Old *Pinus massoniana* forests benefit more from recent rapid warming in humid subtropical areas of central-southern China

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Abstract Trees progress through various growth stages, each marked by specific responses and adaptation strategies to environmental conditions. Despite the importance of age-related growth responses on overall forest health and management policies, limited knowledge exists regarding age-related effects on dendroclimatic relationships in key subtropical tree species. In this study, we employed a dendrochronological method to examine the impact of rapid warming on growth dynamics and climatic sensitivity of young (40–60 years) and old (100–180 years) *Pinus massoniana* forests across six sites in central-southern China. The normalized log basal area increment of trees in both age groups increased significantly following rapid warming in 1984. Trees in young forests further showed a distinct growth decline during a prolonged severe drought (2004–2013), whereas those in old forests maintained growth increases. Tree growth was more strongly influenced by temperature than by moisture, particularly in old forests. Spring temperatures strongly and positively impacted the growth of old trees but had a weaker effect on young ones. Old forests had a significantly lower resistance to extreme drought but faster recovery compared to young forests. The "divergence problem" was more pronounced in younger forests due to their heightened sensitivity to warming-induced drought and heat stress. With ongoing warming, young forests also may initially experience a growth decline due to their heightened sensitivity to winter drought. Our findings underscore the importance of considering age-dependent changes in forest/tree growth response to warming in subtropical forest management, particularly in the context of achieving "Carbon Peak & Carbon Neutrality" goals in China.

Keywords Tree rings · *Pinus massoniana* · Age effects · Drought resilience · Subtropical forests · Rapid warming

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Introduction

In recent decades, climate warming has emerged as a crucial factor influencing the maintenance or alteration of forest morphology (Bauman et al. 2022; Martinez-Sancho et al. 2022). Previous studies have demonstrated that rapid warming significantly impacts tree vigor, species distribution, and the structure, function, and productivity of forests (McDowell et al. 2015; Rozenberg et al. 2020; Cherubini et al. 2021). Understanding how forests or trees respond to recent climate warming is key to predicting future forest dynamics and formulating effective forest management strategies (Carrasco et al. 2022; Zhang et al. 2023; Hu et al. 2024).

Annual rings are reliable indicators of growth dynamics and natural environments (Cherubini et al. 2021; Gao et al. 2022). Tree rings have been widely used to explore tree growth-climate relationships and the ways in which forests respond to climate change (Begovic et al. 2022; Martinez-Sancho et al. 2022; Zhang et al. 2023). Existing dendrochronological studies indicate that the impacts of climate warming on tree growth remain uncertain, even controversial (Camarero et al. 2015; Bauman et al. 2022). For example, while numerous studies report a generally positive effect of global warming on tree growth or forest productivity due to shifts in plant phenology and increased atmospheric CO_2 concentrations (Begovic et al. 2022; Huang et al. 2023), some studies show that rapid warming may also increase respiration rates and drought stress, negatively affecting tree growth or leading to large-scale mortality (McDowell et al. 2015; Bauman et al. 2022). Some studies also indicate that climate warming does not necessarily stimulate tree growth (Clark et al. 2010; Van der Sleen et al. 2015).

Ontogeny is one of the most significant factors influencing tree growth-climate relationships (Au et al. 2022; Begovic et al. 2022). Trees undergo physiological changes as they age and increase in size, developing different strategies to cope with changing environmental conditions (Carrer and Urbinati 2004; Martínez-Vilalta et al. 2007). The climatic sensitivity of forests/trees may undergo diverse changes with increasing age, including enhanced or weakened sensitivity, or no changes (Carrer and Urbinati 2004; Foster et al. 2014; Jiao et al. 2020; Peng et al. 2023). In general, the climatic sensitivity of radial growth increases with age until the tree reaches its maximum height, with some environmental specificity (Carrer and Urbinati 2004; Martínez-Vilalta et al. 2007). For instance, young trees exhibit greater sensitivity than older trees during dry summers due to their developing root systems and low water absorption capacity (Bond 2000; Carrer and Urbinati 2004). However, in temperature-limited environments, old trees may show higher climatic sensitivity than younger ones as a result of their increased use of resources to defend against stress and maintain survival (Carrer and Urbinati 2004). Alternatively, shorter growing seasons result in delayed basipetal movement of growth hormones (Rossi et al. 2008). Therefore, understanding the age-related growth responses of forests/trees to climate warming is crucial for predicting changes in forest productivity, ecosystem services, and carbon sequestration capacity (Camarero et al. 2015; Huang et al. 2021).

Pinus massoniana Lamb. is widely distributed in subtropical regions of China and is commonly used in afforestation in southern China. It plays an important role in the regional carbon balance, in wood production, and in ecosystem services (Ni et al. 2023; Zhang et al. 2023). The species has been widely used for tree ring-based paleoclimate reconstructions for the past two decades due to its sensitivity

to climate (Chen et al. 2012; Duan et al. 2012). Given its regional importance, there is a need to understand how its growth reacts to climate change (Liang et al. 2019; Jing et al. 2022b). However, age-dependent growth responses of *P. massoniana* to climate change remain unexplored. In this study, a dendrochronological investigation of *P. massoniana* on six sites in the Zhangjiajie region of Hunan Province was undertaken to: (1) determine the impact of rapid warming on the growth of trees in young and old age-class sites, (2) identify any differences in their growth-climate relationships and drought resilience, and (3) examine the variation of their climate-growth relationships over time.

Materials and methods

Study area and climate

This study was conducted in the Zhangjiajie region (29.38°–29.74° N, 109.77°–111.29° E) of Hunan Province in central-south China (Fig. 1). The area has a humid subtropical continental monsoon climate with hot rainy summers and cold dry winters. According to climate data (1976–2019) from the Sangzhi meteorological station (29.4° N, 110.17° E, 600 m a.s.l.), annual mean temperatures range from 15.7 to 17.2 ℃. The coldest and warmest months are January (4.8 ℃) and July (27.0 ℃), respectively (Fig. 2). Annual total precipitation ranges from 825 to 2,229 mm, with 68% occurring from April to August. The peak monthly mean temperature (July) and precipitation (June) are not synchronized (Fig. 2). The year 1984 marks an abrupt negative peak in temperature for the period 1976–2019. Since 1984, there has been a significant increase in annual mean temperatures at a rate of 0.2 ℃ per decade ($R^2 = 0.279$, $p < 0.05$). The region experienced a period of prolonged drought stress, as indicated by a high vapor pressure deficit and low relative humidity during 2004–2013, defined as a "drought period" (Fig. 2). The forest vegetation in this area mainly consists of subtropical evergreen conifers and broadleaved species. It is dominated by *P. massoniana*, admixed *Cunninghamia lanceolata* (Lamb.) Hook., *Liquidambar formasana* Hance, *Lithocarpus glabra* (Thunb.) Nakai, and *Cinnamomum camphora* (Linn.) Presl. The predominant soils are Ferralsols and Cambisols (Zhao et al. 2009).

