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Divergent growth and responses of conifer and broad-leaved trees to warming-drying climate in a semi-arid region, northern China

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Abstract

Forests provide irreplaceable ecosystem services for human society and prevent environmental degradation but climate change has substantially undermined these fundamental functions. It is therefore important to examine the responses and adaptation of different tree species to climate warming. Here, we investigated how climate warming has affected tree growth patterns and growth-climate responses of a conifer (*Pinus tabuliformis*) and two broad-leaved species (*Populus davidiana* and *Betula platyphylla*) in a temperate semi-arid region in the northern China. Our results showed that *P. tabuliformis* had a similar regional growth pattern and two broad-leaved species shared an interspecific growth similarity at the same site. Broad-leaved trees had a higher recovery and resilience to drought than the conifer while conifers were more resistant to drought compared to broad-leaved trees, indicating a faster drought-response of broad-leaved species than that of conifers. The warming climate has hindered the tree growth by exacerbating water-deficit, and in particular, water availability has become the limiting factor for the growth of pines in the area. Trees coped with the water-deficit by taking advantage of non-growing season water to compensate the water source for tree growth. The study not only revealed the differences of growth-climate responses between species but also highlighted the necessity to consider species-specific adaptation to climate warming and diversify forest management strategies.

Highlights

- The conifers and broad-leaved trees had divergent growth patterns and growth-climate response in temperate semi-arid China.
- Trees coped with the warming-drying climate by taking advantage of non-growing season water.
- The warming climate had a discriminatory effect on conifers and broad-leaved trees in temperate semi-arid regions.

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Introduction

Forests provide a wide array of ecosystem services for human society while many of which have been disrupted with economic development, and the remains are currently threatened by population expansion and environment deterioration (MacKenzie and Mahony 2021; Van Mantgem et al. 2009). Climatic warming compounded by human activities and environment changes have influenced the structure, function, growth, and dynamics of forest ecosystems (Allen et al. 2010; Reichstein et al. 2013). Forests are vulnerable to a wide range of climate events where droughts and the associated disturbances were particularly considered to be one of the greatest threats globally (Reichstein et al. 2013). The increases in air temperature due to global warming have made droughts more frequent and intense (IPCC 2021; Novick et al. 2016; Trenberth et al. 2014). The increasing drought events have induced massive trees' growth decline and mortality (Allen et al. 2015; Carnicer et al. 2011; Choat et al. 2018; Schwalm et al. 2017). Therefore, it is of great importance to examine the effects of droughts on tree growth and disentangle the drought-resisting strategies of co-occurring trees.

The warming-drying climate hindered tree growth by reducing water availability (Au et al. 2022; Moore et al. 2016; Shen et al. 2020; Trahan and Schubert 2016). Severe drought events even caused mortality due to hydraulic failure or carbon starvation (Anderegg et al. 2012; McDowell et al. 2010; Schwalm et al. 2017). However, trees have natural capacities and strategies to adapt and cope with droughts, for example, trees can adjust their water-use strategies to against with the warming-drying climate (McDowell et al. 2010; Ponce Campos et al. 2013). The adaptability of trees to climate change is a complex process and usually exhibits spatial heterogeneity with species-specific traits (Gazol et al. 2018; McDowell et al. 2010; Yuan et al. 2021). Conifers usually showed a stronger resistance while broad-leaved trees showed a stronger recovery and resilience to extreme drought (Rahman et al. 2019; Yuan et al. 2021). The adjusted water-use strategies also showed species-specific characteristic between conifers and broad-leaved trees and led to different growth patterns (Martínez-Sancho et al. 2018; Yuan et al. 2021). Temporal instability of correlations between tree-ring width index and climate variables also existed, which reflected some strategies that trees adapt to cope with climate warming (Moore et al. 2016; Shen et al. 2020). Studies focus on above inter-species contents and strategies of trees are still insufficient. Crystallizing these inter-species differences and temporally specific variations will improve our understanding of the warming-drying climate effects on forests, especially for forests growing in arid or semi-arid regions that are frequently influenced by climate warming

and recent increasing drought events (Deng et al. 2016; Sun et al. 2018).

The semi-arid regions in the northern China are the major regions for afforestation (National Forestry and Grassland Administration 2019). Given that the regions have experienced significant warming-drying trends with frequent drought events (Huang et al. 2017; Kursar et al. 2009; Zhang et al. 2022) which disturbed the existing forests dramatically (Liu et al. 2013; Zhang et al. 2021), it raised concern about nurturing the existing forests and selecting accurate tree species for reforestation. Broad-leaved trees are the dominant species in the region, yet our understanding of the growth-climate relationships of these trees remains incomplete, and there is ambiguity regarding the distinctions between the growth-climate relationships of broad-leaved trees and conifers. It is necessary and urgent to explore the divergent forest-climate response of conifers and broad-leaved trees for the benefit of regional forest ecosystems in the northern China.

In this study, we aim to understand how climate warming has affected tree growth in the northern China and what strategies trees have taken to cope with it. We selected representative forest stands and tree species including both conifer and broad-leaved trees in semi-arid region to: (1) reveal the divergence of species-specific growth patterns and responses to climate extremes in temperate semi-arid areas; (2) clarify the exclusive and common adaptability of different trees to a warming-drying climate; and (3) provide theoretical basis on the management for the existing forests and the references on tree species selection for reforestation.

