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Radial growth responses of three conifers to climate in Lugu Lake, Northwestern Yunnan

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Introduction: Climate change significantly influences tree radial growth, particularly in high-elevation forests. As a typical plateau lake in the Hengduan Mountains, Lugu Lake lacks sufficient dendrochronological research, hindering the understanding of regional conifers' responses to climate change.

Methods: Using dendrochronological methods, we constructed residual chronologies from tree-ring width data of *Larix potaninii* Batalin. (Chinese larch), *Picea likiangensis* Franch. (Lijiang spruce) and *Pinus yunnanensis* Franch. (Yunnan pine) collected around Lugu Lake. We used Response Function Analysis (RFA) and Redundancy Analysis (RDA) to quantify growth–climate relationships. We further identified the key climatic drivers of radial growth for the three conifers.

Results and discussion: The radial growth of *L. potaninii*, *P. likiangensis*, and *P. yunnanensis* around Lugu Lake was jointly influenced by temperature and precipitation. Specifically, the mean minimum temperature (T_{min}) of previous September, current January precipitation, the mean temperature (T_{mean}) of current May, and the mean maximum temperature (T_{max}) of current September were common factors influencing the radial growth of three conifers. *L. potaninii* was more influenced by temperature in the early growing season (April–May) and moisture conditions in the post growing season (September–October). Elevated growing-season temperatures were detrimental to the growth of *P. likiangensis*. *P. yunnanensis* was more affected by spring drought stress and summer precipitation. Under projected warming with slightly reduced precipitation, the observed climate sensitivities suggest that growth of *L. potaninii* and *P. likiangensis* may respond differently, whereas the response of *P. yunnanensis* is likely more complex. RFA and RDA demonstrated consistency and could effectively complement each other in dendroclimatological studies. This study provides new tree-ring evidence from northwestern Yunnan and insights into potential future growth responses in the region under climate change.

KEYWORDS

climatic factors, dendrochronology, Hengduan Mountains, Lugu Lake, radial growth

1 Introduction

Climate change is accelerating with detectable impacts on high-elevation forests. Studies have demonstrated that global surface temperatures will continue to rise at least until the middle of this century (Ma et al., 2022; Scafetta, 2024). Without substantial reductions in carbon dioxide and other greenhouse gas emissions over the next few decades, global warming is projected to exceed 1.5–2°C within this century (Masson-Delmotte et al., 2021). Climate change alters tree regeneration, growth, and migration in high-elevation regions (Pepin et al., 2015; Kharal et al., 2017). These changes can reshape the structure, productivity, and dynamics of alpine forests (Yadava et al., 2017; Cailleret et al., 2014). Meanwhile, as the main body of terrestrial ecosystems, forests play a crucial role in global carbon sink resources. Forests mitigate climate change through carbon sequestration. They also regulate regional climate, conserve water resources, and provide substantial ecological and economic benefits (Peng, 2023). Therefore, studying the impacts of climate change on forest ecosystems provides a scientific basis for developing effective mitigation and adaptation strategies (Wei et al., 2013).

Dendrochronology overcomes limitations associated with conventional meteorological observations, such as sparse station coverage and short records. By reducing non-climatic influences (e.g., genetics and age-related trends), tree-ring width indices retain key signals of past climate variability. Therefore, they are widely used to examine climate responses and reconstruct past climate (Lin et al., 1995; Fritts, 1991; Wu, 1990; Hu, 2007). Tree rings document annual growth patterns and capture interannual climatic fluctuations. This allows tree rings to be used to assess climate impacts on ecosystems and to support scenario-based discussion of potential future changes (Peng et al., 2023). In earlier investigations, the relationships between multiple tree species and climatic variables have been validated (Li et al., 2024; Yang et al., 2022; Jin et al., 2013). These efforts have further revealed that different species exhibit varied growth response mechanisms to climate change.

The Hengduan Mountains are located on the southeastern edge of the Qinghai-Tibet Plateau, with northwestern Yunnan at its core. As a critical transition zone from the plateau to lower elevations, this area exhibits extreme vertical relief and complex topography, making it a biodiversity hotspot and a region highly sensitive to climate change (Wang, 2021; Zhang et al., 2020). In recent years, scholars have used tree-ring data to investigate the responses of tree radial growth to climate change in this area, clarifying the relationships between radial growth of coniferous species and climatic factors. In the central Hengduan Mountains, *Abies georgei* growth was affected by both temperature (positive effects) and precipitation (negative effects) (Yin et al., 2018). Research on *Tsuga dumosa* in Wuliang Mountain found that water availability was the main limiting factor for radial growth (Yin et al., 2023). In addition, dendrochronological studies have been successively carried out in Laojun Mountain and Jianhu areas (Cao et al., 2020; Deng et al., 2024). However, despite these advances, dendroclimatological evidence remains scarce around Lugu Lake, a representative plateau-lake ecosystem in northwestern Yunnan with well-preserved montane forests (Canham and Murphy, 2016). Unlike climatically extreme environments (e.g., treeline or semi-arid regions), forests around Lugu Lake develop under

relatively favorable hydrothermal conditions, where tree growth may be regulated by multiple climatic factors rather than a single dominant limitation. The lack of tree-ring studies in this region limits our understanding of how dominant tree species respond to climate variability under such non-extreme but ecologically important conditions.

Notably, *Larix potaninii*, *Picea likiangensis*, and *Pinus yunnanensis* are key constructive, dominant and representative species of subalpine forests in northwestern Yunnan. With their distinct annual ring boundaries, clear climate sensitivity, and strong chronology signals, they are preferred species for dendroclimatological research (Shen, 2019; Yuan and Yu, 2013). Furthermore, these three species have different biological characteristics, a multi-species tree-ring comparison may enable understand insights of common and species-specific response to climate change, and then understand their adaptable mechanisms. Existing studies have found that *P. yunnanensis* in Haba Snow Mountain was primarily limited by drought in May of the current year (Zhang et al., 2020). For *L. potaninii* in the middle section of the Hengduan Mountains, warm climate and sufficient heat during the early growing season (May and June) were crucial for its radial growth (Yue et al., 2023). The radial growth of *P. likiangensis* in Shika Snow Mountain was jointly influenced by temperature and precipitation, whereas *Pinus densata* showed a significant correlation only with temperature (Zhang et al., 2018). However, these studies were mostly conducted at individual sites and focused on single species, limiting direct interspecific comparisons under a shared climatic background. Accordingly, coordinated multi-species tree-ring analyses provide a direct basis for identifying shared climatic controls versus species-specific sensitivities, which is essential for assessing relative vulnerability under future climate change and for informing species-specific conservation and adaptive management aimed at maintaining conifer diversity and subalpine forest stability.