Fieldwork and dendrochronological methods

Two age groups were established, young (40–60 years, YOUNG) and old (100–180 years, OLD) classes of *P. massoniana* forests, considering that the oldest tree was less than 200 years old. Three replicate sites were designated for each age group to mitigate the impact of site conditions on results. In July 2021, six forest stands with elevations ranging from
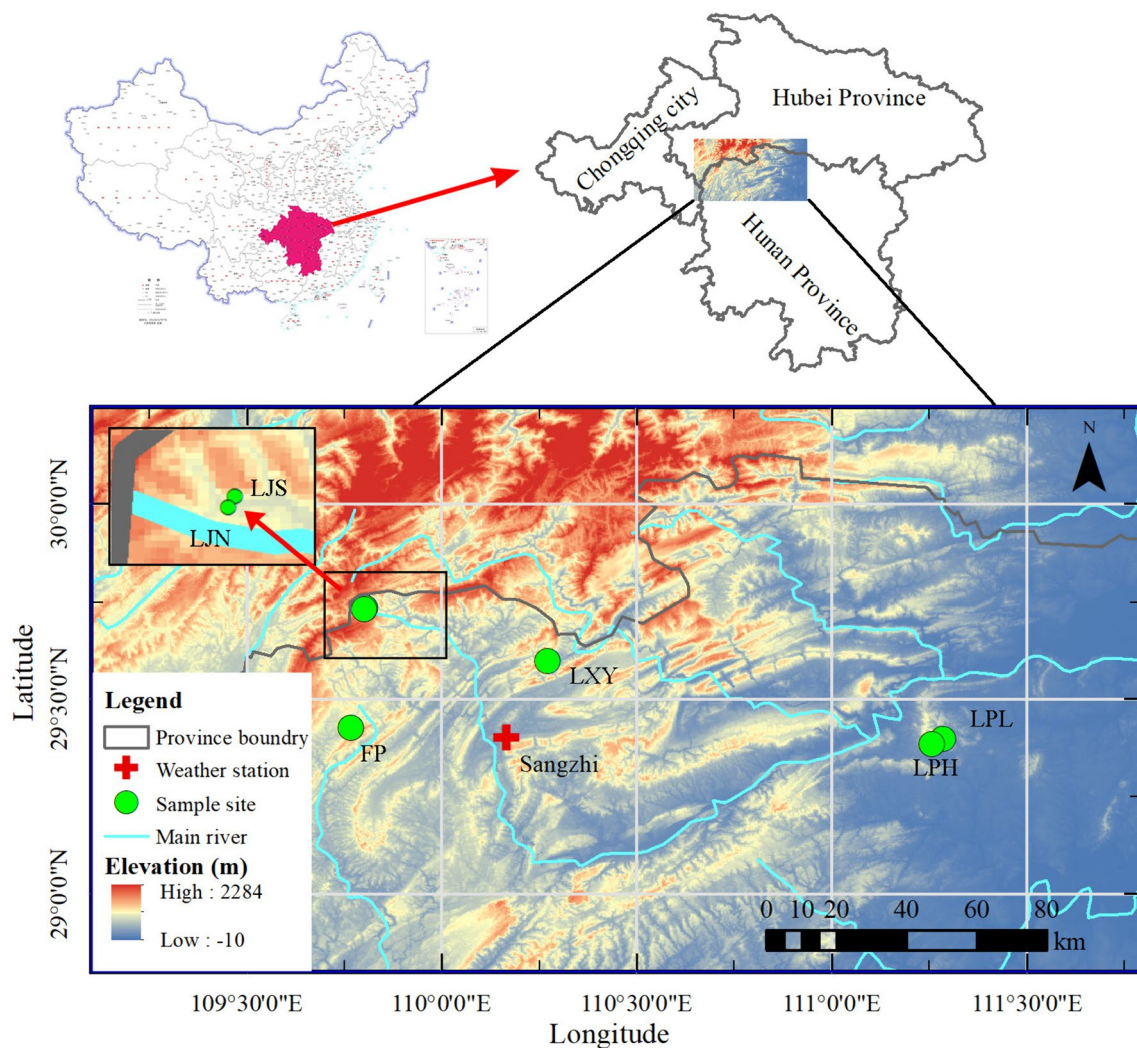
Fig. 1 Distribution of sampling sites and weather station. All maps used in this figure were prepared using the 2023 edition of the standard map of China [censor code: GS(2023)2767]. The map was released by the Ministry of Natural Resources of China and downloaded from National Platform for Common Geospatial Information Services (http://bzdt.ch.mnr.gov.cn/)

270 to 831 m were selected as sampling sites (Table 1). At each site, at least 20 healthy *P. massoniana* trees were sampled in stands with minimal disturbances. Two increment cores per tree were taken at breast height (1.3 m) using a 5.15 mm inner diameter increment borer (Haglöf, Sweden). In some cases, only one core was sampled to reduce the damage to particularly small trees. All cores were numbered, stored in straws, and transported to the laboratory.

In the laboratory, all samples were air-dried and glued onto wooden mounts. Core surfaces were sanded with progressively finer grades of sandpaper until tree-ring boundaries were clearly visible under the microscope. Each tree's annual rings were visually cross-dated to identify possible absent or false rings and assigned an accurate calendar year using the skeleton-plot method (Stokes and Smiley 1968). Ring widths were measured to an accuracy of 0.01 mm using the LINTAB™ 6 tree-ring width measuring system (Frank Rinntech, Germany). The accuracy of measurements and cross-dating was statistically tested with the COFECHA program (Holmes 1983). Samples younger than 15 years or with poor cross-dating quality were excluded from the study. A total of 287 cores from 164 trees were used for further analysis (Table 1).

Raw ring width sequences were detrended by fitting a negative exponential curve or linear regression function (ModNegExp) with the "dplR" package (Bunn 2008) in R software (R Core Team 2021). All tree-ring indices from each site were then combined into a single standard chronology using Tukey's biweight robust mean to minimize the effects of abnormal values (Fig. 3) (Cook 1985). The arithmetic mean method was used to calculate the regional tree-ring chronologies of *P. massoniana* for