Materials and methods

Study area and tree species

The study area (42.1–43.6°N, 117.7-118.3°E) had two sampling sites at the northern China where Reshui in the south of Great Xing'an Mountains and Laofu in the east of Yinshan Mountains. The landform is mountainous, and the altitudes of our sampling sites range from 1150 to 1426 m above sea level (Fig. 1a). The region is semi-arid with a typical Asian monsoon climate. The mean monthly temperatures range from −15.3°C in January to 19.3°C in July (-17.7°C to 18.5°C in Reshui and −12.7°C to 20.9°C in Laofu). Precipitation concentrates in summer (June-August) and Reshui receives less summer precipitation than that of Laofu. The monthly self-calibrating Palmer drought severity index (scPDSI) in Reshui is higher than that of Laofu (Fig. 1b). During 1950–2019, annual mean temperature and annual precipitation was respectively 1.3°C and 368 mm in Reshui, and 5.1°C and 419 mm in Laofu. The regional annual mean
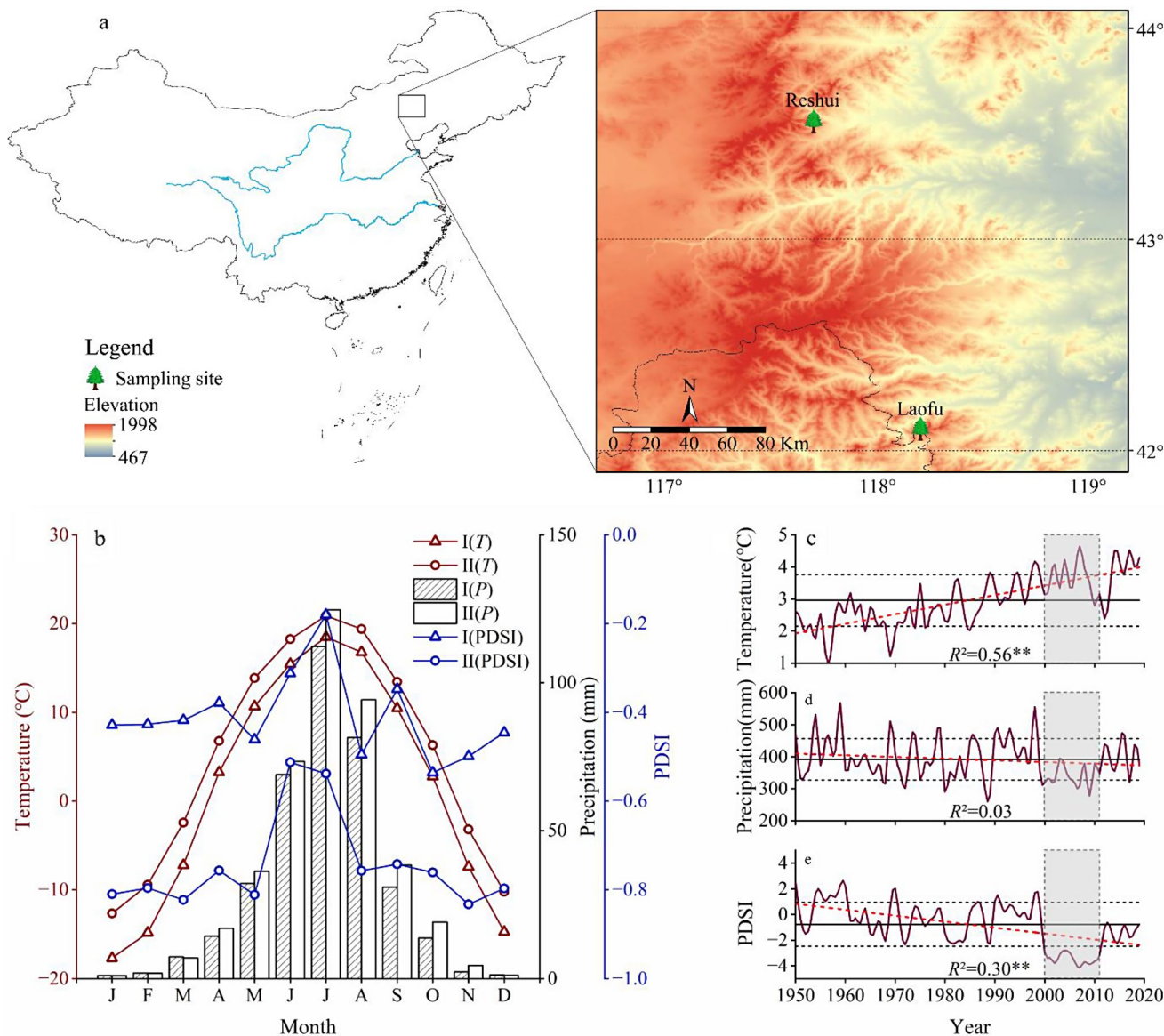
Fig. 1 Locations of sampling sites (**a**), monthly mean temperatures (*T*), precipitation (*P*) and scPDSI of two sites (I: Reshui, II: Laofu) (**b**), and annual mean temperature (**c**), annual precipitation (**d**) and annual scPDSI (**e**) in the study area. The horizontal solid and dashed line in subplot **c**, **d** and **e** represents the corresponding the mean and the mean ± 1 standard deviation, respectively. The red dashed line and equation in subplot c, d and e represents the linear trend of annual mean temperature, annual precipitation, and annual scPDSI during 1950–2019, respectively. The asterisks "**" represented the linear regression model with 99% confidence interval

temperature increased significantly at a rate of 0.3 °C/decade ($R^2 = 0.56$, $p < 0.01$) (Fig. 1c) while annual precipitation did not show a long-term change (Fig. 1d). The annual scPDSI decreased significantly ($R^2 = 0.30$, $p < 0.01$) (Fig. 1e), indicating a warming-induced drought in the region.

The tree species are scarce and decreased from southeast to northwest for the harsh climatic conditions in our study area. The main evergreen conifers are *Pinus tabuliformis*, *Pinus sylvestris* var. *mongolica* with a deciduous conifer *Larix gmelinii*. *Populus davidiana*, *Betula platyphylla*, *Ulmus davidiana* and *Quercus mongolica* are the dominant deciduous broad-leaved tree species. The two sampling sites, without river courses nearby, showed homogeneously environmental characteristics.

Tree ring data

We sampled one evergreen conifer (*P. tabuliformis*) in monospecific plantation stands and two deciduous broad-leaved trees (*P. davidiana* and *B. platyphylla*) in mixed secondary forest stands at two sites (Reshui and Laofu) in July 2019. The three tree species were sampled at shady aspect in each site with similar slopes. Both sampling sites had minimal human disturbance and we only sampled mature,

upright trees without obvious insect pests or fire scars. One to two cores were drilled into each tree using a 5.15 mm inner diameter borer at breast height (1.3 m). At each site, a minimum of 20 tree individuals for each species were sampled. The sampling cores of each tree species were labeled, placed in plastic straws and taken back to the laboratory for further analysis. With the standard dendrochronological procedure (Cook and Kairiukstis, 1980; Stokes and Smiley, 1968), sampling cores were fixed in a wooden trough using latex and make sure that the dark side of the core is upward. After drying, each core was polished by a series of coarse to fine sand paper until the annual ring boundaries were clearly visible.

The tree cores were cross-dated under a microscope and measured using a LINTAB 5 tree-ring width measuring system (Rinntech Heidelberg, Germany) at 0.01 mm accuracy. The reliability of the measurement series was tested by the COFECHA program (Holmes 1983). A total of 272 cores from 143 trees were used for the tree-ring chronologies development (Table 1). The measurement series were standardized with the ARSTAN program by fitting a negative exponential curve or linear regression function (in order to retain more climatic signals) to minimize the age-related influence on radial tree growth. For some measurement series could not be fitted by negative exponential curve or linear regression function, a spline function with step size greater than 2/3 of its series length was used for fitting. Eventually, six standard chronologies for three tree species were employed in subsequent analyses with a common time span of 1988–2018 (EPS > 0.85). Among the six chronologies, the shortest and the longest ones are 31 years (*P. tabuliformis* and *P. davidiana* in Laofu) and 69 (*P. tabuliformis* in Reshui) years in length, respectively (Table 1; Fig. 2). The mean sensitivity (MS) and expressed population signal (EPS) of each chronology indicate that our chronologies share a common signal, which are suitable for dendroclimatology analysis (Table 1).

Meteorological data

The monthly mean temperature, monthly maximum temperature, monthly minimum temperature, and monthly precipitation from 1950 to 2019 were obtained from the Climatic Research Unit (CRU TS 4.04) (http://climexp.knmi.nl) with a resolution of 0.5°×0.5° covering the study region between 42.0°~44.0° N and 117.5°~118.5° E. Monthly snow-cover data during 1967–2020 were obtained from above website with a resolution of 1°×1°. Also, the monthly self-calibrating Palmer Drought Severity Index (scPDSI) series from CRU TS 4.04 with a resolution of 0.5°×0.5° was selected as aridity index in in this study, as it is the most appropriate index in defining droughts for China (Yang et al. 2017) and is the proxy index of soil moisture.

The monthly mean temperature and precipitation form CRU TS 4.04 were calibrated by data form the nearest meteorological station to the sample sites (Linxixian station for Reshui and Chifeng station for Laofu). The monthly mean temperature and precipitation form CRU TS 4.04 were extremely significant correlated to that from meteorological station with correlation coefficient from 0.70 to 0.97 ($p < 0.01$, Fig. S1), which indicating the homogeneity.