We analyzed tree-ring samples from sites around Lugu Lake, focusing on three study species: *L. potaninii*, *P. likiangensis*, and *P. yunnanensis*. By employing dendroecological methods, we aimed to: (1) find the interspecific differences in the climate-response patterns of the three conifers and identify the main climate factors affecting tree growth, (2) discuss the potential growth implications of these species in the context of climate change.

2 Materials and methods

2.1 Study area and species

Lugu Lake is situated on the border between Yunnan and Sichuan Provinces, China, with geographical coordinates ranging from 100°43' to 100°50'E and 27°37' to 27°45'N. This lake extends across Ninglang County and Yanyuan County, which belong to the two aforementioned provinces (Figure 1; Xie et al., 2020). The surrounding area is characterized by tectonic erosion, denudation, and karst landforms, dominated by mid-to-high mountain tectonic erosion terrain with elevations ranging from 2,657 m to over 3,800 m (Wu, 2023). Brown soil is distributed in the area with an elevation of 2,800–3,600 m, and the main soil types are red-brown soil, brown soil, black limestone soil, and brown felt soil. The soil

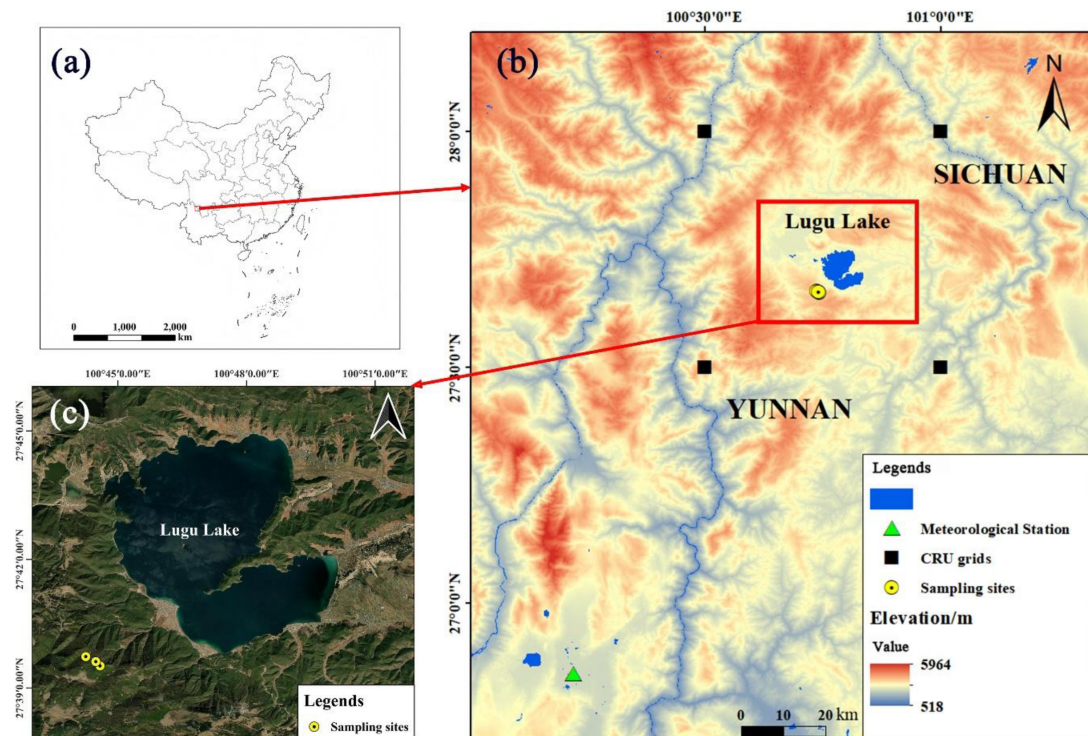


FIGURE 1

Study area location and sampling sites. (a) Location of Lugu Lake in China; the red rectangle indicates the extent shown in (b). (b) Regional topography (DEM) around Lugu Lake showing lakes, meteorological station, CRU grids, and sampling sites; the red rectangle indicates the extent shown in (c). (c) Satellite image of the Lugu Lake area showing the sampling sites.

above 3,600 m above sea level is dark brown, mainly including dark brown soil, humus-accumulated bleached soil, and brown felt soil.

Vertical vegetation zonation is evident in the mountains surrounding Lugu Lake. Along the elevation gradient from the lake surface up to the mountain summits, the vegetation types appear in the following sequential order: cold-temperate mountain sclerophyllous evergreen broad-leaved forests, cold-temperate broad-leaved forests, warm-temperate coniferous forests, cool-temperate coniferous forests, and cold-temperate coniferous forests (Xie, 2020). Below 3,000 m around Lugu Lake, large areas of *P. yunnanensis* forests are distributed, with local development of *Quercus delavayi* forests. Between 3,000 and 3,500 m, the landscape is dominated by *P. densata*, *P. yunnanensis*, *P. likiangensis* and *A. georgei*. Above 3,500 m, *Abies delavayi* and *L. potaninii* are the dominant species (Sheng, 2015). All three study tree species were dominant species at each sampling site. In the *L. potaninii* site, rhododendrons (e.g., *Rhododendron bureavii* and *Rhododendron leptothrium*), together with *Lyonia ovalifolia* and *Salix takasagoalpina*, were the dominant shrubs. The herb layer consisted of *Viola delavayi*, *Saxifraga epiphylla*, and *Rhodiola yunnanensis*. In the shrub layer of the *P. likiangensis* site, common species included *R. bureavii* and *Rhododendron uvarifolium*. The herb layer was dominated by *Pteris dactylina*, with companion species such as *Impatiens delavayi* and *Triplotelia grandiflora*. In the *P. yunnanensis* site, the shrub layer was dominated by cold- and drought-tolerant alpine oaks (e.g., *Quercus monimotricha* and *Quercus pannosa*), with companion species including *Rhododendron decorum* and *Rhododendron racemosum*. The herb layer included *Argentina lineata*, and *Sedum yunnanense*.