Fig. 2 a, b Climatic diagrams for the study area and variations in (**c**) precipitation, **d** mean temperature, **e** vapor pressure deficit (VPD), and **f** relative humidity 1976–2019. The straight lines in **c–f** represent linear fitted trends before and after the abrupt increase in mean temperatures in 1984. The *R*-squared and slope (*k*) of each model are listed. The yellow-shaded area highlights a long-term drought during 2004–2013. *T*, mean temperature; *Tmin*, minimum temperature; *Tmax*, maximum temperature; *P*, precipitation. *$p < 0.05$
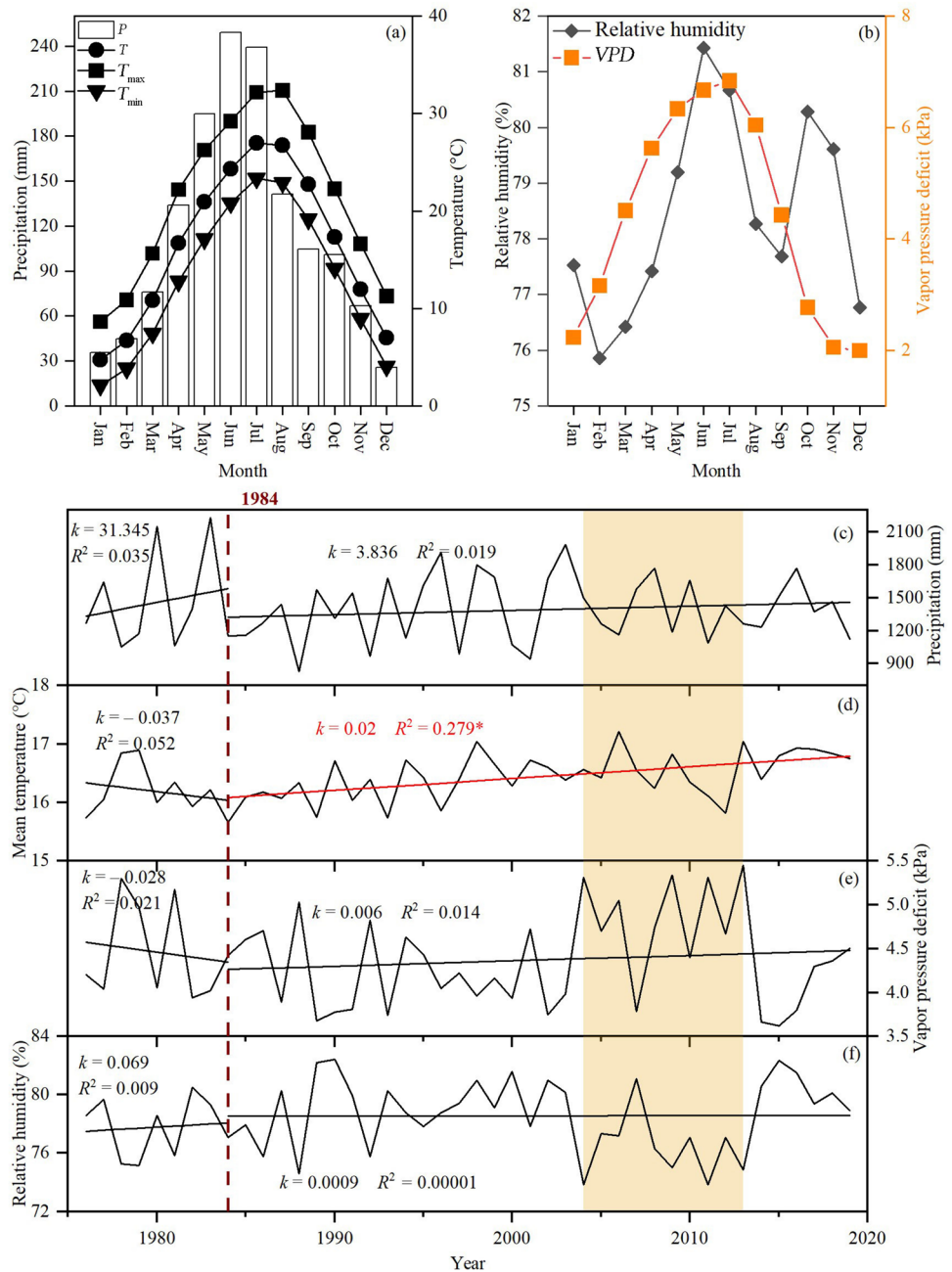

Table 1 Site descriptions and statistics for *Pinus massoniana* chronologies from six sampling sites

Site code	Latitude	Longitude	Ele. (m)	C/T	Age ± SD	MRW ± SD (mm)	Rbar	EPS
FP	29.425° N	109.767° E	642	69/38	49 ± 23	6.30 ± 2.20	0.49	0.90
LJN	29.731° N	109.800° E	698	67/36	40 ± 22	4.04 ± 2.18	0.51	0.94
LJS	29.735° N	109.802° E	698	54/30	46 ± 13	4.89 ± 2.45	0.41	0.93
LPH	29.384° N	111.259° E	831	30/21	111 ± 84	2.65 ± 1.84	0.33	0.72
LPL	29.397° N	111.286° E	270	35/20	101 ± 83	4.47 ± 3.34	0.45	0.80
LXY	29.597° N	110.272° E	654	32/19	120 ± 81	2.53 ± 1.37	0.35	0.86

C/T = cores/trees, Rbar = series intercorrelation, EPS = expressed population signal. Rbar and EPS are calculated for 1976–2019
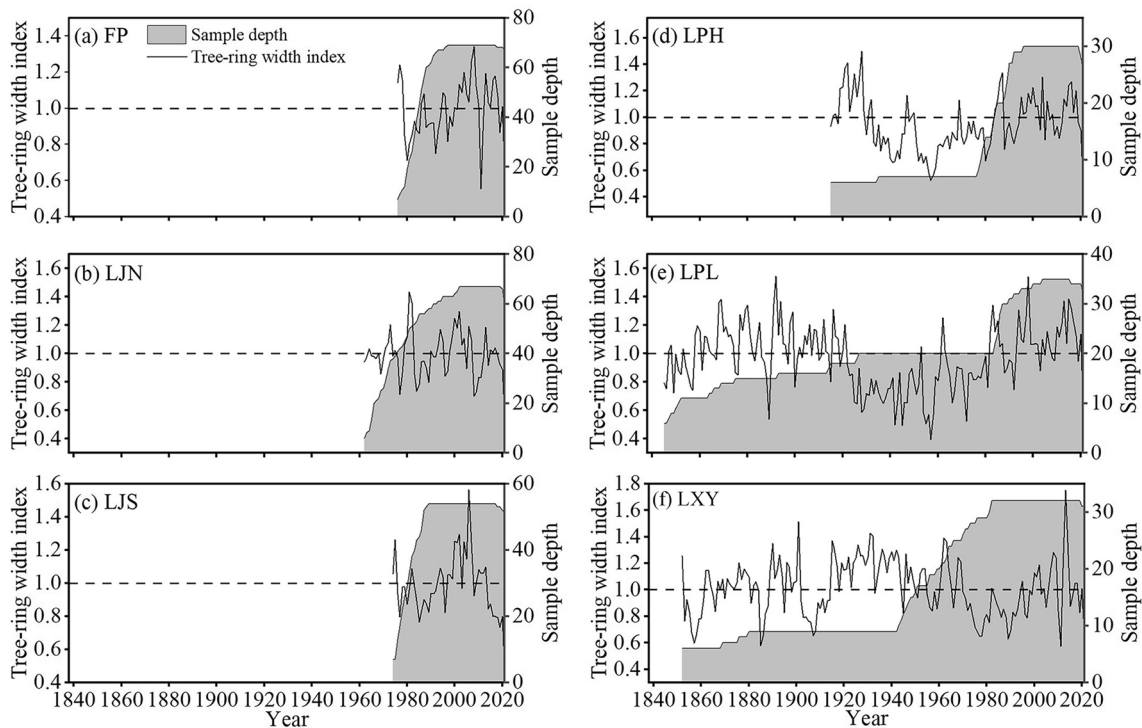
Fig. 3 Tree-ring width index of *P. massoniana* at six sampling sites. Young age-class sites include FP, LJN, and LJS; old age-class sites include LPH, LPL, and LXY. The grey-shaded area indicates the number of cores

young (YOUNG) and old (OLD) age classes. Statistical characteristics of the ring width chronologies for each site are shown in Table 1.

Basal area increment measurements

Basal area increment (*BAI*) provides a more accurate representation of growth than tree-ring width because it eliminates variations in growth due to increasing stem circumference and size adjustments in growth (Zhu et al. 2018a; Jing et al. 2022b). The ring width measurements were converted to *BAI* using the formula:

$$BAI = \pi \left(R_n^2 - R_{n-1}^2 \right) \tag{1}$$

where, R_n^2 and R_{n-1}^2 are the squared stem radial increments corresponding to rings formed in years n and $n-1$, respectively. After implementing the pith offset (Rozas 2003), raw ring widths were converted to *BAI* values using the BIAPlt software (available at http://www.ldeo.columbia.edu/treer ing-laboratory/resources/software). For a more intuitive comparison of *P. massoniana* BAI growth at different sites, the *BAI* sequence was log-transformed and normalized using the Z-core method (Jing et al. 2022b).

Climate data

Instrumental climate data from the nearby Sangzhi Meteorological Station were obtained from the China Meteorological Data Service Centre (http://data.cma.cn). Monthly climate data from 1976 to 2019 were used in this study because the shortest chronology started in 1976. Climate variables included total precipitation (*P*), relative humidity (*Rh*), and mean (*T*), minimum (*Tmin*), and maximum (*Tmax*) temperatures.