Statistical analysis

Principal component analysis (PCA) was performed to investigate the main variance of the six standard chronologies at the two sites. Pearson correlation analysis was employed to examine the correlations between different variables, including different tree-ring width chronologies, and tree-ring width index and climatic variables. The first-order difference of tree-ring width index and climatic variables was used in the correlation analysis to reduce the effect of the autocorrelation of the tree-ring widths and the climatic variables. The measured tree-ring widths of the three tree species in the drought period were compared to study the responses between conifers and broad-leaved trees. Here, the wide ring was defined as the tree-ring width in that year is greater than its mean, the narrow ring as the tree-ring width in that year is maller than its mean, and the extremely wide/narrow rings as its tree-ring width in that year is greater/smaller than its mean + 1SD/ mean − 1SD, respectively. Seasonal climate variables were defined according to the climate condition in the study area: growing season

Table 1 Basic information of tree species in the two sites and tree-ring chronology statistics

Site and tree species	Tree type	No. of cores/trees	Time span (EPS > 0.85)	MC	MS	SD	SNR
I (PT)	Evergreen conifer	48/24	1950–2018	0.87	0.52	0.46	58.3
II (PT)	Evergreen conifer	39/21	1988–2018	0.75	0.38	0.33	21.3
I (PD)	Deciduous broad-leaved	46/25	1965–2018	0.69	0.61	0.43	15.0
II (PD)	Deciduous broad-leaved	47/26	1988–2018	0.57	0.48	0.32	23.8
I (BP)	Deciduous broad-leaved	42/22	1956–2018	0.65	0.77	0.51	28.7
II (BP)	Deciduous broad-leaved	50/25	1953–2018	0.54	0.62	0.40	19.8

Note I: Reshui, II: Laofu, PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*. MC: mean correlation coefficients among all series, MS: mean sensitivity, SD: mean standard deviation, SNR: signal-to-noise ratio

Fig. 2 Tree-ring indices of three tree species at two sites and their sampling depths (shading area). The red dashed lines represented the year of 2000 and 2001 (the first and second year of drought period). The species codes are PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*
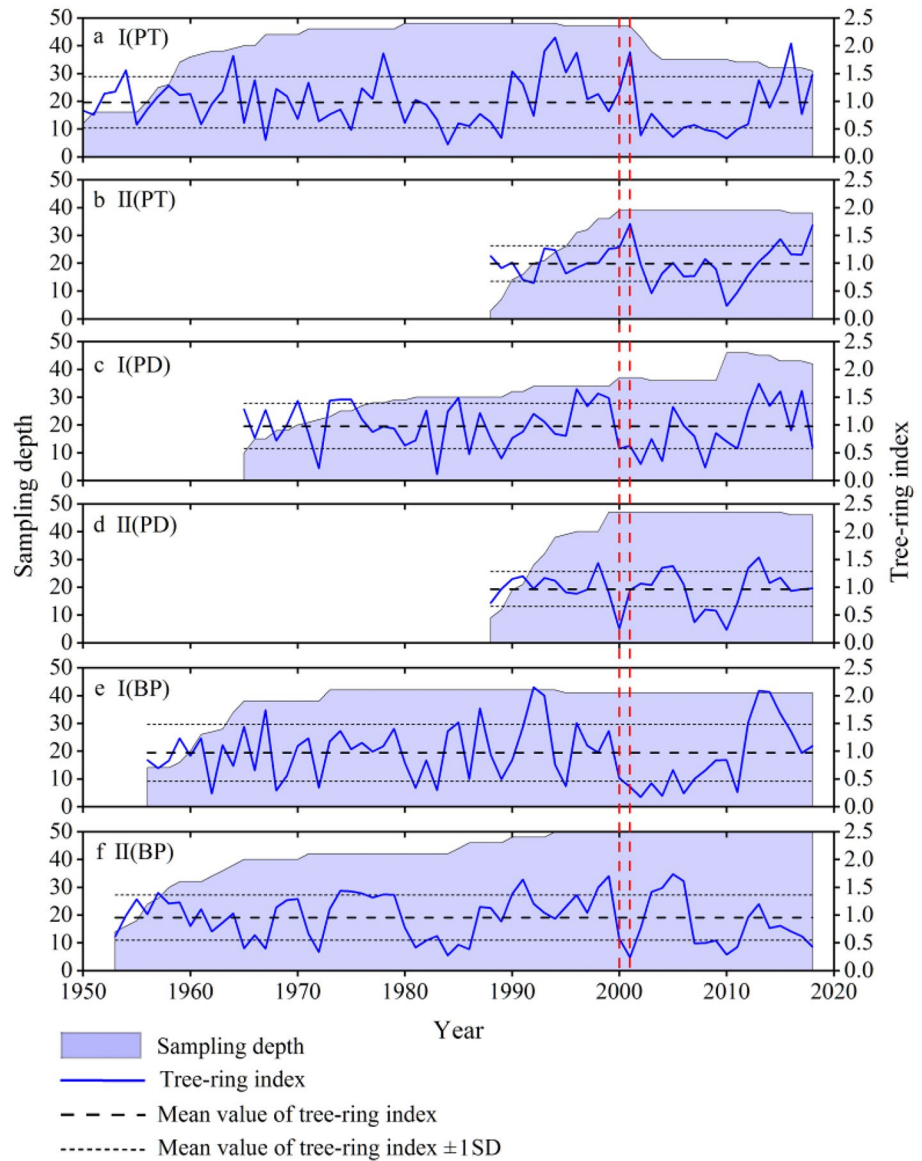
(April–September, G) and non-growing season (November–March, NG).

We used moving correlations with a 31-years window to examine the temporal stability of the first-order difference correlations between tree-ring width index of trees and climate variables (Biondi and Waikul 2004). As the snow-cover data was available from 1967 to 2020, only four out of the six chronologies were suitable for the moving correlations analysis, including three chronologies in Reshui and one *B. platyphylla* chronology in Laofu (Table 1; Fig. 2). To examine how increasing temperature impacts the climate-growth relationship, we used the logistic function with the maximum iterations of 400 to examine the relationship between 31-years moving correlation coefficients and climatic warming as defined by interval mean temperature. We choosed the mean temperature in the two sample sites during

the corresponding time span as the interval mean temperature (e.g. the interval mean temperature of 1968–1998 is the mean temperature of Reshui and Laofu during 1968–1998).

The growth-climate responses of trees to extreme drought were examined with resistance (Rt), recovery (Rc) and resilience (Rs), which represent the capacity of trees to endure disturbance-related changes during extreme events, the trees' ability to bounce back from disturbance, and trees' elasticity or adaptation to disturbance, respectively (Lloret et al. 2011). The three indices were calculated as follows:

$$Rt = Dr/PreDr \tag{1}$$

$$Rc = PostDr/Dr \tag{2}$$

$$Rs = PostDr/PreDr \tag{3}$$

where *Dr* is the tree-ring width index during extreme drought year, *PreDr* and *PostDr* were mean tree-ring width index over three years prior and post the extreme drought year, respectively (Dorado-Liñán et al. 2019; Gazol et al. 2018). Also, the mean tree-ring width index prior and post to the extreme drought year over four and five years were calculated for the *PreDr* and *PostDr*. The mean of *Dr* was calculated for certain consecutive drought years. We defined years with scPDSI < -3.0 as extreme drought years (Yang et al. 2017). These are 2001, 2002 and 2005–2010 in Reshui, and 2001, 2002, 2007 and 2009 in Laofu. We also examined the growth-climate responses of trees to mild drought during the years with scPDSI < the mean − 1 SD. The differences of *Rt*, *Rc* and *Rs* among tree species were compared by ANOVA and Tukey's test.

The basal area increment (BAI) series of trees was calculated using the raw measurement data (Biondi and Qeadan 2008) and the formula is as follows:

$$BAI_n = \pi \left(R_n^{\ 2} - R_{n-1}^{\ 2} \right) \tag{4}$$

where *R* is the radius at the breast height of trees and *n* is the year of tree-ring formation. The growth status of trees during the common time span (1988–2018) was assessed and compared by their linear trend coefficient, respectively.