The Lugu Lake area (~27°N) lies within a southwest monsoon climate zone but, due to its high elevation, exhibits an atypical subtropical climate (Chang et al., 2018). The region experiences abundant sunlight, relatively small annual temperature fluctuations, and distinct wet and dry seasons (Wu, 2023). The wet season spans from June to October, accounting for approximately 89% of the annual precipitation (929.7 mm), while the dry season extends from November to the following May, with January and February receiving minimal rainfall. Based on 1950–2023 data from the Lijiang Meteorological Station, the area has an annual mean temperature of 12.7°C, with maximum and minimum averages of 18.9 and 6.7°C, respectively. In addition, the Palmer Drought Severity Index (PDSI) shows a decreasing trend, suggesting a gradual shift toward drier conditions in the region (Figure 2).

2.2 Climate data

Five climate factors were used in the analysis of climate-growth relationship, including mean minimum temperature (T_{min}), mean temperature (T_{mean}), mean maximum temperature (T_{max}), precipitation ($Prec$), and PDSI. T_{min} and T_{max} for the Lijiang meteorological station (100.22°E, 26.85°N, elevation 2,380 m) were obtained from the National Oceanic and Atmospheric Administration (NOAA), covering the period 1950–2023. Considering the incomplete and short-term records from nearby meteorological stations, the Lijiang meteorological station was chosen for its long-term and continuous dataset, despite being geographically more distant. Its representativeness for the study

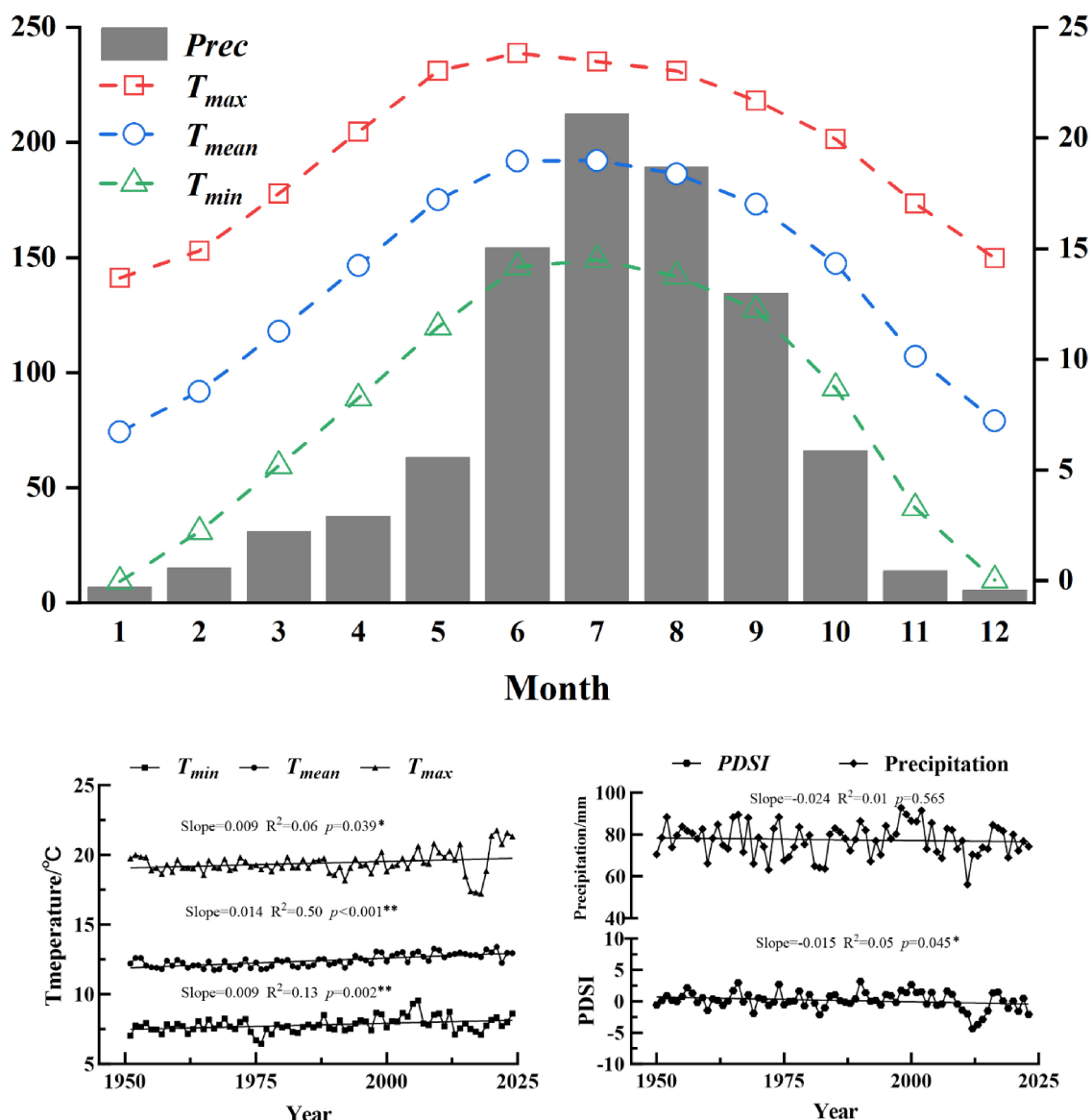


FIGURE 2

Climate data from 1950 to 2023. * $p < 0.05$ and ** $p < 0.01$.

area was evaluated and deemed acceptable, making it the most reliable data source available at present. *Prec* and T_{mean} datasets were sourced from the Climatic Research Unit (CRUTSv.4.07, <https://crudata.uea.ac.uk/cru/data/hrg>) with a spatial resolution of $0.5^\circ \times 0.5^\circ$. *PDSI* data were derived from the global CRU gridded monthly dataset,¹ also at a resolution of $0.5^\circ \times 0.5^\circ$.