Vapor pressure deficit (*VPD*), the amount of vapor stored in the air until the saturation point at a given temperature is reached, is a proven indicator of drought (Martinez-Sancho et al. 2022). Monthly *VPD* data were calculated from the monthly mean temperature and relative humidity using the formula:

$$VPD = 0.61078 \times e^{\frac{17.27 \times Ta}{Ta + 237.3}} \times (1 - Rh) \tag{2}$$

where *Ta* is air temperature, and *Rh* is relative humidity.

Seasonal climate data were defined as previous winter (*pWin*, previous December–current February), current spring (*SPR*, March–May), current summer (*SUM*, June–August), and current autumn (*AUT*, September–November).

Extreme drought events and indices of resistance and recovery

Based on previous studies (Jing et al. 2022b) and our correlation analysis, we found that autumn drought plays an important role in tree growth. Extreme drought years were characterized based on the averaged autumn *VPD* values (Martinez-Sancho et al. 2022). First, the first order differences of *VPD* in autumn from 1976 to 2019 were calculated. Years in the first order differences series with values higher than the mean plus 1.5 times the standard deviation were defined as extreme drought years (Fang and Zhang 2019; Zhu et al. 2023). The years 1988, 1990, 2001, and 2019 were identified as extreme drought years.

The ability of trees to continue growing under drought stress is represented by the resistance (*Rt*), which is the reduction of radial growth during drought compared to before the drought. The capacity of trees to restart growth following drought is represented by the recovery (*Rc*), the post-drought radial growth compared to that during the drought (Lloret et al. 2011; Fang and Zhang 2019; Zhu et al. 2023). Tree resilience to drought was estimated using the two components (*Rt* and *Rc*), calculated for each tree following the formulas provided by Lloret et al. (2011):

$$Rt = Dr/PreDr \tag{3}$$

$$Rc = PostDr/Dr \tag{4}$$

where *Dr* indicates the ring width indices or raw ring widths in the drought year, and *PreDr* and *PostDr* indicate the mean ring width indices or raw ring widths during the three years before and after the drought. The year 2019 was not considered in calculating drought resilience as data for the three subsequent years were not available.

Statistical analysis

A segmented test was conducted to examine long-term trends in temperature using the R package 'segmented' (Muggeo 2008). The year 1984 was identified as an abrupt point of temperature increase between 1976 and 2019. A linear regression model was used to investigate temporal trends in climate variation and radial growth before and after 1984. Pearson correlation coefficients (*R*) between main climatic variables and ring width chronologies were calculated to reveal the impact of climate change on tree growth. In this study, growth-climate relationships were calculated for a 12-month period from the previous December to the current November, and for a 4-season period from the previous winter to the current autumn. Moving correlation analysis between seasonal climate and tree growth was also applied to the period 1976–2019 with a 20 year moving window to detect temporal changes in growth-climate relationships. Correlation and moving correlation analyses were performed using the R package 'treeclim' (Zang and Biondi 2015).

Results

Growth characteristics and drought resilience of *P. massoniana*

The LXY chronology showed a positive correlation with the LPH ($R = 0.36$, $p < 0.05$) and LPL ($R = 0.4$, $p < 0.01$) chronologies. Additionally, the LPL ($R = 0.55$, $p < 0.01$) was positively correlated with the LPH chronology ($R = 0.4$, $p < 0.01$). The LJS and LJN chronologies also demonstrated a positive correlation ($R = 0.51$, $p < 0.01$) (Table 2). The normalized log *BAI* sequences revealed that tree growth on old and young age-class sites significantly increased after the onset of rapid warming in 1984. Trees in old age-class sites still maintained a similar trend of growth enhancement during the long-term severe drought period 2004–2013, while trees in young age-class sites showed a slight decline in the dry period (Fig. 4). The OLD group trees have a significantly lower resistance ($p < 0.0001$) to drought but higher recovery ($p < 0.05$) than the YOUNG group trees (Fig. 5).

Relationship between tree growth and climate

Tree growth in old and young age classes had a strong positive correlation with temperatures (*T*, *Tmax*, and *Tmin*) in January to May and the current spring, especially for trees

Table 2 Pearson correlation (*R*) matrix of tree-ring chronologies among six sites during 1976–2019

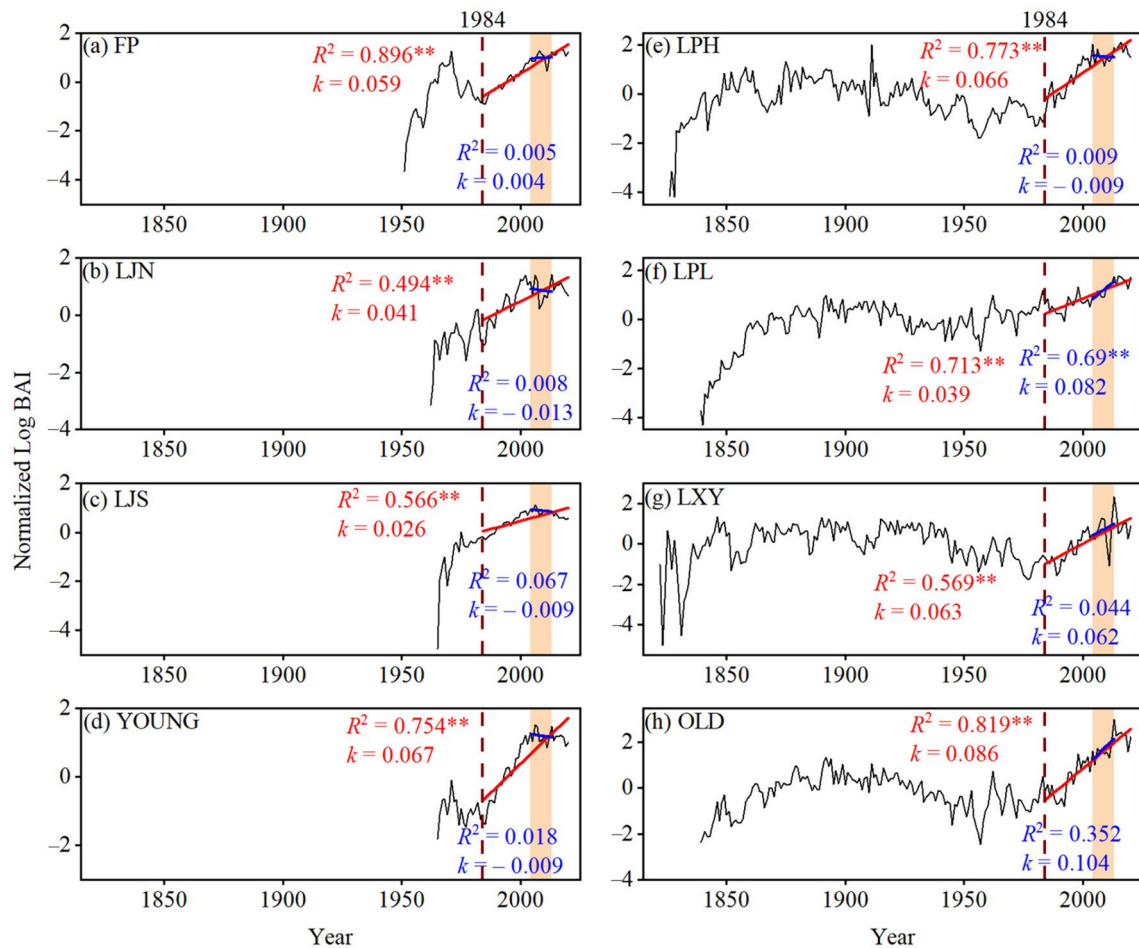|	FP	LJN	LJS	LPH	LPL	LXY
FP	1					
LJN	−0.09	1				
LJS	0.1	0.51**	1			
LPH	0.4**	0.08	0.1	1		
LPL	0.04	0.08	0.15	0.55**	1	
LXY	0.47**	0.27	0.33*	0.36*	0.4**	1