Results

Growth characteristics and the responses to extreme drought

The chronologies of conifer (*P. tabuliformis*) of the two sites significant positively correlated to each other ($r = 0.54$, $p < 0.01$). The chronologies of two broad-leaved trees (*P. davidiana* and *B. platyphylla*) were significant positively correlated with each other at the same site, with correlation coefficient of 0.67 in Reshui and 0.62 in Laofu ($p < 0.01$). The interspecific correlation within the same site was higher than that of intraspecific between two sites (Table 2). The

Table 2 Correlations between the standard chronologies of the three tree species in two sites during the common period, 1988–2018

	I(PT)	II(PT)	I(PD)	II(PD)	I(BP)
II(PT)	**0.54***				
I(PD)	0.22	0.13			
II(PD)	0.22	0.19	**0.41***		
I(BP)	0.33	0.19	**0.67***	0.31	
II(BP)	0.02	-0.20	**0.38***	**0.62***	0.14

Note The bold indicates the correlation coefficient reaches a significant level. The asterisks "**" and "*" respectively indicates 99% and 95% confidence level. The species codes are

PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*

BAI of *P. tabuliformis* significantly decreased ($p < 0.05$) in Reshui but significantly increased ($p < 0.01$) in Laofu, respectively, during the common time span (1988–2018), while the BAI of the two broad-leaved trees were insignificantly varied except *P. davidiana* in Laofu (Fig. S2).

The principal component analysis (PCA) of the six chronologies also showed specific attributions. The first (PC1), second (PC2) and third (PC3) principal components explain 86.4% of the total variance of the six chronologies during 1988–2018, with the variance explanation of 46.2%, 23.8%, 16.4% for PC1, PC2 and PC3, respectively. The chronologies of the conifer and the broad-leaved trees were divided in two groups with PC2 scores, reflecting a contrasting growth pattern between tree types. As indicated by PC3, the two groups of broad-leaved trees, *P. davidiana* and *B. platyphylla*, reflected a similar growth pattern at interspecific level at the same site (Fig. 3).

A drought period appeared during 2000–2011 with lower scPDSI than the mean − 1 standard deviation (Fig. 1e) and the extreme drought years were included in this period. The year of 2000 and 2001, first and second year of the drought period, respectively corresponded to wide rings or extremely wide rings of *P. tabuliformis* from two sites, whereas the rings were narrow or extremely narrow in the two broad-leaved trees except for *P. davidiana* in Laofu in 2001. *P. tabuliformis* maintained narrow rings in the rest years (except the year of 2008 in Laofu) in the drought period especially in Reshui and the two broad-leaved trees' rings fluctuated notably (Fig. 2). The *P. tabuliformis* had the strongest resistance (*Rt*) to stress compared to broad-leaved trees, while *P. davidiana* and *B. platyphylla* had a stronger recovery (*Rc*) and resilience (*Rs*) (higher than 1) than *P. tabuliformis* (lower than 1), over three years prior and post extreme drought year. The difference of *Rc* between *P. tabuliformis* and *B. platyphylla* was significant ($p < 0.05$, Fig. 4). The results of *Rt*, *Rc* and *Rs* were similar over four and five years prior and post to the extreme drought year compared to the three years (Fig. S3).

Relationships between radial growth and climatic variables

The correlations between tree-ring width index of three tree species and mean temperature were mainly negative in two sites while the correlations with precipitation, scPDSI and snow-cover were mainly positive (Fig. 5). The temperature had a negative effect on the radial growth of both conifer and broad-leaved trees during non-growing season (November–March, NG) and growing season (April–September, G), respectively. For example, *P. tabuliformis* tree growth showed a significantly negative correlation with temperatures over NG ($r = -0.52$, $p < 0.01$) in Reshui while
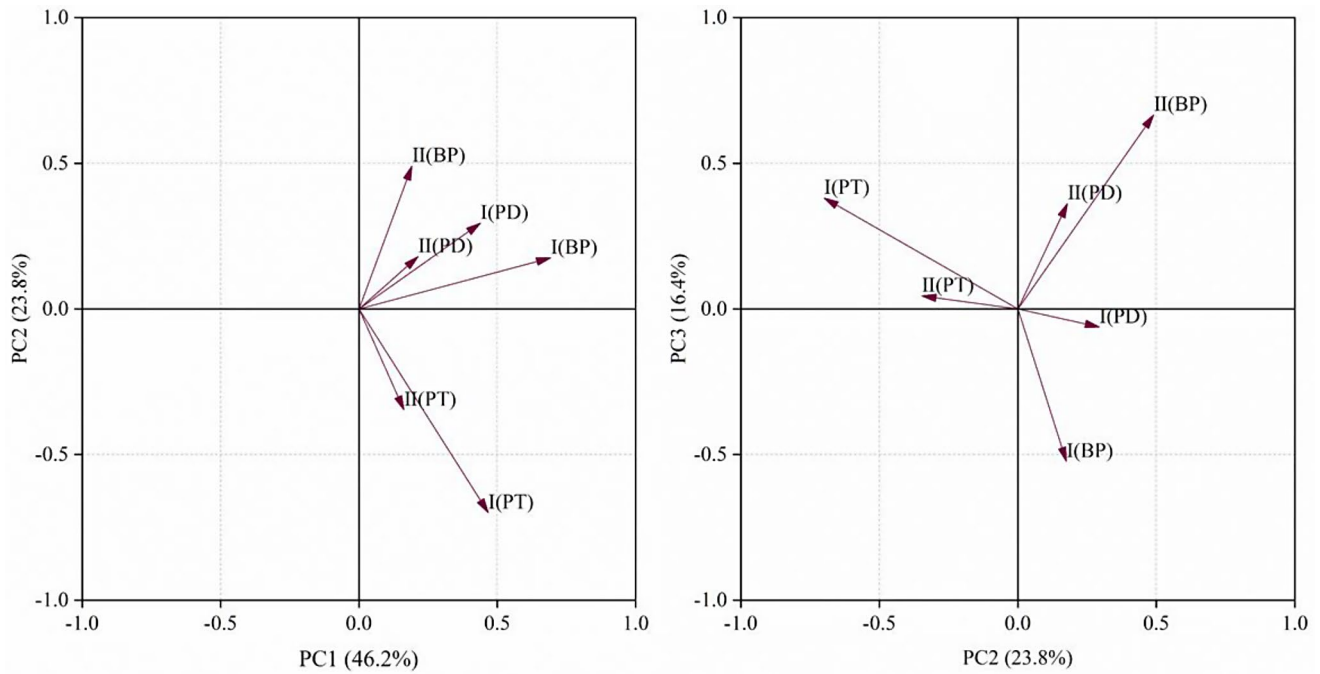
Fig. 3 The PCA loadings on the first three principal components of six chronologies during the common period of 1988–2018. The species codes are PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*
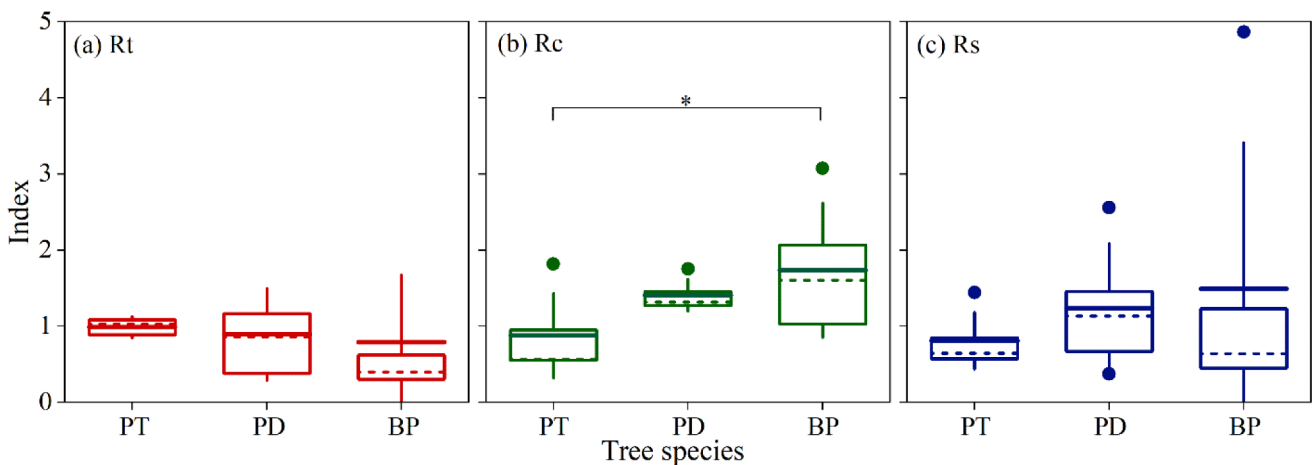

