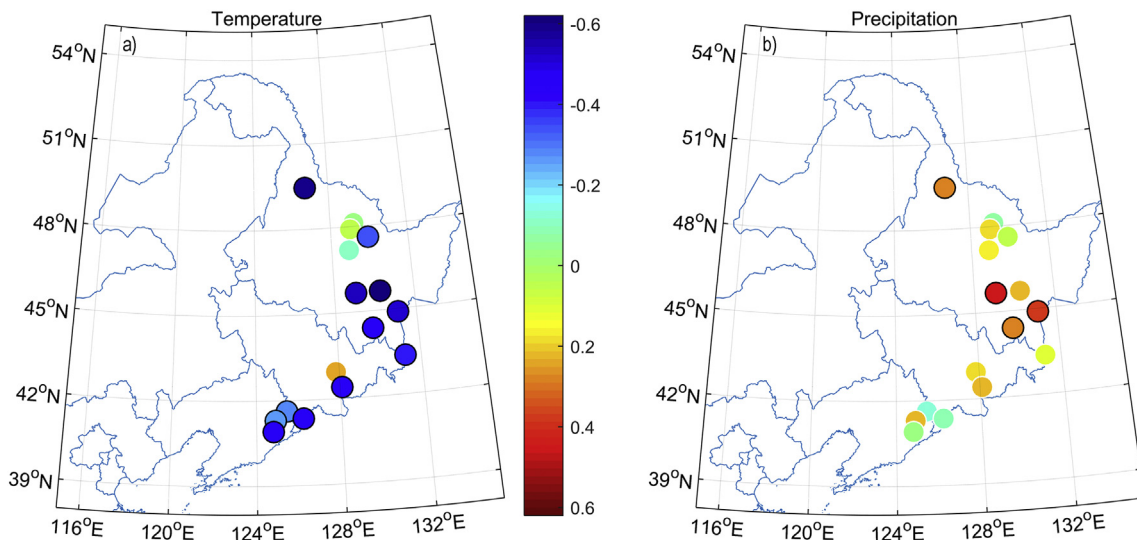
Fig. 6. Pearson's correlation coefficients between Korean pine tree-ring chronologies and growing season (May–Sep) mean temperature (a) and total precipitation (b). Positive (negative) coefficients are represented by red (blue) colors, and circles with black edge (>0.26 or less than −0.26) are significant at α = 0.05.
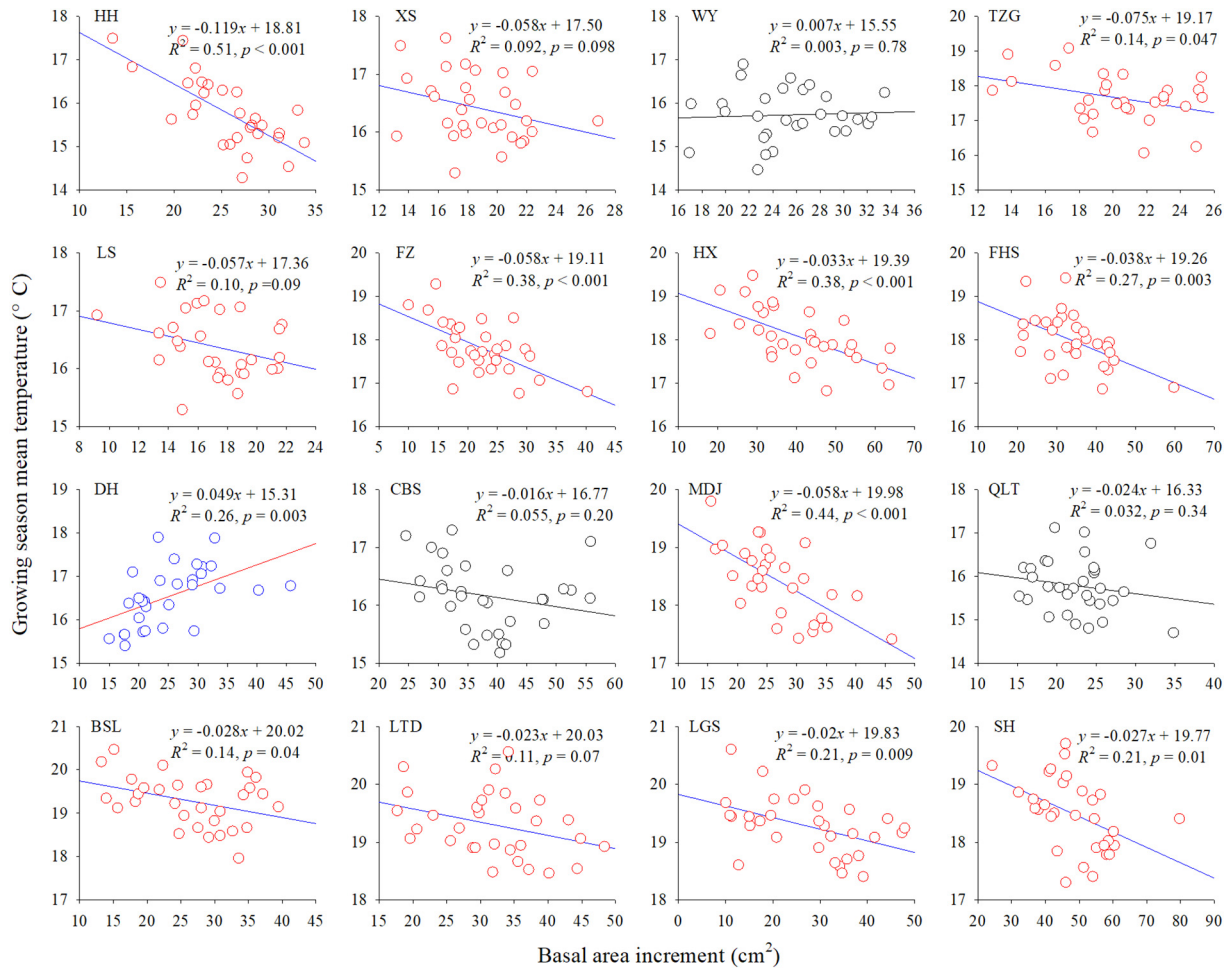
Fig. 7. Relationships between site-level basal area increment (BAI) and growing season temperature (May–Sep) at the 16 sampling sites during the period 1983–2013. The sampling site code is the same as in Table 1.