*$p < 0.05$, **$p < 0.01$

Fig. 4 Temporal variation of normalized log basal area increment (*BAI*) for *Pinus massoniana* in the study area. Growth patterns for young and old age classes are fitted by linear regressions from 1984 to 2020 (red) and 2004 to 2013 (blue). 1984 marks the abrupt negative peak of the mean annual temperature. Yellow-shaded areas (2004–2013) indicate drought years. The *R*-squared and slope (*k*) of each model are listed. The data for YOUNG and OLD groups were obtained by averaging the raw *BAI* values corresponding to the same age-class sites and then logarithmically normalizing them. **$p < 0.01$

in old age-class sites (Fig. 6). However, trees in old and young age classes responded differently to *Tmin* in September, with a negative correlation ($p < 0.05$) with growth in the young LJN and LJS sites but a weak correlation with old age-class sites (Fig. 6).

Drought in autumn had a strong effect on the radial growth of trees in old age-class sites, but no effect on the growth of trees in young age-class sites (Fig. 6). The *Rh* and *VPD* in November had a significant ($p < 0.05$) positive and negative correlation with the radial growth of trees in old age-class sites, respectively (Fig. 6). Precipitation had slight impacts on radial growth on all sites. The consistency of tree growth-climate relationships on old age-class sites was stronger than on young age-class sites.

Temporal stability of tree growth-climate relationships

A moving correlation analysis revealed a clear shift in growth-climate relationships around 1984, a year of rapid warming (Fig. 7). The relationships between temperatures (*T* and *Tmin*) during the current spring and tree growth on the OLD age group maintained a stable, and positive correlation. However, the relationship shifted from a significant ($p < 0.05$) positive correlation to a weak one in the YOUNG age group (Fig. 7). The negative impacts of *Tmin* in the current autumn on tree growth in the OLD and YOUNG age groups strengthened in recent decades, with the OLD age group trees shifting from positive ($p < 0.05$) to negative correlations, and the YOUNG age group trees

Fig. 5 Boxplots of mean resistance (*Rt*) and recovery (*Rc*) indices of trees in young and old age classes to extreme droughts in 1988, 1990, and 2001; resistance and recovery indices are calculated using raw ring widths and tree ring indices. The data for the YOUNG and OLD groups are a mixture of samples from the young and old age-class sites. *$p < 0.05$, ****$p < 0.0001$
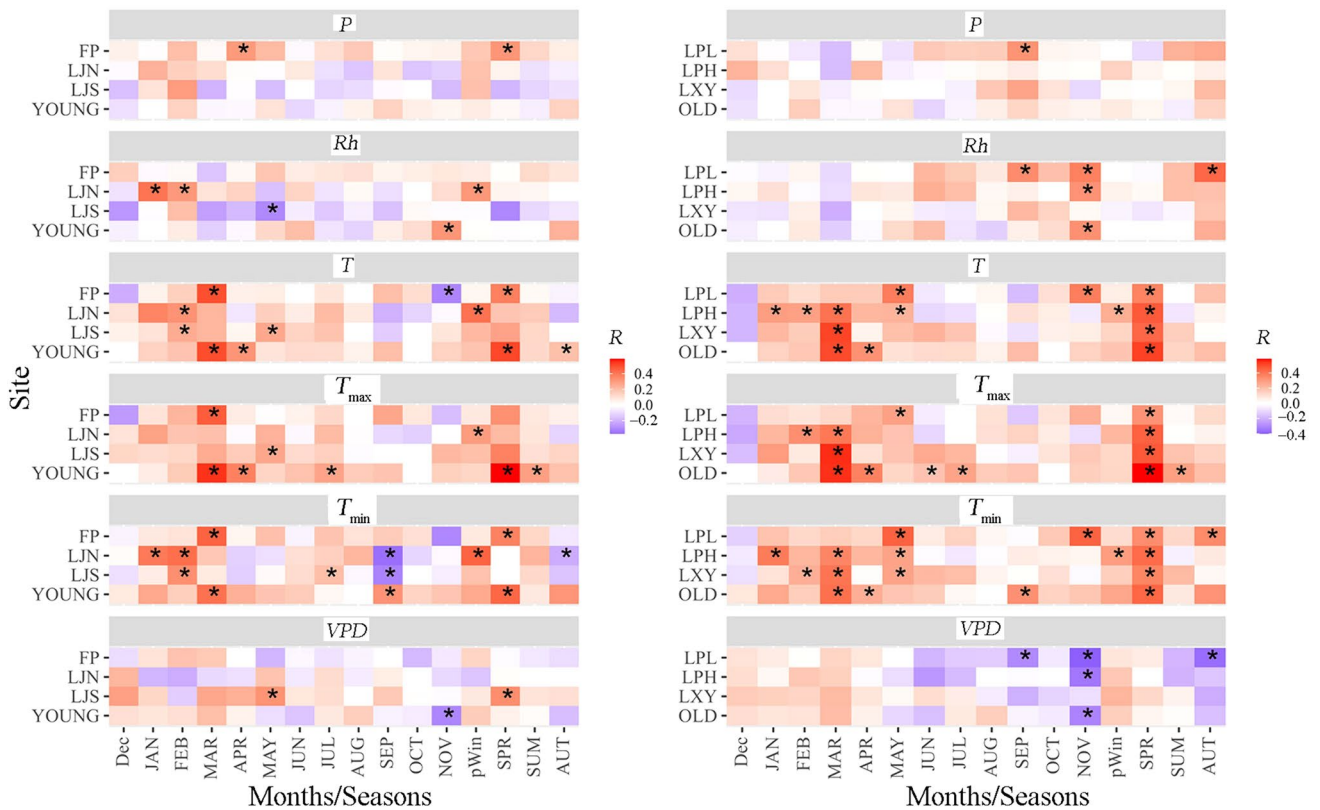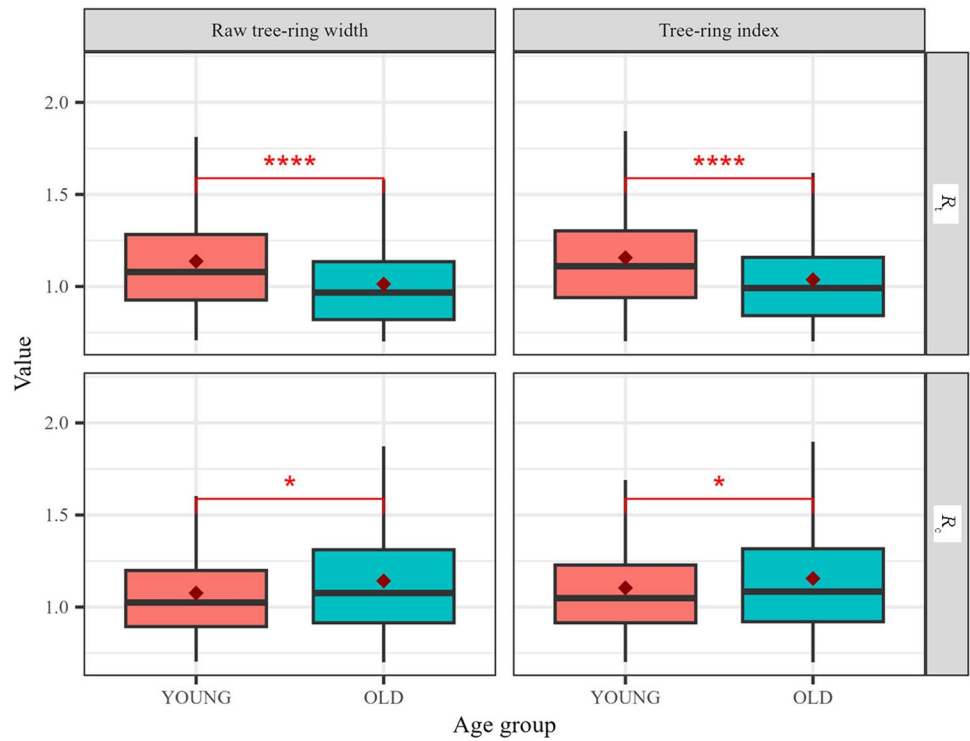