Fig. 4 Comparison of three tree species' growth resistance (*Rt*) (**a**), recovery (*Rc*) (**b**) and resilience (*Rs*) (**c**) to the extreme drought years over three years prior and post to each extreme drought year. The upper and lower limits of the error bars represent the mean ± 1 standard deviation for the *Rt*, *Rc* and *Rs* of each tree species. The horizontal solid and dashed line respectively represent the mean and median. Solid dots in each subplot represent the abnormal values. The differences of *Rt*, *Rc* and *Rs* among tree species were compared by ANOVA and Tukey's test. The asterisk represents the significant difference at the 95% confidence level. The species codes are PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*

P. davidiana and *B. platyphylla* tree-ring width index had negative correlations with temperature in June-August in Reshui, respectively. In particular, the correlation between *P. davidiana* tree-ring width index and August temperature is significant ($r = -0.39$, $p < 0.05$, Fig. 5Ia). The tree growth of *P. davidiana* and *B. platyphylla* had negative correlations with June and July temperatures in Laofu and only the

correlations in June reached significant level (r is -0.42 and -0.44, respectively, $p < 0.05$, Fig. 5IIa).

The precipitation had a divergent influence on conifer and broad-leaved trees at different sites (Fig. 5Ib and IIb). Precipitation had a stronger influence on the growth of conifer compared to broad-leaved trees in Reshui. *P. tabuliformis* tree-ring width index showed positive correlations with precipitation from previous October to current February

where a significant positive association was found in previous November ($r = 0.39$, $p < 0.05$) and in July ($r = 0.50$, $p < 0.01$) as well as during G ($r = 0.41$, $p < 0.05$). *P. davidiana* tree-ring width index showed a significantly positive and negative correlation with previous ($r = 0.42$, $p < 0.05$) and current ($r = -0.40$, $p < 0.05$) October precipitation, respectively (Fig. 5Ib). Precipitation had higher correlations with broad-leaved trees than that of conifer in Laofu. Only October precipitation in the current year had a significantly negative correlation with the tree growth of *P. tabuliformis* ($r = -0.48$, $p < 0.01$). The precipitation in April, June and July had significantly positive correlations with *P. davidiana* tree-ring width index (r is 0.47, 0.60 and 0.37, respectively, $p < 0.05$). Also, June precipitation significantly positive correlated to *B. platyphylla* tree-ring width index ($r = 0.38$, $p < 0.05$; Fig. 5IIb).

The correlations between scPDSI and broad-leaved tree species were higher than that of conifer. The scPDSI showed significantly positive ($r = 0.37$, $p < 0.05$) correlation with *P. tabuliformis* tree-ring width index during G in Reshui. The positive correlations between scPDSI and *P. davidiana* and *B. platyphylla* tree-ring width index were similar—significant ($p < 0.05$) in most single months and the merging months such as G and NG (Fig. 5Ic and IIc).

In addition, the influence of snow-cover on the radial growth of conifer is stronger than that of broad-leaved tree species. The tree growth of *P. tabuliformis* showed significantly positive correlation with snow-cover over NG ($r = 0.61$, $p < 0.01$) in Reshui (Fig. 5Id). For broad-leaved trees, only *B. platyphylla* tree-ring width index significantly correlated to snow-cover variation in March ($r = 0.42$, $p < 0.05$) and November ($r = 0.40$, $p < 0.05$) in Reshui and December ($r = 0.38$, $p < 0.05$) in Laofu (Fig. 5Id and IId).

Responses to warming-drying climate

The correlations between tree-ring width index of three tree species and climate variables varied with the warming-drying climate (indicated by the significantly decreased annual scPDSI, Fig. 1e) in the two sites during 1950–2018. The moving correlations for *P. davidiana* and *B. platyphylla* in Reshui were similar, and which was different form *P. tabuliformis* in Reshui and *B. platyphylla* in Laofu (Fig. 6). Some moving correlations between tree-ring width index and climate variables reached significant level and varied evidently. This included the moving correlations of *P. tabuliformis* tree-ring width with precipitation in G, as well as temperature, precipitation and snow-cover in NG in Reshui, *P. davidiana* tree-ring width with temperature in NG in Reshui, *B. platyphylla* tree-ring width with precipitation in NG in Reshui, and *B. platyphylla* tree-ring width with temperature in NG and precipitation in G in Laofu.

Each significant moving correlations exhibited a S-shaped curve with increasing temperature. The correlations of temperature in NG and precipitation in G and NG with *P. tabuliformis* tree-ring width index showed a abruptly decreasing pattern, which were different from that of the two broad-leaved trees—a gradually decreasing pattern (except the correlations between *B. platyphylla* tree-ring width with precipitation in NG in Reshui) (Fig. 7). The other insignificant correlations between tree-ring width index of the two broad-leaved trees and climate variables also showed a gradually decreasing pattern, such as the moving correlation coefficients of *B. platyphylla* tree-ring width with temperature in NG and precipitation in G in Reshui, and *P. davidiana* tree-ring width with precipitation in G and NG (Fig. S4). The correlations of temperature in NG maintained negatively with *P. tabuliformis* and *P. davidiana* tree-ring width index in Reshui (Fig. 7a and b), and transformed from significant positive to negative with *B. platyphylla* tree-ring width index in Laofu (Fig. 7c). The moving correlation coefficients of *P. tabuliformis* decreased from insignificant negative to extremely significant negative ($p < 0.01$) and remained stable (Fig. 7a), while the moving correlation coefficients of *P. davidiana* decreased from insignificant negative to significant negative ($p < 0.05$) and remained stable (Fig. 7b). The extremely significant positive ($p < 0.01$) correlation coefficients between precipitation in G also decreased with increasing temperature for *P. tabuliformis* in Reshui and *B. platyphylla* in Laofu (Fig. 7d, e). The moving correlation coefficients respectively were stable above significant positive level ($p < 0.05$, Fig. 7d) and faded out the significant level (Fig. 7e). The moving correlation coefficients of precipitation in NG with *P. tabuliformis* and *B. platyphylla* in Reshui changed inversely, respectively faded out the significant level (Fig. 7f) and transformed from insignificant to significant positive level ($p < 0.05$, Fig. 7g). The positive correlation between snow-cover in NG and *P. tabuliformis* tree-ring width index in Reshui increased from insignificant to extremely significant ($p < 0.01$) and remained stable with increasing mean temperature (Fig. 7h).