larger trees in subtropical China were more stressed than smaller ones by the warming and drying environment. Similarly, young trees in the Pyrenees experience longer seasons today than older trees did when they were in their juvenile phase, which was reported to result in larger growth rates in juvenile ages (Way and Oren, 2010). In addition, young *Pinus taiwanensis* were the most sensitive to reductions in relative growth rates, but absolute growth in older trees was strongly reduced under increased temperature (Ruiz-Benito et al., 2015). This was, however, not found in our study results.

Several reasons could explain the age-related Korean pine growth decline induced by climate warming. First, tree species trait: When young, Korean pine is a very shade-tolerant tree that cannot survive under the full light. In juvenile ages, Korean pine prefer a mild and humid climate and have more stringent requirements for soil moisture than older trees. Therefore, high growing season temperatures in combination with less precipitation caused sharper growth decline in younger than in older trees. Second, competition: The sign and magnitude of age-related growth responses may change at the individual level due to stand structure and competitive environment (Linares et al., 2009; Linares et al., 2010). Linares et al. (2010) found trees suffering from competition were predisposed to decline given an additional a severe drought stress. Madrigal-González and Zavala (2014) reported that negative impacts of increasing drought frequency were disproportionally higher in younger trees under high competition. Younger trees tend to occupy the same ecological niche and may experience greater competition for space and nutrients, resulting in a high vulnerability to external stress such as temperature-induced drought