2.3 Tree-ring sampling and processing

Tree core sampling was carried out in the Lugu Lake area in May 2020 and March 2024. A total of 168 cores were obtained from 83 individual trees, which covered the three target species in this study (Table 1). Sampling followed standard dendrochronological protocols (Fritts, 2012). Specifically, conifers

with minimal anthropogenic disturbance were selected within the study area. Cores were extracted at breast height (1.3 m above ground) using an increment borer with an inner diameter of 5.15 mm, and efforts were made to reach the pith. Each tree was cored 1–3 times from different directions. The three species were sampled from sites with comparable topographic settings (similar elevation and generally south to southeast aspects) to reduce potential non-climatic influences. All cores were placed in plastic straws and labeled with unique identifiers. Following the tree-ring processing methods described by Stokes and Smiley (Stokes and Smiley, 1996), the cores were brought to the laboratory, mounted on custom wooden troughs (1 cm thick, 1.5 cm wide) using white latex with auxiliary fixation via tape, air-dried naturally, and sanded sequentially with grit sandpaper ranging from 240 to 1,200 mesh until tree rings were clearly visible before being scanned using an EPSON Scan (Expression 11000XL) with parameters set to 24-bit full color and 3,000 dpi resolution. The tree ring widths were

¹ <https://crudata.uea.ac.uk/cru/data/drought>

TABLE 1 Sampling sites information.

Tree species	Latitude	Longitude	Elevation	Aspect	Slope (°)	No. (tree/core collected)
<i>L. potaninii</i>	27°39'44"N	100°44'15"E	3,623 m	SE	10	30/61
<i>P. likiangensis</i>	27°39'31"N	100°44'35"E	3,670 m	S	9	27/56
<i>P. yunnanensis</i>	27°39'37"N	100°44'29"E	3,575 m	S-SE	7	26/51

measured using CDendro and CooRecorder ver 7.3 software with a precision of 0.001 mm (Larsson, 2010), and the measurement results were validated by using the COFECHA program (Holmes, 1983), with poor-quality samples excluded, ultimately retaining 151 cores from 83 trees for the master chronology. Tree-ring chronologies were developed by using the ARSTAN program (Cook, 1986), with a 67% spline function applied to remove the effects of individual tree growth trends. This resulted in three types of chronologies [standard chronology (STD), residual chronology (RES), and autoregressive chronology (ARS)] for each coniferous species, and residual chronologies were used for further analyses to detect climate-growth relationships (Figure 3).

2.4 Data analysis

Given that tree radial growth exhibited a “lag effect” in response to climate, which means its growth is not only related to climatic factors in the current year but also influenced by those in the previous year (Fritts et al., 1965), such as previous September to December. Considering that the tree growing season typically spans from April to October, correlation analyses were conducted between the tree-ring indices of the three conifers and climatic factors, including T_{min} , T_{max} , T_{mean} , $Prec$, and $PDSI$ from September of the previous year to October of the current year. Additionally, to assess the cumulative effects of climate conditions on tree growth, the same set of climatic variables was analyzed for specific phenological periods: the post growing season (September–October) of the previous year, the early growing season (April–May) of the current year, the growing season (June–August) of the current year, and the post growing season of the current year. Here, “post growing season (September–October)” refers to a late-season period potentially associated with carry-over effects on the subsequent year’s growth, rather than implying direct ring formation after growth cessation. These analyses aimed to explore the correlations between tree growth and climatic factors, as well as to identify the primary limiting factors for tree growth. Response function (RFA) was performed by using DendroClim2002 software (Biondi and Waikul, 2004). The response function first extracted principal components from climatic factors before conducting regression analysis, enabling a more accurate reflection of the extent to which sample data are influenced by environmental variables (Blasing et al., 1984). RDA in CANOCO 5 software (Ter Braak and Smilauer, 2002) was then used to further validate the relationships between tree growth and climatic factors. In total, 70 examined climate variables were included in the RDA, consisting of monthly T_{min} , T_{mean} , T_{max} , $Prec$ and $PDSI$ from September of the previous year to October of the current year (14 months $\times$ 5 climatic variables). As a multivariate environmental gradient analysis, RDA evaluated the associations between tree radial growth and climatic factors through regression and principal

component analysis of chronologies and climatic variables (Ter Braak, 1994). Graphs were generated using Origin 2025, GraphPad Prism 10.1.2, and QGIS 3.34.

3 Results

3.1 Chronology statistics

Based on the analysis of the chronology characteristics and statistical features within the common interval (1950–2020) of the three conifers (Table 2), the chronology lengths of *L. potaninii* and *P. yunnanensis* were similar, measuring 121 years and 105 years, respectively, whereas that of *P. likiangensis* was the longest, reaching 237 years. The residual chronology of *L. potaninii* showed higher values in terms of mean sensitivity (MS), variance in the first eigenvector (VFE), standard deviation (SD), signal-to-noise ratio (SNR), and expressed population signal (EPS) compared with those of *P. likiangensis* and *P. yunnanensis*. This indicated that the residual chronology of *L. potaninii* was of better quality and contained more environmental information. Although the mean sensitivity (MS) values of the three residual chronologies were relatively low, this was consistent with the relatively favorable hydrothermal conditions in the Lugu Lake region, where tree growth was not strongly constrained by a single climatic factor. Moreover, the high values of EPS (0.89–0.96) and SNR (8.37–25.95) indicated strong common signals and reliable climatic information in the chronologies. Therefore, the residual chronologies were considered robust and suitable for subsequent climate-growth relationship analyses.