Fig. 6 Correlations between tree ring width indices and monthly (from the previous December to the current November) and seasonal climate variables. YOUNG and OLD mean regional tree-ring chronologies of *Pinus massoniana* at young and old age-class sites.

P, precipitation; *Rh*, relative humidity; *VPD*, vapor pressure deficit; *T*, mean temperature; *Tmax*, maximum temperature; and *Tmin*, minimum temperature; *pWin*, previous winter; *SPR*, current spring; *SUM*, current summer; *AUT*, current autumn. *$p < 0.05$
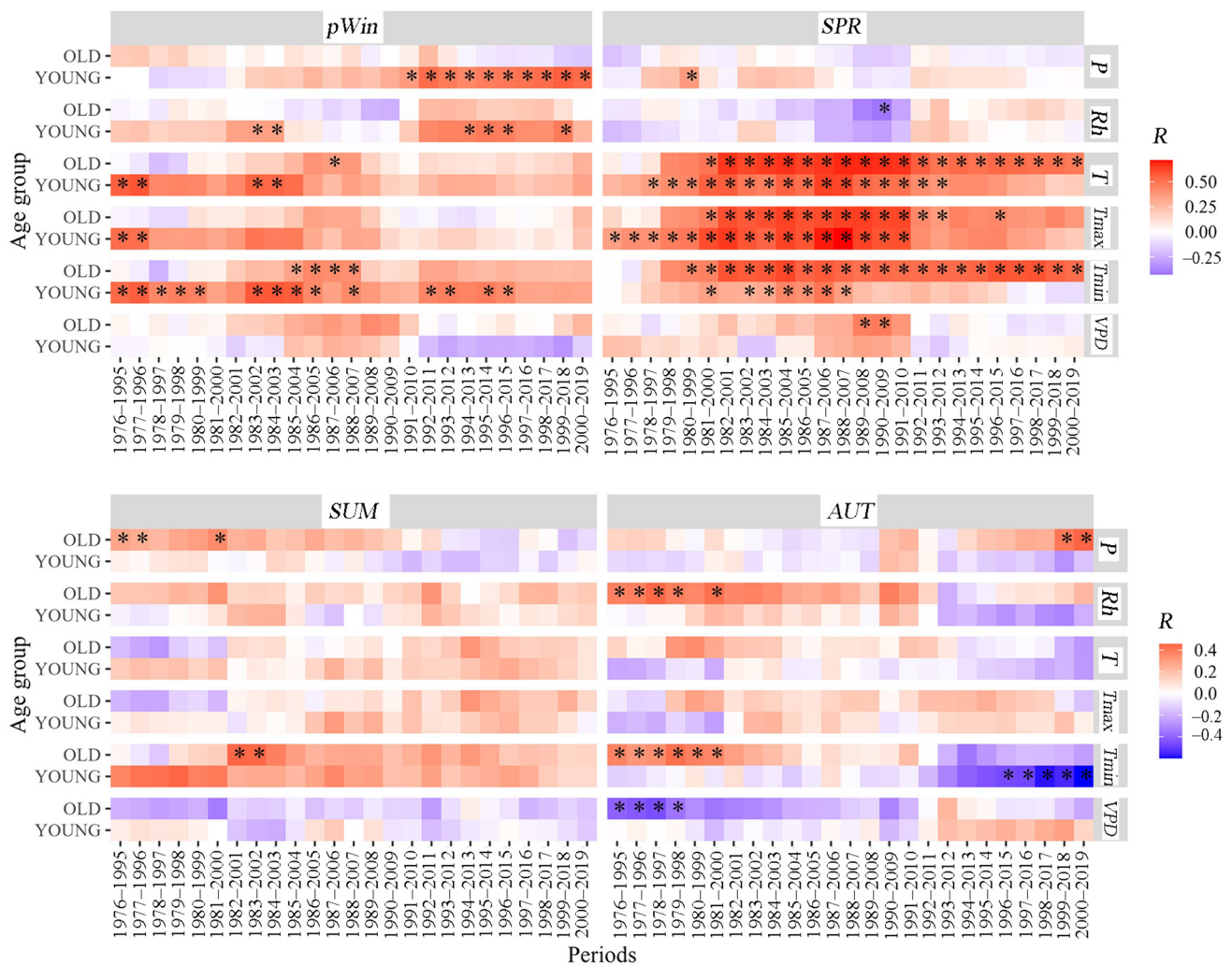
Fig. 7 Moving correlation analysis between tree-ring chronologies and main seasonal climate factors during 1976–2019. Pearson correlation coefficients were computed for 20-year moving windows. YOUNG and OLD mean regional tree-ring chronologies of *Pinus massoniana* at young and old age-class sites. *P*, precipitation; *Rh*, relative humidity; *VPD*, vapor pressure deficit; *T*, mean temperature; *Tmax*, maximum temperature; and *Tmin*, minimum temperature; *pWin*, previous winter; *SPR*, current spring; *SUM*, current summer; *AUT*, current autumn. *$p < 0.05$

transitioning from weak correlations to negative ($p < 0.05$) ones.

The correlation between previous winter precipitation and tree growth in the OLD age group gradually shifted from weak positive to negative in recent decades. In contrast, it turned from weakly negative to significantly ($p < 0.05$) positive for trees in the YOUNG age group (Fig. 7). The negative impacts of relative humidity in the current autumn for trees in both YOUNG and OLD age groups strengthened with time; specifically, their correlations shifted from positive to negative or from significantly positive to weakly positive. The correlation between autumn *VPD* and tree growth in the YOUNG and OLD age groups was gradually opposite to the relationships between autumn *Rh* and tree growth (Fig. 7).