(Luo and Chen, 2013). Younger Korean pine, which require more shade, are under more competitive stress than older trees. The higher amount of competition could make them more sensitive to rapid warming and reduced precipitation, thus inducing declining growth rates. Third, growth rate and duration: In young trees, cells are usually smaller, due to the shorter root-leaves path length and associated hydraulic constraints linked to tree height (Ryan and Yoder, 1997). In climatologically unfavorable periods, the cambium is prone to produce fewer cells, thereby decreasing tree growth (Konter et al., 2016). However, older and taller trees produce only a few larger cells per ring which decrease to a lesser degree under unfavorable conditions, due to slower and shorter xylogenesis (Rossi et al., 2008). This could make older trees more complacent, especially during warming periods (Carrer et al., 2015). In contrast, young trees tend to be more sensitive to climate and respond more rapidly to favorable and unfavorable conditions (Rozas et al., 2009). In addition, earlywood and whole ring width of *Pinus pinaster* were more sensitive to climate influence, while the response of latewood ring width to climate was stronger in older trees (Vieira et al., 2009). Young trees start the growing season earlier, thus a time window delay occurs between young and old trees during which wood cells of young trees integrate environmental signals. Young trees usually have a longer growing season and respond faster to climate conditions (Vieira et al., 2009). Fourth, root system: Under water-limited conditions, the lateral root spread of trees tends to be strongly related to the above-ground tree size (Magnani et al., 2002). This indicates that less-developed lateral roots in young (or small) trees would exacerbate water stress during a drier period (Rozas et al., 2009).
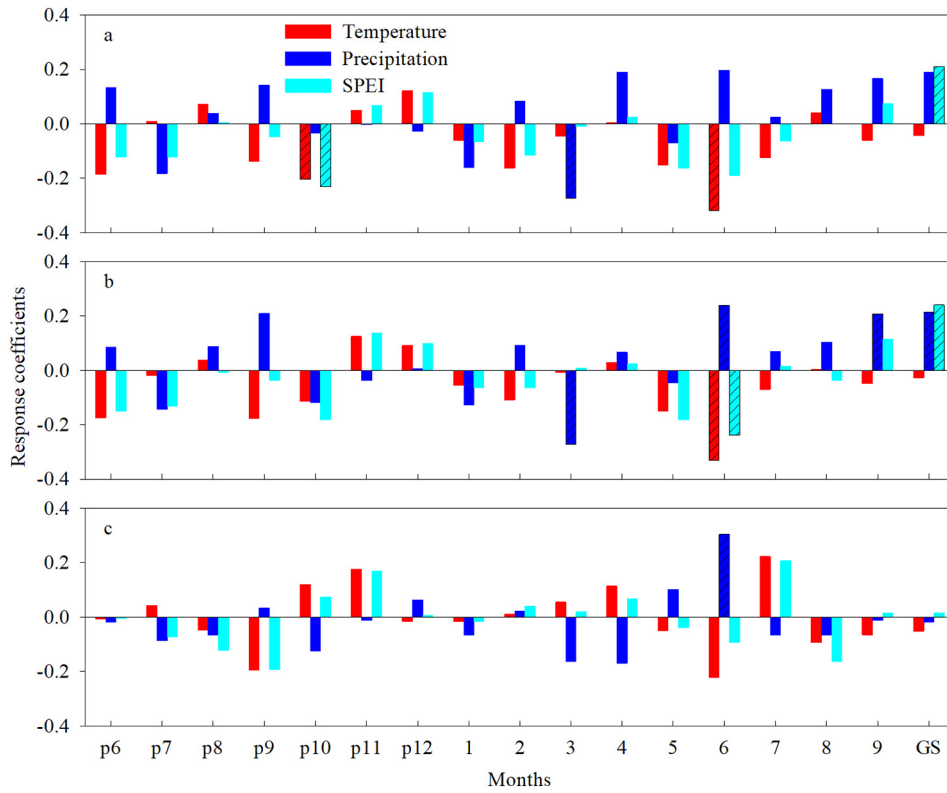
Fig. 8. Response function analysis between the (a) young, (b) middle, and (c) old chronology and monthly mean temperature (red bar), total precipitation (blue bar) and standardized precipitation-evapotranspiration index (SPEI, cyan bar) during the period 1959–2008. The bar with oblique lines represents the significance level at α = 0.05. The letter "p" in X tick label represents the previous year, e.g. "p6" is the previous June. The letter "GS" represents the growing season (May–Sep).

Also, Korean pine is a shallow root tree species, with less developed main roots but well developed horizontal lateral roots. In juvenile ages, when the root system is not fully developed, pine is more sensitive to drought caused by rising temperature. Fifth, physiological mechanism: Age is closely related to tree size and height, which can stimulate or reduce secondary growth due to higher light accessibility, reduced competition (Bond, 2000), increased hydraulic resistance in water transport, and increased respiration (Meinzer et al., 2011; Ryan and Yoder, 1997). Cambium activity and secondary growth are intrinsically controlled by gene expression and hormonal signals (Meinzer et al., 2011), and extrinsically by environmental factors, including temperature and precipitation (Deslauriers et al., 2008; Konter et al., 2016). Several physiological processes are affected by tree age, including reduced foliar efficiency, lower photosynthetic rates, delayed onset of reproduction, and movement (Rossi et al., 2008). Accordingly, the climatic sensitivity of tree-ring growth consistently increases during the juvenile phase of exponential height growth. The maximum sensitivity is reached when the tree reaches its maximum height limit
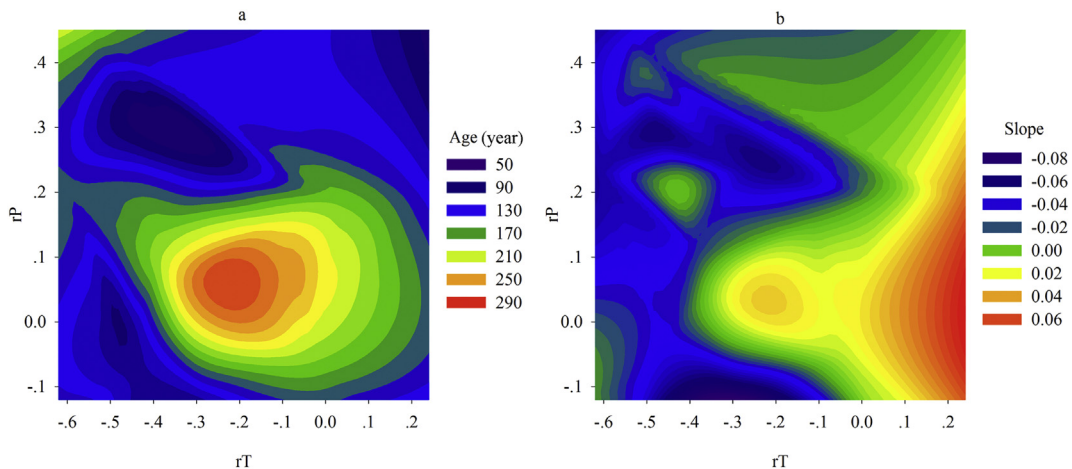
Fig. 9. Relationships between tree age (a) and the standardized BAI slope (b) and the correlation coefficients of chronologies and the growing season temperature (rT) and precipitation (rP). The slope is the slope of fitting line of the standardized BAI from 1983 to 2013.