3.2 Response function analysis of tree growth to climate

The response function analysis (RFA) between the residual chronologies and climatic factors (Figure 4) showed that significant relationships were identified at $p < 0.05$. *L. potaninii* was significantly and negatively correlated with September T_{min} of the previous year ($p < 0.05$), and positively correlated with T_{min} from April to May of the current year ($p < 0.05$). The radial growth of *P. likiangensis* showed a significant and negative correlation with February $PDSI$ and September $Prec$ of the current year ($p < 0.05$), while exhibited a significant and positive correlation with September T_{max} of the current year ($p < 0.05$). For *P. yunnanensis*, a significant and negative correlation was found between its radial growth and January $Prec$, as well as May T_{mean} and T_{max} of the current year ($p < 0.05$). Conversely, a significant and positive correlation was observed with November T_{min} of the previous year ($p < 0.05$).

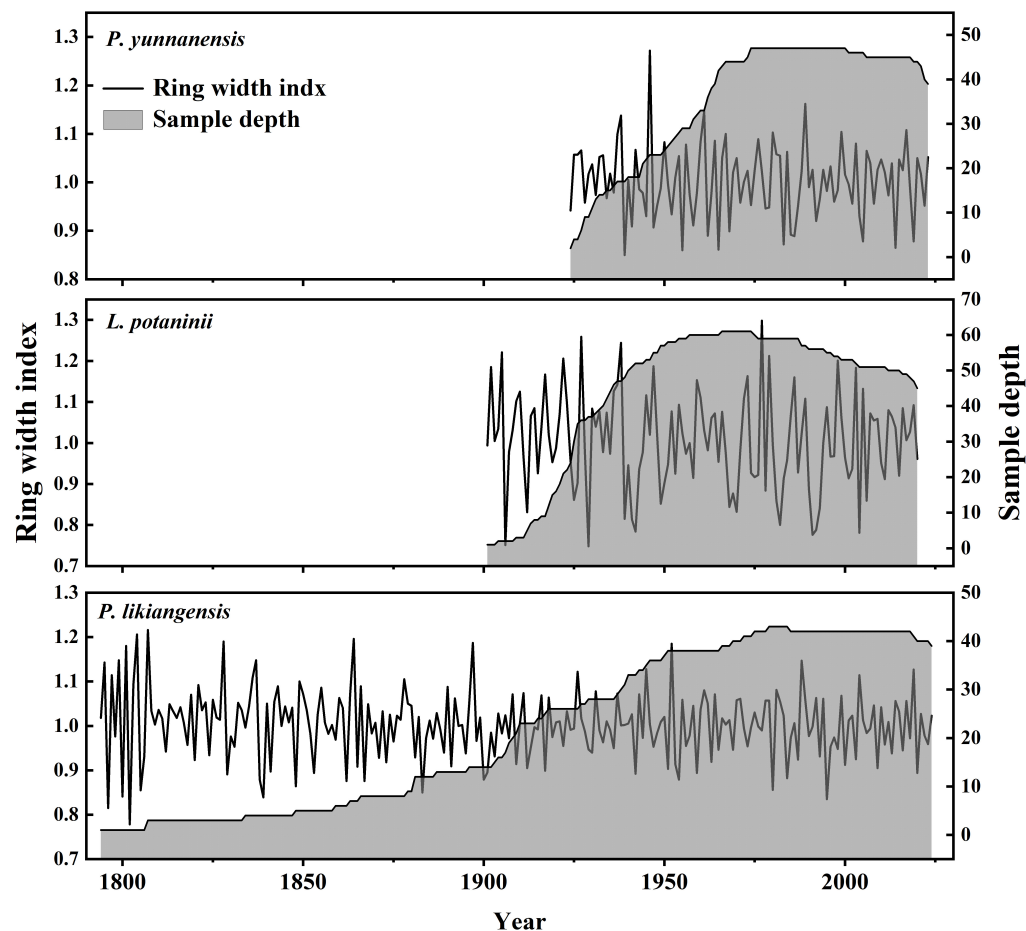


FIGURE 3
Residual tree-ring chronology and sample size.

TABLE 2 Statistics of residual chronologies and common interval analysis.

Residual chronologies	<i>L. potaninii</i>	<i>P. likiangensis</i>	<i>P. yunnanensis</i>
Sample no (trees/cores retained after quality control)	30/61	27/43	26/47
Chronology span/a	1899–2020	1787–2024	1918–2023
Mean sensitivity (MS)	0.13	0.07	0.08
Statistics of common interval analysis		1950–2020	
Variance in the first eigenvector/% (VFE)	39.92	29.68	31.10
Standard deviation (SD)	0.12	0.06	0.07
Signal-to-noise ratio (SNR)	25.95	12.56	8.37
Expressed population signal (EPS)	0.96	0.93	0.89

For the results of correlation analysis between radial growth and growing-season (Table 3), significance was assessed at $p < 0.05$, and *L. potaninii* was significantly and negatively correlated with early growing season *Prec* of the current year ($p < 0.05$) and showed positive correlations with early growing season T_{min} and T_{mean} ($p < 0.05$), as well as post growing season *Prec* and *PDSI* of the current year ($p < 0.05$). For *P. likiangensis*, negative and positive correlations with T_{min} were found in the current growing season and post growing season, respectively ($p < 0.05$). *P. yunnanensis* exhibited a significant and negative correlation with growing season *Prec* of the current year ($p < 0.05$), and a significant and positive

correlation with early growing season *PDSI* of the current year ($p < 0.05$).