Discussion

Growth enhancement of young and old *P. massoniana* forests

The normalized log *BAI* of *P. massoniana* significantly increased after 1984 across all sites. This growth enhancement has been reported by Li et al. (2020), and similar patterns have been observed with other subtropical tree species (Carrasco et al. 2022). These studies are in agreement with the general belief that subtropical forest ecosystems are likely to benefit or at least withstand rising temperatures (Boisvenue and Running 2006; Reyes-Fox et al. 2014). In recent decades, increasing atmospheric CO_2 has been an important factor contributing to enhanced

growth (Camarero et al. 2015; Zhu et al. 2021). As early as 1984, Lamarche et al. (1984) attributed the improved growth of high elevation *Pinus aristate* Engelm and *Pinus longaeva* Bailey in the western United States during the late twentieth century to higher atmospheric CO_2. Elevated CO_2 levels may increase photosynthetic rates and light energy utilization efficiency (Reyes-Fox et al. 2014) and improve intrinsic water-use efficiency (Martinez-Sancho et al. 2022). Additionally, temperature has been identified as a key factor driving cambium reactivation in conifers in the Northern Hemisphere (Gao et al. 2022; Huang et al. 2023). Rapid warming promotes an earlier start and later finish of cambium activities, extending the growing period, which could be another important factor contributing to the growth enhancement of *P. massoniana* (Duan et al. 2012). Gao et al. (2022) also found that the prolonged growing season from climate warming significantly promoted growth in humid areas but not arid ones. Other possible reasons for growth enhancement of *P. massoniana* require further investigation. For example, the El Niño-Southern Oscillation has been shown to significantly increase the growth of *P. massoniana* in subtropical China by delaying the arrival of summer monsoons (Li et al. 2020). Moreover, no detrending process was applied to BAI data in this study. The substantial growth improvement of trees in young age-class sites may be partly attributed to the age-related trend in BAI growth. According to the typically sigmoidal pattern of BAI growth in individual trees, this rapid growth increase in young trees could occur because of an increasing canopy as the trees age (Johnson and Abrams 2009).

Furthermore, the radial growth of trees in young age-class sites showed a clear decline during the long-term drought of 2004–2013, while trees in old age-class sites basically enhanced growth. It suggests that trees in old age-class sites still benefit from warming, even under severe drought. This is understandable because trees in young age class exhibit increasing sensitivities to winter droughts as climate warming intensifies, while trees in old age class do not (Fig. 7) (Carrer and Urbinati 2004; Au et al. 2022). Winter drought may weaken tree hydraulic-carbohydrate systems, resulting in slower growth in the following growing season (Earles et al. 2018). A plausible explanation is that older trees have a higher water absorption capacity and can access water from deeper soil layers because of their more developed and extensive root systems (Puhe 2003). To some extent, these root systems buffer the adverse effects of winter drought (Au et al. 2022; Zhu et al. 2023). Additionally, competition is a major factor affecting tree growth. Competition for resources between neighboring trees adversely affects growth and may even lead to decline or death, especially for saplings with limited competitiveness (Gómez-Aparicio et al. 2011; Liang et al. 2019).

However, our results do not agree with previous studies in China's subtropical forests that reported a significant decline in radial growth of *P. massoniana* in recent decades due to warming-related drought (Li et al. 2019; Jing et al. 2022b). Elevated temperatures may enhance respiration and drought stress, increasing the consumption of limited water resources and resulting in a decline in growth (Zhu et al. 2018a; Jiao et al. 2020). In contrast to these studies, our study area experienced lower annual temperatures that did not exceed the optimal threshold for limiting *P. massoniana* growth. Furthermore, the contrasting findings may also be attributed to differences in intensity of solar radiation (photosynthetic capacity) (Muller-Landau et al. 2021) and soil characteristics (water and nutrient holding capacity) between different regions (Li et al. 2019; Jing et al. 2022b). There are still some intriguing possibilities to explore, such as a comparative study between healthy and declining pine forests to verify whether the evidence of growth decline on sensitive sites exposed to extreme drought and thermal stress is conclusive. More research is needed to thoroughly understand the processes and implications of warming on *P. massoniana* growth in southern China.

Growth-climate relationships of *P. massoniana* in young and old forests

The radial growth of *P. massoniana* was more strongly associated with temperature than precipitation. This is consistent with studies on *P. massoniana* in other subtropical areas of China (Chen et al. 2012; Duan et al. 2012) and other temperate tree species in northeast China (Zhu et al. 2020). Precipitation is typically not a limiting factor for tree growth in humid environments, especially in mountainous regions (Duan et al. 2012; Jevšenak et al. 2021). Our study area, characterized by a humid subtropical climate with 1412 mm of rain annually, satisfies the water needs for tree growth. This is why existing paleoclimate reconstructions based on tree ring widths of *P. massoniana* in subtropical areas of China are primarily focused on temperature rather than precipitation or drought indices (Chen et al. 2012; Duan et al. 2012).

Spring temperatures, especially in March, had a significant positive effect on *P. massoniana* growth, particularly for trees in old age-class sites (Fig. 6). This result agrees with the observation that warm spring conditions boost *P. massoniana* growth (Duan et al. 2012; Fu et al. 2017). A rise in spring temperatures is typically associated with an early onset of cambial activity (Duan et al. 2012) and high photosynthesis (Reyes-Fox et al. 2014). Warm, early spring temperatures promote the activity of microorganisms, enhancing litter decomposition and nitrogen mineralization and thereby releasing more nutrients to support growth (Fu et al. 2017). High early-spring temperatures also protect trees from frost

damage (Duan et al. 2012). Trees in old age-class sites were more sensitive to spring temperatures than those in young age-class sites because they have well-developed organs and are more able to take advantage of favorable early spring conditions. For example, the extensive foliage and deep root systems of older trees allow more efficient access to water and nutrients and to synthesize photosynthates (Bond 2000; Puhe 2003). In addition, older trees, having experienced numerous spring seasons, might have developed specific resilience to typical spring temperature changes. This adaptation could demonstrate a positive relationship with spring temperatures. For example, older trees exhibit more stable and predictable phenological patterns, including the timing of bud burst and flowering, which are often triggered by temperature cues (Rollinson and Kaye 2012). This stability leads to tree growth being more synchronized (strong positive correlation) with spring temperatures.

Furthermore, September VPD exhibited a strong negative correlation, and Rh exhibited a strong positive correlation with *P. massoniana* trees in old age-class sites, but no correlation with trees in young age-class sites. This suggests that older trees were more sensitive to drought towards the end of the growing season. A plausible explanation is that younger trees store carbon during periods of high stress and allocate it more towards respiration than growth, potentially increasing resistance to external mortality factors (McDowell et al. 2011) and avoiding drought-induced carbon starvation (Huang et al. 2021). However, older trees may prioritize allocating resources to maintaining existing structures and metabolic functions over active growth (Malhi 2012). Towards the end of the growing season, the transition to dormancy and the need to store resources for winter may alter resource allocation, potentially making older trees more sensitive to water stress (Schultz et al. 2013). Additionally, drought stress toward the end of the growing season may impact various phenological processes influenced by water availability such as leaf senescence and nutrient reabsorption, making older trees more vulnerable (Estiarte and Peñuelas 2015). Moreover, differences in the growth-climate relationships of *P. massoniana* among sites within the same age group might be attributed to heterogeneous microenvironments caused by topography and elevation, including factors such as solar radiation, air humidity, and soil properties (Gómez-Aparicio et al. 2011; Zhu et al. 2018b; Rozenberg et al. 2020). These factors could immediately or eventually affect radial growth, leading to diverse tree growth responses to climate among sites (Zhu et al. 2018a, 2021; Jing et al. 2022a). For example, trees at the high-elevation LPH site exhibited a significant positive correlation with temperature from January to March, whereas trees at the low-elevation LPL site showed a weak correlation. This is in agreement with that high-elevation trees are usually more sensitive to temperature than those at lower elevations (Rozenberg et al.

2020; Jing et al. 2022a). Additionally, trees on the shady slope at the LJN site had positive correlations with temperature and Rh in winter. In contrast, trees on the sunny slope at the LJS site were weakly correlated with these factors. This difference may be related to variations in winter microclimates between sunny and shady slopes, including factors like sunshine hours, temperature, evapotranspiration, and snow cover (Branson and Shown 1990; Tang and Fang 2006).