(Martínez-Vilalta et al., 2007; Rozas et al., 2009). Therefore, varying physiological processes might result in various levels of climate sensitivity throughout a tree's lifespan.

We listed the five possible reasons that rising temperature caused the age-related growth decline, but we don't have detailed data to support each of them. Competition may be the most important reason for the decline of younger Korean pine. The Korean pine is a shade-tolerant species and thus susceptible to show a great impact of competition once a certain size/age level is reached. The competence is a sufficiently negative factor to trigger growth decline, such as other authors have described in other shade tolerant species (Becker et al., 1989; Linares et al., 2009; Linares et al., 2010). That is to say, if there is no global warming, the younger Korean pine growth still will decline because of competition. Nothing but the growth decline is even more serious because of climate warming. We cannot be sure of the respective contribution of competition and climate warming to the younger Korean pine growth decline. However, the ultimate cause of age-related growth decline induced by global warming is still unclear (Linán et al., 2012). Further studies are needed to determine the exact cause of the decline of younger Korean pine.

4.4. Implications for forest management under climate change

Our key finding was that climate warming, especially since the 1980s, induced a significant Korean pine growth decline in younger trees across its distribution area in China. This age-related climate response must be considered when forecasting Korean pine forest changes under future climate change. Growth decline of younger trees could possibly intensify with continued warming and result in reduced stand density and tree number in many locations. We do not anticipate a complete decline across the region given that some of our populations did not fully show decline and one increased. However, in the most vulnerable sites, it seems likely that species composition, forest structure, and ecosystem functions of the broadleaved Korean pine forests will change. This change will occur unless there is a reversal of moisture availability, which could compensate for the adverse effects of climate warming. As documented in western North America, climate warming and drought can lead to a growth decline and reduced tree vigor, which renders the forest prone to certain insect pests or plant disease outbreaks like bark beetle (Bentz et al., 2009). Growth decline might be more serious in northeast China than in the western US because younger trees could be more prone to die. The reduced vitality of young pines would limit the potential for Korean pine to recover from the adverse effects of climate warming by natural regeneration.

A significant shift in climate towards warmer, drier conditions has important implications for the ecosystem services that Korean pine provides to the region. Analyses between NDVI and BAI showed that vegetation productivity and Korean pine growth closely interacted in the northwestern Xiaoxing'an Mountains and southwestern Changbai Mountains during the period 1982–2006 (Fig. S6). This may have led to the observed forest productivity decline in recent decades in northeast China (Peng et al., 2011; Piao et al., 2011). If the observed trend continues, there is a good chance that the degree of future terrestrial carbon storage will decrease as predicted by Zhang et al. (2015a). The higher susceptibility of young Korean pine to warming compounds the potential for a long-term decline of the carbon sink in the region, particularly if no other species fill this niche. It is reasonable to consider that this change in the carbon sink could result in a positive feedback that accelerates climate warming.

We found age to be a crucial factor for tree growth and persistence under climate change. In contrast to recent assumptions, the decline in productivity was higher in juvenile ages than in mature ages. Since forest distribution models predict that young trees will have a higher productivity, this result would reverse the outcome of modelled forecasts in Korean pine growth. Age-related growth responses to climate warming need to be further studied in order to more fully understand the mechanisms and various impacts of warming on pine growth in northeast China.

Conflict of interest

The authors declare no conflict of interests.

Data availability

Data available from the International Tree-Ring Data Bank (ITRDB): https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring.

Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.08.393.

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