The negative correlation between temperature in NG and *P. tabuliformis* tree-ring width index reached a significant level when the interval mean temperature was about 3.0 °C (Fig. 7a). This temperature was coincident with the positive correlation between snow-cover in NG and *P. tabuliformis* where it reached a significant level (Fig. 7h) as well as with the negative correlation between temperature in NG and *P. davidiana* in Reshui where the correlation started to decrease (Fig. 7b). The positive correlation between precipitation in G and *B. platyphylla* in Laofu also decreased when the interaval mean temperature at 3.0 °C (Fig. 7e).
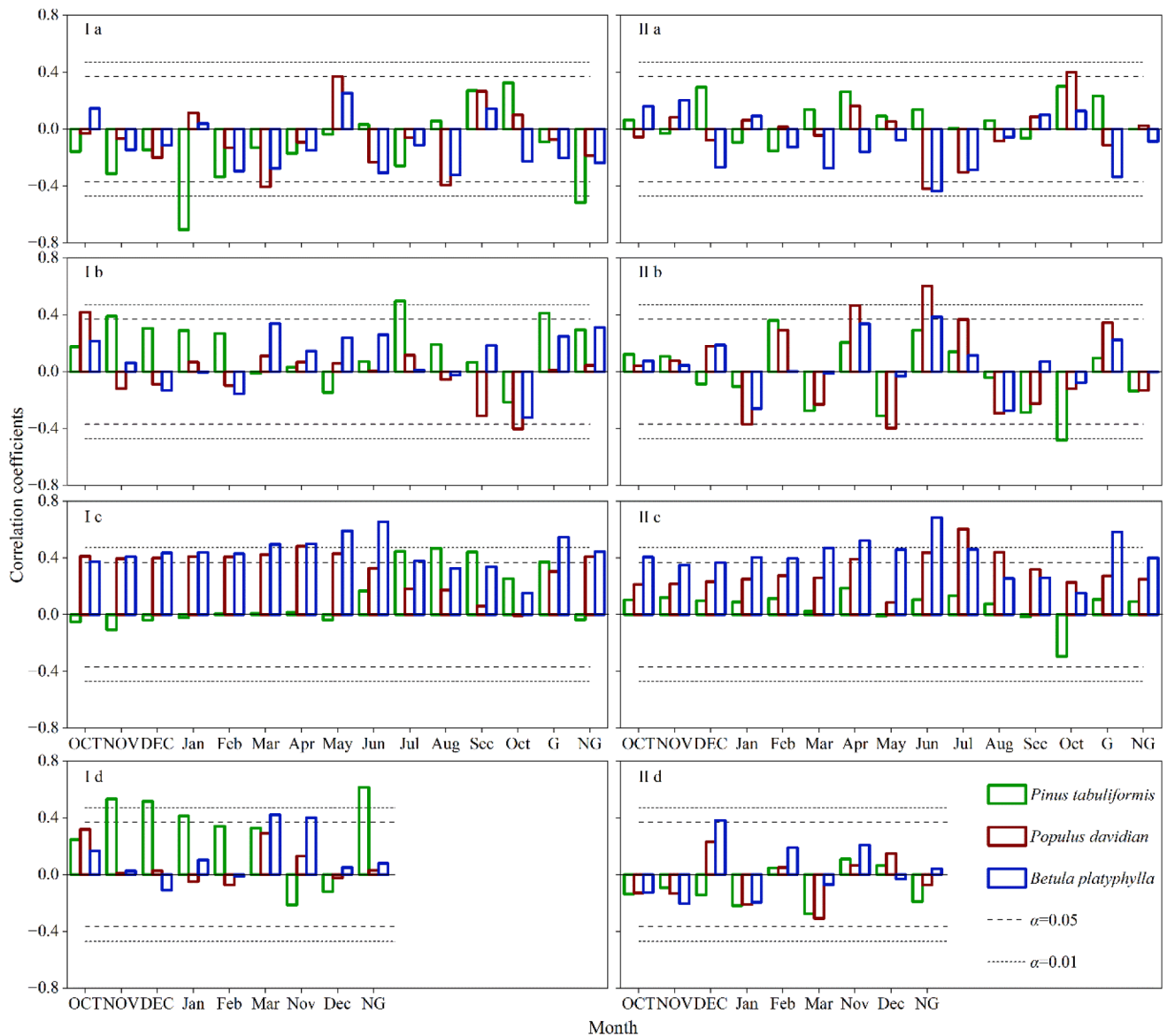
Fig. 5 Correlation coefficients of the first-order difference between tree-ring width index of the trees in Reshui (I) and Laofu (II) with mean temperature (**a**), precipitation (**b**), scPDSI (**c**) and snow-cover (**d**). Capital letters represent months of the previous year, G: growing season, NG: non-growing season

Discussion

Specific radial growth and responses to extreme climate

Our two study sites, Reshui and Laofu experienced different hydrothermal conditions—a lower temperature and precipitation but higher scPDSI in Reshui compared to Laofu (Fig. 1b), which resulted in specific growth-climate response of three species within these two sites (Fig. 5). *P. tabuliformis* shared similar growth pattern between different sites while the growth of two broad-leaved tree species showed interspecific consistency at the same site (Table 2; Fig. 3). The study area is the northern boundary of *P. tabuliformis* (National Forestry and Grassland Administration 2019) and the geographic distribution limits might be the overwhelming environment factor that lead to the growth similarity along or around their northernmost distribution. Our findings were supported by previous demonstration that conifers usually exhibited consistent radial growth patterns at regional scale, whereas it was more common for broad-leaved trees at the stand level (Pacheco et al. 2020; Yuan et al. 2021). The two broad-leaved trees were sampled in the same stand at each site, and their interspecific growth consistency might be due to their uniform wood property (diffuse-porous wood) and identical externally environmental
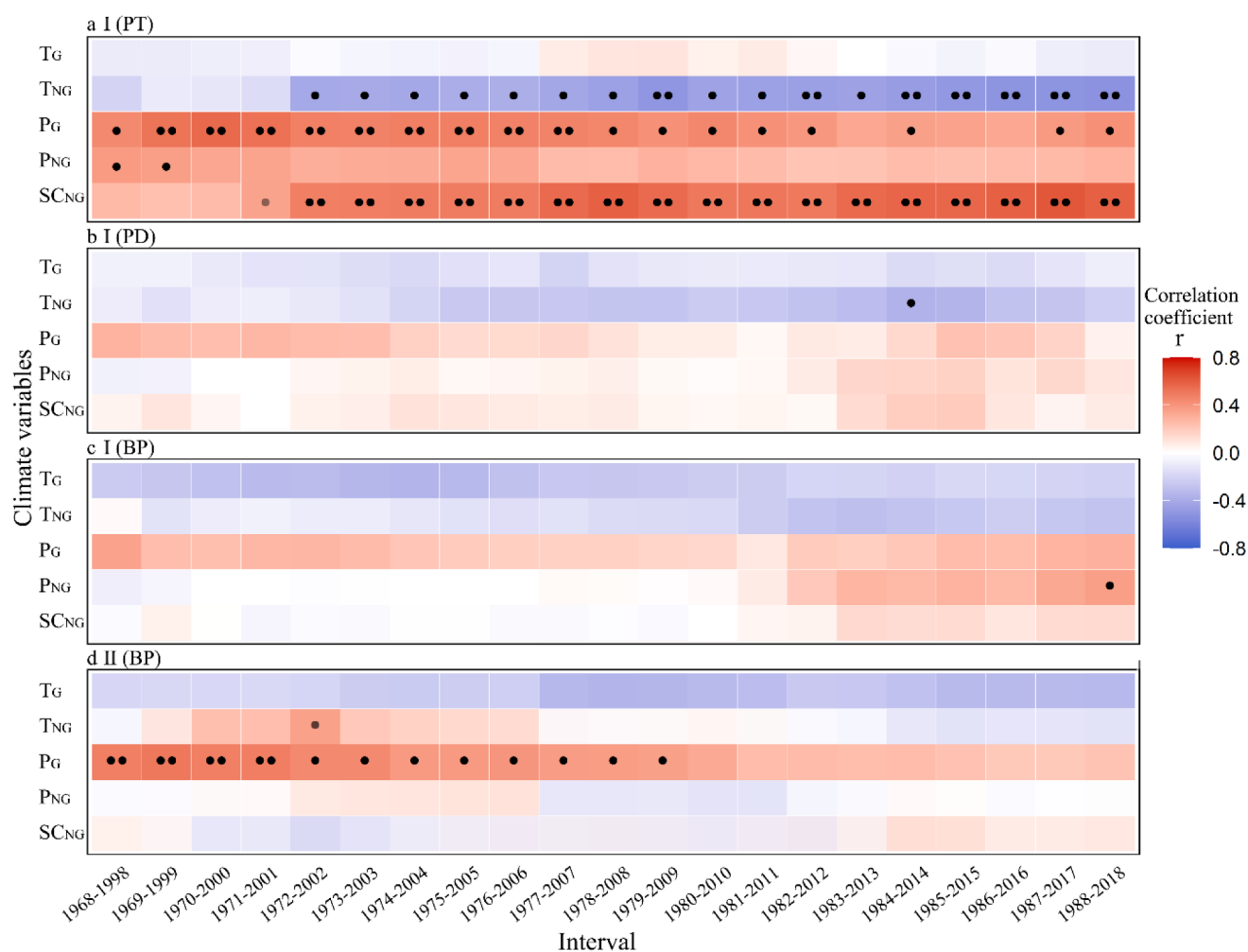
Fig. 6 Moving correlations in 31-years interval between the first-order difference of four standard chronologies of three tree species and climate variables in Reshui (I) and Laofu (II). T_G: mean temperatures of growing season, T_{NG}: mean temperature of non-growing season. P_G: precipitation of growing season, P_{NG}: precipitation of non-growing season. SC_{NG}: snow-cover of non-growing season. "λλ" and "λ" indicates significance at the 0.01 and 0.05 level, respectively. The species codes are PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*