3.3 Redundancy analysis of tree growth to climate

The RDA results (Figure 5) showed that the first and second axes collectively explained 19.27% of the variance in the response variables, with the first axis accounting for 11.50% and the second axis for 7.77%. Among the 70 examined climate

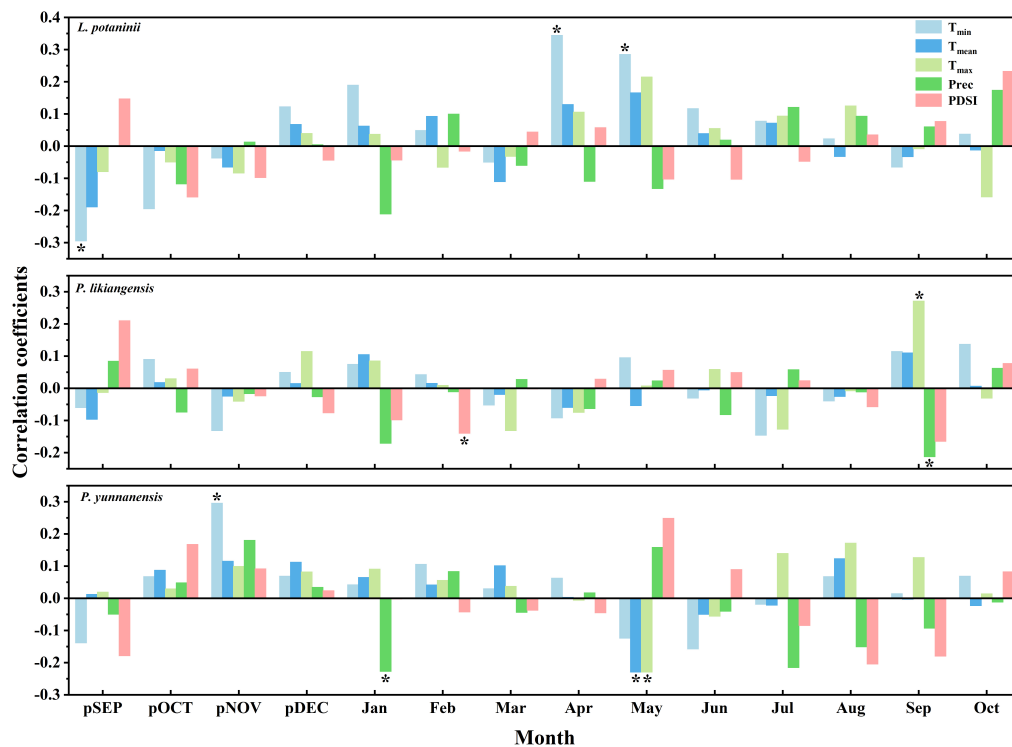


FIGURE 4

Correlation analyses of response function between the residual chronologies and the 630 monthly climatic factors. p: previous year, *indicates a significant correlation at $p < 0.05$ based on 631 bootstrap significance tests implemented by DendroClim2002.

variables, four factors significantly affected tree growth ($p < 0.05$), and temperature-related factors outnumbered precipitation-related ones, indicating that temperature exerted a stronger influence on radial growth. September T_{min} of the previous year and January $Prec$ of the current year had a similar impact on tree growth, as they showed a significant and negative correlations with three conifers. In contrast, September T_{max} of the current year exhibited a significant and positive correlation with three conifers. Current May T_{mean} had a positive effect on the radial growth of *P. likiangensis* and *L. potaninii*, but a negative effect on *P. yunnanensis*.

4 Discussion

4.1 Common responses in climate–growth relationships of study species

Previous September T_{min} showed a significant negative association with the radial growth of *L. potaninii*, while the other two species exhibited negative but non-significant trends. These results suggest that the radial growth of *L. potaninii* may be influenced by both current-year and previous-year temperature conditions, indicating a lag effect (Fritts et al., 1965; Yu et al., 2005). Although trees were in the post growing season, their physiological activities (such as water transport and nutrient accumulation) still persisted (Li et al., 2014). Elevated nighttime temperatures could

lead to enhanced respiration and transpiration, this is detrimental to organic matter accumulation. To meet the water demands of transpiration, trees mobilized stored water within their tissues. Thus, increased temperatures exacerbated water stress, this likely slowed tree growth (Wang et al., 2019). Similar results have been reported in tree-ring studies of *Picea koraiensis* in coniferous forest of northeastern China, as well as in subalpine forests of adjacent Shika Snow Mountain (Zhang et al., 2018; Yuan et al., 2020).

Regarding daytime temperature effects, RDA indicated that current September T_{max} was positively associated with radial growth in all three species at the multivariate level. In contrast, RFA revealed a negative but non-significant relationship between September T_{max} and the growth of *L. potaninii* at the monthly scale. Late-season temperature responses in *P. yunnanensis* was method-dependent. September corresponds to the end of the growing season, during which cambial activity may not have fully ceased in this region. Moderate increases in daytime temperature during this period may favor photosynthesis and carbon assimilation. They may also extend the effective growing season, contributing to the growth variability observed at the multivariate level (Tan et al., 2011). Similar results have been observed in studies of adjacent areas, such as Pudacuo National Park and Small Zhongdian of Shangri-La, and Miyaluo Forest in western Sichuan (Yu et al., 2017; Xu et al., 2013; Zhao et al., 2012).

Given that January precipitation had a significant negative correlation with growth, while temperature showed a positive correlation, this suggests that tree growth was limited by temperature. Winter snowfall was often accompanied by low temperatures. Together with partial freezing of surface soil moisture, these conditions can damage root and impair nutrient

TABLE 3 Correlation analyses between the residual chronologies and the climatic factors in 643 growing season.

Growing season	L. potaninii				P. likiangensis				P. yunnanensis						
	Tmin	Tmean	Tmax	Prec	PDSI	Tmin	Tmean	Tmax	Prec	PDSI	Tmin	Tmean	Tmax	Prec	PDSI
Post growing season of the previous year	-0.086	-0.054	-0.034	-0.024	-0.025	0.013	-0.020	0.023	-0.016	0.036	-0.006	0.046	0.032	0.000	0.004
Early growing season of the current year	0.099*	0.114*	0.017	-0.080*	-0.059	0.053	-0.021	0.058	-0.005	-0.015	-0.002	-0.052	-0.052	0.069	0.117*
Growing season of the current year	0.038	0.016	0.064	0.054	-0.049	-0.123*	0.004	-0.010	-0.021	-0.017	-0.025	0.049	0.050	-0.092*	-0.085
Post growing season of the current year	0.002	-0.009	-0.042	0.072*	0.092*	0.115*	0.039	0.042	-0.035	-0.027	0.051	0.015	0.040	-0.020	-0.027

*Indicates a significant correlation at $p < 0.05$.

uptake. As a result, growth may be reduced and rings become narrower (Zhang et al., 2009; Yue et al., 2022). In addition, increased winter snowfall prolonged spring snowmelt and shortened the tree growth period, thereby restricting radial growth (Vaganov et al., 1999). The negative impacts of winter precipitation on tree growth have also been observed in studies of *Larix gmelinii* in northern Greater Khingan Mountains of northeastern China and *Abies spectabilis* in the Manaslu Range of central Himalaya (Sun et al., 2019; Gaire et al., 2020).