Drought resilience of young and old *P. massoniana* forest trees

There were significant differences in drought resistance and recovery between young and old trees. It is important to clarify that older trees are generally considered more resistant to drought than younger ones due to their more extensive root systems and greater accumulation of water and nutrient reserves (Puhe 2003; Zhu et al. 2023). However, we found that trees in the YOUNG group exhibited higher resistance to but lower recovery from drought compared to trees in the OLD group (Fig. 5). This is in agreement with research on ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) in remote forests of the Rocky Mountains (Lloret et al. 2011) and certain angiosperm and gymnosperm species across North and South America, Eurasia, Africa, and Oceania (Au et al. 2022).

The lower resistance in older trees may indicate a reduction in vitality, consistent with the extensively documented age-related reduction in tree growth (Lutz et al. 2018) and the frequently disproportionate mortality of older trees (Foster et al. 2014; McDowell et al. 2015). This could also reflect growth and survival tradeoffs, whereby stress-induced growth reductions in older trees reflect a survival strategy (Dobbertin 2005; Körner 2017; Piovesan and Biondi 2021). Another explanation involves non-structural carbohydrates: during periods of drought, older trees may have a bias to converting non-structural carbon to starch for recovery growth, while younger trees may convert it to soluble sugars to defend against the negative effects of drought (Dietze et al. 2014; Martínez-Vilalta et al. 2016).

Moreover, older trees, being more resilient, may have experienced cumulative stress over the years such as damage from pests, diseases, or previous drought events. This accumulated stress could make them more susceptible to additional stressors, including drought, especially toward the end of the growing season (Niinemets 2010). As noted previously, older trees allocate resources differently than younger ones (Malhi 2012), potentially making older trees more vulnerable to drought (Schultz et al. 2013). However, older trees usually have a larger storage capacity, accumulating considerable nutrients, carbohydrates, and water. These resources enable the canopy and the root system to continue

functioning or to re-establish after the stress period, resulting in better recovery from extreme drought (Linares et al. 2010; Begovic et al. 2022).

The tradeoff between resistance and recovery can be related to the mathematical relations between *Rt* and *Rc*. A significantly decreased *Dr* in the presence of similar *PreDr* and *PostDr* levels will invariably produce low *Rt* and high *Rc* values. Galiano et al. (2011) found that if both resistance and recovery following periods of drought partly depend on the amount of accumulated reserves, a tradeoff between resistance and recovery might happen, leading to high resistance and low recovery, or vice versa. The observed enhanced tree growth in old age-class sites could be attributed to high recovery. Nevertheless, it is important to note that the response of trees to drought stress is complex and can vary significantly based on species, environmental conditions, and individual tree characteristics. More research at a larger regional scale is needed to test the findings of age-related differences in the responses of *P. massoniana* to extreme drought and the mechanisms behind them.

Temporal variability in dendroclimatic relationships of *P. massoniana*

The positive correlations between winter-spring temperatures and tree growth on young age-class sites gradually weakened after the onset of rapid warming in 1984. This reduced growth sensitivity to temperature is known as the "divergence problem" (D'Arrigo et al. 2008). Wang et al. (2014) found that five subtropical tree species, including *P. massoniana*, *Pinus taiwanensis* Hayata, *Schima superba* Gardn et Champ., *C. lanceolata* (Lamb.) Hook., and *Castanopsis eyrei* (Champ. ex Benth.) Tutcher, in southeastern China have a weaker response to temperatures in recent decades than in the early decades of the twentieth century.

A high winter-spring temperature can increase drought stress by accelerating air/soil water evaporation and plant transpiration (Atkin et al. 2007). In addition, photosynthetic enzyme activity may decrease as temperatures increase beyond a particular threshold (Lindner et al. 2010), resulting in a narrow growth ring. Increased water use efficiency may also be a key reason for the diminished effect of temperature on trees (McMahon et al. 2010; Van der Sleen et al. 2015). The results of a study by Cai et al. (2020) show similar responses by *P. massoniana* at low elevations, whereas at high elevations, it showed a positive correlation with temperature. Trees typically benefit from warming in cold, high elevation environments (Zhu et al. 2018a; Rozenberg et al. 2020). The strong correlation between temperature and tree growth at high elevations suggests that warming may eventually encourage the expansion of the tree line and provide a more favorable environment. However, the "divergence problem" was not found in older *P. massoniana* trees (OLD

group), possibly as a result of their weaker sensitivity to warming-related drought (Carrer and Urbinati 2004; Au et al. 2022).

In general, climate warming significantly increased the carbon fixation of *P. massoniana*, especially by older forests, which indicates that they benefit more from climate warming (Begovic et al. 2022) or suffer less damage in a warming climate than younger forests (Wang et al. 2019). Furthermore, the negative effects of warming are mainly caused by drought. Because older trees can recover quickly from drought, they are less affected by warming. These factors could also help explain why older forests benefit more from warming. However, drought stress in our study area will increase if warming continues, reducing photosynthesis and increasing respiration (Lindner et al. 2010). The growth of young trees will likely decrease due to warming-related drought stress, resulting in a long-term decline in the carbon sink of young *P. massoniana* forests in the subtropical region. Old *P. massoniana* forests are likely to continue removing atmospheric carbon at increasing rates for many decades beyond 100 years (Lutz et al. 2018).

Pinus massoniana is one of the most important afforestation tree species in southern China. Therefore, from a climate mitigation perspective, the preservation of older forests/trees should be prioritized because of their greater capacity for carbon sequestration and storage (Körner 2017). It is also crucial to choose different tree species to develop an optimal species portfolio to compensate for the different degrees of carbon capture of different age classes due to continued warming. Some moisture conditions also should be changed, such as irrigation or watering, when carrying out afforestation, which could offset the negative impacts of global warming. Moreover, when dealing with extreme droughts, more focus should be given to post-drought protection for young *P. massoniana* forests/trees, while preventative measures should be prioritized for older forests/trees to maintain higher productivity. These findings could help the Chinese government implement "Ecosystem Conservation and Restoration Projects" and achieve the "Carbon Peak & Carbon Neutrality" goals, the most important national policies now being implemented by the Chinese government.

Conclusion

In this study, a dendrochronological approach assessed the impact of rapid warming on the growth of *P. massoniana* in old and young forests. Trees in both young and old age-class sites exhibited significant growth enhancement (*BAI*) after 1984. The radial growth of *P. massoniana* was generally more strongly linked with temperature than with moisture, indicating that temperature was the key factor influencing growth in the study area. The growth of older trees was

more sensitive to climate factors, such as spring temperatures (positive) and autumn vapor pressure deficits (negative). Different climate-growth responses of *P. massoniana* on nearby sites with similar ages might be caused by heterogeneous microenvironments. Trees in older forests recover faster from extreme droughts, while those in younger forests are more resistant to drought stress.

The "divergence problem" of *P. massoniana* was found in young forest sites but not in old forest sites due to differences in drought sensitivity. Trees in old age-class sites had a positive correlation with spring temperatures after warming, in line with their continuing growth enhancement even under long-term severe drought. The results suggest that trees in old forests may be able to enhance growth under continued warming in coming decades, but those in younger forests may experience more severe growth decline or increased mortality. Our findings may provide new perspectives on paleoclimate reconstructions as well as on the estimation of the effects of climate warming on forest dynamics and biomass accumulation in subtropical forests. They may be helpful in formulating sustainable forest management strategies for subtropical forests of different ages in southern China.

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