conditions. The higher sensitivity of broad-leaved trees to drought than the pines could also cause the interspecific growth consistency in the same site and intraspecific growth divergence at different site, such as the faster response to drought, indicated by the wide rings of *P. tabuliformis* in 2000 and 2001 (the first and second year of drought period), as well as the consecutively narrow rings in other years compared with the remarkably fluctuated rings of *P. davidiana* and *B. platyphylla* (Fig. 2).

The different response to drought between conifers and broad-leaved trees, such as the opposite resistance and recovery: low resistance and high recovery of broad-leaved trees vs. high resistance and low recovery of conifer (Fig. 4 and S3), might be related to their different ecological and physiological attributes resulting in the divergent water-use strategies (Choat et al. 2012a; Li et al. 2020), reflected by the different correlations to precipitation and snow-cover

between the pines and broad-leaved trees in the two sites (Fig. 5). Broad-leaved trees, with low water retention capacity (Carnicer et al. 2013; Firn et al. 2019), usually adopt risky embolism-tolerance strategies in response to drought stress to maintain photosynthesis (Choat et al. 2012a; Li et al. 2020), but would also cause a rapid decrease in water potential and lead to the hydraulic dysfunction in severe or persistent droughts (Carnicer et al. 2013; Firn et al. 2019; Liu et al. 2017). Conifers usually have greater hydraulic safety thresholds (Choat et al. 2012b) and adopt a more conservative water-use strategy, such as stomatal closure to increase water retention and avoid drought-induced xylem cavitation, and protect themselves from drought stress (Brodribb et al. 2014; Li et al. 2020). The studied pines were able to take advantage of thesnowmelt water of previous non-growing season or rainwater of the highest precipitation month (July) for their growth in Reshui (Fig. 5Ib and Id).
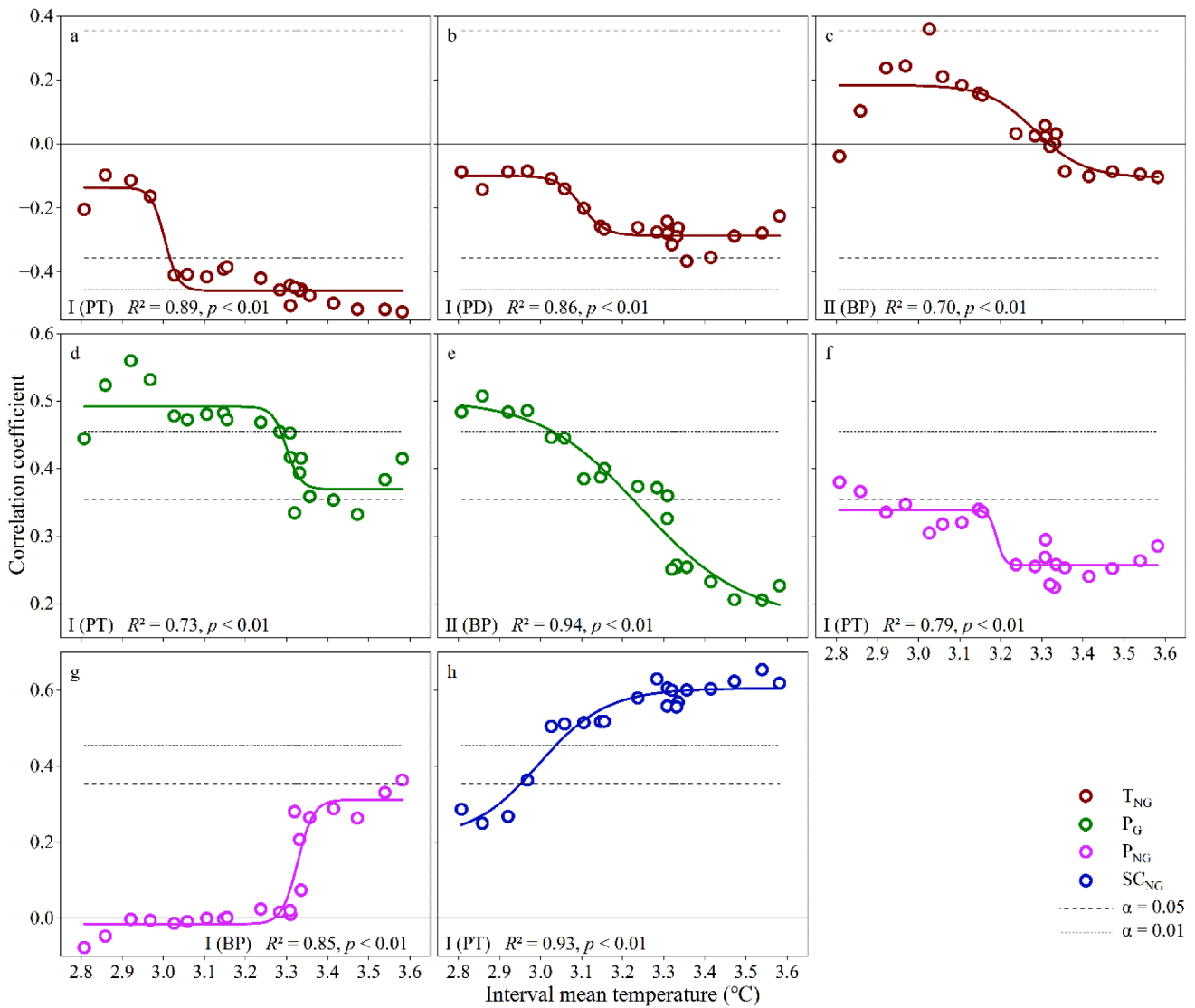
Fig. 7 The relationship between 31-years interval mean temperature and moving correlation coefficients of the tree-ring width from three tree species and climate variables (T_{NG}, P_G, P_{NG} and SC_{NG}) from 1968 to 2018. T_{NG}: mean temperature of non-growing season; P_G: precipitation of growing season; P_{NG}: precipitation of non-growing season; SC_{NG}: snow-cover of non-growing season. The smooth curve in each subplot was fitted by a logistic equation. The dashed and dotted line respectively represented the moving correlation coefficients reached significant ($p < 0.05$) and extremely significant ($p < 0.01$) level. The species codes are PT: *Pinus tabuliformis*, PD: *Populus davidiana* and BP: *Betula platyphylla*. I: Reshui, II: Laofu

The different responses of hydraulic function to winter frost between conifer and broad-leaved trees might also induce their different response to drought. Conifers exhibited less embolism and frost fatigue than broad-leaved trees over winter (Dai et al. 2020; Sass-Klaassen et al. 2011), which would prolong the intraannual influence of hydrothermal condition on the pines, and alleviate their response to drought. Moreover, the forest type: monospecific plantation for pines and naturally mixed stands for broad-leaved trees, might induce the different response to drought between conifers and broad-leaved trees. In general, conifers can resist the short-term drought with their water retention capacity and broad-leaved trees are sensitive to drought in the study area.