Both RDA and RFA results indicated that the number of temperature-related factors exceeded that of precipitation factors, further highlighting the importance of temperature for tree growth. This was consistent with the high sensitivity of alpine tree species to thermal conditions (Zhao et al., 2024).

4.2 Divergent responses among species to climatic factors

The temperature (T_{mean}) in current May promoted the growth of *L. potaninii* and *P. likiangensis*, particularly for *L. potaninii*, which was also positively influenced by T_{min} and T_{mean} during the early growing season (April–May), highlighting the critical role of spring temperatures in tree growth. For *L. potaninii*, in the early growing season, leaf buds begin to sprout, and xylem cambial cells start to divide and elongate. High temperatures, combined with ample sunlight, create favorable conditions for photosynthesis, thereby increasing the formation of carbohydrates needed for branch development and bud growth (Zhang et al., 2020; Yin et al., 2018). In addition, higher temperatures can increase enzyme activity in plants and promote the activity of soil microorganisms, enabling trees to start growing earlier and have a longer growing season, thereby promoting radial growth (Bhuta et al., 2009; Tang et al., 2018). Spring warming can accelerate the onset of cambial reactivation and advance phenological stages such as budburst and shoot elongation, which are essential for earlywood formation (Rossi et al., 2007; Bhuta et al., 2009). Reports from high-altitude areas such as Haba Snow Mountain and western Sichuan have documented the positive effects of early-season temperature on tree growth (Zhang et al., 2020; Sun et al., 2010).

In contrast, moist conditions during early growing season were crucial for the growth of *P. yunnanensis*, and higher temperature during this period (particularly in May) inhibited its growth. The radial growth of *P. yunnanensis* relies on spring moisture conditions, likely due to its high water demand (Shen et al., 2025). *PDSI* reflected the availability of soil moisture, which directly affected cambial activity and, consequently, xylem formation (Dai et al., 2004; Gruber et al., 2010). *P. yunnanensis* had a high water demand at the beginning of the growing season to promote the expansion of xylem cells. However, high temperatures and low precipitation during this period (Figure 2) made soil moisture availability a key limiting factor for tree growth (Yang et al., 2018). The sensitivity of *P. yunnanensis* to spring drought may be attributed to its high water demand during early growth stages and limited surface moisture availability. Although it possesses a relatively deep root system, insufficient early-season precipitation combined with high evaporative demand can restrict water uptake. Additionally, its high

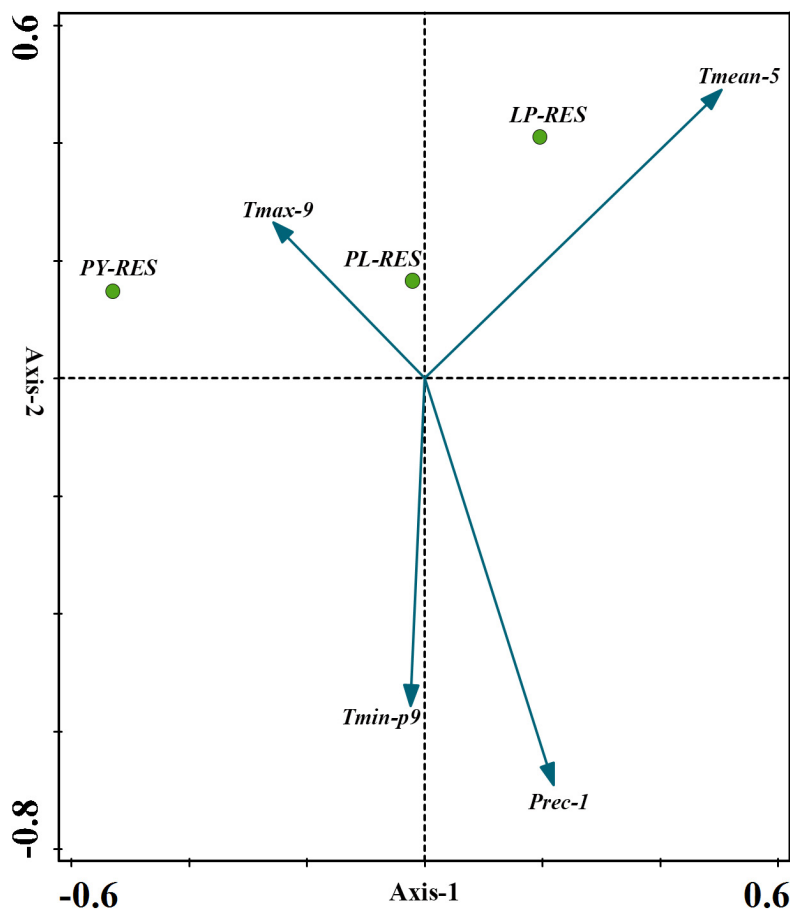


FIGURE 5

The RDA between three chronologies and the climate variables for the common period (1950–2020). Only significant ($p < 0.05$) climate variables were presented. The longer vector of the climate factor indicated the greater contribution. The shorter perpendicular line between the chronology and the climate vector (itself, or the extension line) indicated a higher correlation between them. Chronology and climate vectors pointing the same direction represented a positive correlation, and in opposite directions, indicated a negative correlation.

stomatal conductance increases water loss through transpiration, exacerbating drought stress under warming conditions (Shen et al., 2025). The negative impact of spring drought on the radial growth of *P. yunnanensis* has also been reported in other areas of northwestern Yunnan, such as Haba Snow Mountain and Yulong Snow Mountain (Zhang et al., 2020; Yang et al., 2018).

4.3 Species-specific responses to climate variability

For *L. potaninii*, *Prec* and *PDSI* in the post growing season positively influenced radial growth (Table 3). Favorable moisture conditions toward the end of the growing season may promote carbon storage, bud formation, root activity, and soil moisture recharge prior to dormancy, thereby exerting carry-over effects on radial growth in the subsequent growing season (Xu et al., 2021).

Elevated temperatures during the growing season (June–August) were detrimental to the growth of *P. likiangensis*. On the one hand, the growing season had a high water demand. If nighttime temperatures rose without a corresponding increase in precipitation, it would increase tree transpiration, leading

to a water balance disorder in the trees, thereby inhibiting the enlargement and division of cambial cells and ultimately affecting radial growth (Lu et al., 2015; Hou et al., 2024). On the other hand, higher nighttime temperatures enhanced respiration, consuming photosynthetic products and thus restricting tree growth (Zhao et al., 2016). Notably, this negative response contrasts with the positive temperature–growth relationships reported for *P. likiangensis* at nearby high-altitude treelines (e.g., Yulong and Haba Snow Mountains) (Yang et al., 2018; Zhang et al., 2020), suggesting a shift in climatic limiting factors: while warming can benefit colder treelines by extending the growing season (Rossi et al., 2007). At our sites, higher temperatures were more likely to increase evaporative demand and respiratory carbon costs, and may be further amplified by relatively closed-canopy competition for water (Zhang et al., 2009). Additionally, the radial growth of *P. likiangensis* showed a significant correlation with the entire growing season, but not with individual months (June–August), indicating the importance of the cumulative effect of temperature on the radial growth of *P. likiangensis*. *P. yunnanensis* showed a significant and negative correlation with growing-season *Prec*, possibly because after water accumulation in the early stage, excessive water during the growing season caused anaerobic respiration in

the roots, consuming photosynthetic products and producing harmful substances such as alcohol, which affected growth (Kreuzwieser and Rennenberg, 2014). Similar conclusions have been confirmed in previous studies (Zhang et al., 2018; Li et al., 2014).

In this study, the results of RDA and RFA were largely consistent. RDA offered distinct advantages over traditional RFA, as it could more precisely delineate the response patterns, thereby identifying the critical impacts of temperature in September of the previous year, May and September of the current year, and *Prec* in January on the three species. In the RFA, September T_{min} of the previous year exhibited negative correlations with all three species, although statistical significance was only observed for *L. potaninii*. Similarly, January *Prec* of the current year showed negative correlations with all three species, but significance was limited to *P. yunnanensis*, which complicated the generalization of patterns. Additionally, while RFA detected that September *Prec* of the current year constrained the growth of *P. likiangensis*, this relationship was not captured by RDA. This discrepancy highlighted both the consistency and complementarity of the two methods. Therefore, their integrated application enabled a more comprehensive and accurate identification of the primary climate factors influencing the radial growth of the three conifers.

Taken together, the results presented above demonstrate pronounced species-specific responses of the three conifers to climate variability, providing a basis for understanding their potential growth responses under future climate change. Building on this, existing climate scenario simulations allow a qualitative discussion of possible growth trajectories and associated adaptation risks. Under the RCP4.5 scenario based on the EC-EARTH model (CMIP5), previous studies suggested that the annual mean temperature in the study area may exhibit an overall upward trend, with relatively pronounced warming in April and May, while precipitation may show a slight decrease (Hazeleger et al., 2010). This model-based information is used here to provide a general climatic context rather than quantitative projections. From a qualitative perspective, reduced precipitation could potentially influence radial growth of the three conifers, particularly for *P. likiangensis* and *P. yunnanensis*. For *L. potaninii*, the growth response to reduced precipitation may be more complex, as potentially beneficial effects associated with reduced moisture stress could partly offset inhibitory effects. The impacts of future warming on the three species may therefore involve both positive and negative effects, potentially favoring *L. potaninii* and *P. likiangensis*, while higher temperatures may constrain the growth of *P. yunnanensis*. In addition, our results indicate that other temperature variables (T_{min} and T_{max}), especially T_{min} , play important roles in regulating conifer growth. Therefore, robust projections of future tree growth would require greater consideration of T_{min} and T_{max} based on bias-corrected and downscaled CMIP6 multi-model ensembles, which is beyond the scope of the present study. Future research could further utilize CMIP6 multi-model ensembles, combined with various emission pathways, to provide quantitative regional projections of temperature and precipitation fluctuations. Such efforts will be essential for enhancing the precision and reliability of climate risk assessments.

5 Conclusion

This study shows that co-occurring conifer species in subalpine forests could share common climatic constraints while exhibiting distinct, species-specific growth sensitivities. Overall, temperature-related factors played a dominant role in regulating radial growth, whereas moisture availability exerted additional controls depending on species and season. The study highlights pronounced species-specificity in conifer growth responses to climate, even among co-occurring species. Under ongoing climate change, continued warming may alleviate cold limitation for cold-limited conifers, but it may also increase drought- and heat-related risks for moisture-limited species by intensifying evaporative demand and carbon costs. Adaptive forest management should account for species-specific climate vulnerability. For *P. yunnanensis*, priorities include using drought-tolerant planting material or companion species, conserving soil moisture, and enhancing dry-season water conservation. For *P. likiangensis*, avoiding over-thinning and protecting moist microsites may buffer heat and evaporative stress. For *L. potaninii*, maintaining mixed-species stands and tracking seasonal moisture can support resilience. Therefore, multi-species dendroclimatological assessments provide critical information for evaluating differential vulnerability and informing species-specific conservation and adaptive forest management strategies in mountain ecosystems. Future work integrating additional sites and physiological evidence would further strengthen regional generalization and mechanistic understanding.

Data availability statement

The original contributions presented in this study are included in this article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

TY: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. YueZ: Conceptualization, Methodology, Visualization, Writing – original draft. YK: Data curation, Investigation, Software, Writing – original draft. SX: Data curation, Funding acquisition, Project administration, Software, Writing – review & editing. CT: Formal analysis, Writing – review & editing. YunZ: Conceptualization, Funding acquisition, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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