Shifting available water

Increasing temperature intensified evaporation and resulted in a continued water-deficit environment (Allen et al. 2010; Choat et al. 2018; Liu et al. 2013; Timofeeva et al. 2017), which threatened the growth and survival of trees in the northern China (Liu et al. 2013; Zhang et al. 2021), including our study area as indicated by a substantial decrease in scPDSI (Fig. 1e). Taking advantage of available water

besides the growing season to cope with the ongoing water-deficit environment is a key for trees to sustain their growth and survival. The temporal instable relationships between tree growth and climate variables reflected a shift of trees' availabile water as the warming-drying climate, with homogeneous trend but different attributes between the conifer and broad-leaved trees (Figs. 6 and 7).

Precipitation during growing season, supplying trees to complete intra-annual radial growth process, is crucial for tree growth in arid and semi-arid regions (Cai et al. 2020; Zhang et al. 2021). However, in our study, the influence of precipitation over growing season was weakening for both conifer and broad-leaved trees, and the difference is that it stabled at the significant level with pines and faded out the significant level with broad-leaved trees (Figs. 6 and 7). The influence of non-growing season temperature and snow-cover on pines simultaneously became significant at the interval mean temperature of 3.0 °C, corresponding to the time span of 1972–2002 and including about 22 years after climate warming (according to the IPCC report that climate warming origined in 1980) (IPCC 2013). That is, the pines broadened its intraannual available water within about 22 years after climate warming, such as taking advantage of the snowmelt water, to compensate lower availabile water over growing season to sustain its growth, and became less dependent on precipitation in G. This result is supported by the isotopic analysis results that trees mostly used winter precipitation for radial growth in semi-arid regions (Allen et al. 2019; Huang et al. 2022; Zhang et al. 2018).

The moving growth-climate relationships of broad-leaved trees were homogeneous with that of pines, such as their decreasing relationship with precipitation in G and increasing relationship with non-growing season water (precipitation and snow-cover) (Fig. 6). Most of the relationships didn't reach a significant level during 1968–2018 especially in Reshui. But the moving correlations between *B. platyphylla* radial growth in Laofu with more precipitation seemed to be undergoing the identical changes as the broad-leaved trees and climate variables in Reshui, such as its decreasing relationship with precipitation in G from significant to insignificant (Fig. 6). The identical changes indicated that these insignificant relationships in Reshui might result form the insufficient analysis time span. For example, the influence of precipitation in G on *B. platyphylla* radial growth in Reshui was significant previously (Fig. S5), then weakened before the pines with climate warming, which was consistent with the broad-leaved trees' faster response to droughts than the pines in our study (Fig. 2). The snowmelt water in the late NG, rather than the whole NG, could supply the radial growth of broad-leaved trees, which is reflected by the significant influence of March snowmelt water on *B. platyphylla* growth in Reshui (Fig. 5Id). This might be due to that the snowmelt water in early spring can saturate into

soil and continuously sustain the growth of trees and the insufficient precipitation in growing season cannot meet the needs of tree growth as the low water retention capacity of broad-leaved trees (Carnicer et al. 2013; Firn et al. 2019). While in the site of Laofu, with relatively high precipitation, the growing season (such as June and July) precipitation, favored the two broad-leaved trees growth (Fig. 5IIb). As a result, the NG water such as snowmelt water, which could last until May in our study area and compensate the water-deficit environment, has been more important for tree growth under global warming, especially in the region with less precipitation (Reshui).

The shifting availabile water was accompanied by the pressure from increasing temperature in NG for tree growth, especially for the pines with significant water-dependence in NG (Figs. 6 and 7). That might be attributed to the different wood structures between conifers and broad-leaved trees where the pines retain their water transport ability in winter while this ability was strictly limited for broad-leaved trees (Dai et al. 2020). On the other hand, warming-induced loss of available water, such as early snowmelt and exacerbated evapotranspiration, amplified drought stress in NG leading to reduced pine growth. Therefore, the conifers would suffer more adversity from the increasing temperature in NG than that of broad-leaved trees in the study area.

Potential growth under warming climate

The forests are projected to change in species composition or structure in this region under future warming climate (Zhang et al. 2022). The growth of pines, especially in the semi-arid region of northern China, would likely decline under the compounded stresses of warming and water-deficit (Cai et al. 2020; Zhao et al. 2021), indicating greater susceptibility to conifers than broad-leaved trees (Seidl et al. 2017). The declines in growth of trees were considered to be a precursor of mortality especially for coniferous (Cailleret et al. 2017, 2019), such as the pines, which reflected an unfavourable growth status of the studied conifers (Fig.S2), as the pines are a long-lived tree species, which can show steady growth and insignificant declines at nearly 300-years old in areas with sufficient rainfall (Chen et al. 2006, 2007). On the one hand, the compounded stress from temperature and water-deficit environment hindered the growth of pines, on the other hand, the lower recovery to drought of pines indicated that the pines were hardly to recover to the pre-drought growth status in a few years. In spite of the forest stand of pines is located at the shady slope with relatively humid condition, the growth of pines was still degenerating, reflecting a deteriorating warming-induced drought impact. Our results suggested that the tree species such as *P. tabuliformis* might be unsuitable for afforestation especially in Reshui with low precipitation. The broad-leaved trees with normal growing status such as *P. davidiana* and *B. platyphylla*

(Fig.S1), with higher recovery strengthen the plasticity of them to warming-induced drought environment (Dai et al. 2020), would still be a practicable choice for afforestation tree species selection. The other broad-leaved tree of *Quercus mongolica* growing in our study area (Gao et al. 2020) reflected a similar climate response to *P. davidiana* and *B. platyphylla*. The better growing status of broad-leaved trees than pines in our study might also result form the forest type, as pines were sampled in monospecific forest stands and broad-leaved trees in mixed forest stands, and tree species diversity could enhance the drought resistance of trees (Liu et al. 2022). In any case, appropriate tree species selection is crucial for afforestation and will bring enormous benefits to local society and achieve sustainability, and the selection of tree species should be not only based on the assessment of the existing trees' growth status but also their potential growth in the future. Although we estimated the future growth status for different trees merely from interaction between climate variables and tree growth, a myriad of other factors such as competition, insect diseases, species composition, land use changes are likely to intensify in the future and alter the tree growth, which should also be carefully considered when selecting tree species for afforestation.

In general, we revealed the homogeneous growth-climate responses of *P. tabuliformis*, *P. davidiana* and *B. platyphylla* to warming-drying environments—taking advantage of non-growing season water to compensate the water source for tree growth, and this process was accompanied by increasing restrictions from non-growing season temperature. This growth-climate responses occurred faster in broad-leaved trees than conifers, and earlier in areas with low precipitation. Our results indicated the ability of trees to adapt the climate warming, and provided a reference for accessing climate warming's threat to the forest ecosystems in the semi-arid areas of northern China.

Declarations

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