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Climatic influences on intra-annual stem variation of *Larix principis-rupprechtii* in a semi-arid region

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Intra-annual monitoring of stem radial growth dynamics of trees and detecting how tree growth responds to changing climatic conditions are crucial for predicting the future growth dynamics under increasing drought conditions. Here, we monitored the intra-annual stem radial growth dynamics of seven *Larix principis-rupprechtii* using point dendrometers to investigate the influence of climate variables on the intra-annual growth of *L. principis-rupprechtii* in the growing season. The average stem radial growth of *L. principis-rupprechtii* started on 29 April and stopped on 17 August based on the sigmoid Gompertz functions. The intra-annual stem radial growth of *L. principis-rupprechtii* showed a parabolic trend, with its growth decreased when the temperature and sunlight duration hours exceeded certain thresholds. The vapor pressure deficits (VPD) strongly influenced tree intra-annual growth over other climatic factors in the growing season. Stem radial growth of *L. principis-rupprechtii* decreased significantly with increasing VPD when VPD ranged from 0.5 to 0.8 kPa. Intra-annual stem radial growth of *L. principis-rupprechtii* was severely inhibited when VPD was higher than 0.8 kPa. In contrast, tree stem radial growth reached the maximum when VPD was lower than 0.5 kPa. Our study highlighted the important influences of major limiting climatic factors on the stem radial growth of trees in semi-arid regions.

KEYWORDS

stem radial growth, point dendrometer, climate response, vapor pressure deficits (VPD), threshold effects, *Larix principis-rupprechtii*

Introduction

Climate changes significantly influenced intra-annual tree growth and eventually affected forest productivity (McDowell et al., 2008; Deslauriers et al., 2017). Changing climatic conditions influenced the stem radial growth of trees to different degrees (Betsch et al., 2011; Cabon et al., 2020; Zhang Q. et al., 2022). Growth declines due to rapid warming have been observed in Dahurian larch populations in the western Daxingan Mountains of northeastern China (Zhang X. L. et al., 2016). High vapor pressure deficits (VPD) due to changes in temperature and moisture conditions has become a significant limiting factor for the intra-annual growth of trees (Battipaglia et al., 2014; Trotsiuk et al., 2021). Therefore, understanding the response of the stem radial growth variation to climate factors is crucial to predict tree stem growth under future climate change.

Dendrometer provides a continuous automatic recording of intra-annual stem radial growth processes without destroying samples (Zweifel et al., 2001; Deslauriers et al., 2003). It is widely used in studies exploring the relationship between intra-annual stem changes in trees and climate change (Zweifel and Hasler, 2000; Oberhuber et al., 2014). Stem radius fluctuations recorded by dendrometer include growth-induced irreversible stem expansion and tree water deficit-induced reversible stem shrinkage (Deslauriers et al., 2007). Tree stem growth can be separated from daily variation in water effects by using a zero-growth model (Zweifel et al., 2016). Temperature was the most important factor limiting tree stem radial growth at high altitudes and latitudes (Turcotte et al., 2009; Li et al., 2013). Stem radial increment was positively correlated with temperature before the growing season, while it was mainly limited by precipitation and relative humidity after early July for Taiwan pine (Liu X. S. et al., 2018). Therefore, exploring the intra-annual radial growth of trees is essential to understand the relationship between tree stem growth and climate.

Many large-scale forestry projects have been recently carried out in northern China (Zhang Y. et al., 2016). *Larix principis-rupprechtii* is one of the main species used in these projects. *L. principis-rupprechtii* is widely distributed in the mountainous areas of north-central China and is the main species in the alpine coniferous forest belt of North China. However, planted forests were sensitive to climate change (Payn et al., 2015). *L. principis-rupprechtii* had significantly lower resistance and resilience than other tree species during extreme drought (Xiao et al., 2021). Rapid warming has led to a growth decline in the southern edge of larch populations (Liu Y. Y. et al., 2018). Traditional dendrochronology usually focuses on analyzing the relationship between inter-annual tree growth and climatic factors (Evans et al., 2017; Jiang et al., 2018). How the intra-annual stem radial growth of *L. principis-rupprechtii* is affected by climate factors is still lacking.

Here, we investigated the intra-annual daily stem growth of *L. principis-rupprechtii* and its responses to climatic factors based on high-resolution dendrometer data. The aims of our study were to: (a) analyze the relationship between the intra-annual growth of *L. principis-rupprechtii* and climate factors to clarify the major limiting climate factors and (b) explore the response of intra-annual stem radial growth of *L. principis-rupprechtii* to changes in major climatic factors.

Materials and methods

Study area

The study area is located in the mountainous regions of north-central China (41.52°N, 117.40°E, **Figure 1A**). It is a semi-arid and semi-humid climate zone. Long-term records (1990–2021) from the meteorological station in WeiChang county (41.58°N, 117.46°E) were obtained from China Meteorological Administration.[1] The annual mean temperature is 5.5°C. The coldest month is January, with an average temperature of -12.4°C and an extreme minimum of 23.7°C. The hottest month is July, with an average temperature of 21.3°C (**Figure 2**). Annual precipitation ranges from 300 to 560 mm. Precipitation is mainly concentrated in summer, with June to August accounting for more than 60% of the annual precipitation. The main types of soil in the mountainous areas of the study region are gray forest soil, black calcium soil, and light black calcium soil (Wang et al., 2015).

L. principis-rupprechtii is the dominant tree species in the study area (**Figure 1B**). The main shrub species are *Padus racemosa*, *Populus davidiana Dode*, *Sorbus pohuashanensis*, *Lespedeza daurica*, *Rosa davurica*, etc. The understory herbs are *Carex lanceolata*, *Juncus effusus*, *Potentilla longifolia*, *Sanguisorba officinalis*, *Thalictrum peticulata*, etc.

Data collection

Dendrometer measurements

Dendrometer can monitor stem radial growth changes in trees and characterize growth-climate relationships with high temporal resolution without substantial damage to the formative layer and woody tissue (Deslauriers et al., 2003). The sensing probe can sense the stem radial variation of the tree and convert it into a current signal, which is transmitted to the dendrometer data logger. Dendrometers could record intra-annual stem radial growth (Deslauriers et al., 2003; Vieira et al., 2013; Oberhuber et al., 2014). In July 2020, we selected seven well-grown *L. principis-rupprechtii* trees with relatively straight trunks in the study area (1308 m). The stem radial variations include reversible and irreversible processes (Zweifel et al., 2006). To retain a more realistic stem radial growth signal, we used a knife to carefully remove the outermost outer bark and dead bark tissue without damaging the cambium to ensure close contact of the dendrometer with the stem to reduce the impact of bark expansion and contraction on the dendrometer data and then installed the dendrometer (Model: D1, measurement range 8890 μm, linearity $<$ 5%, resolution:

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[1] http://data.cma.cn

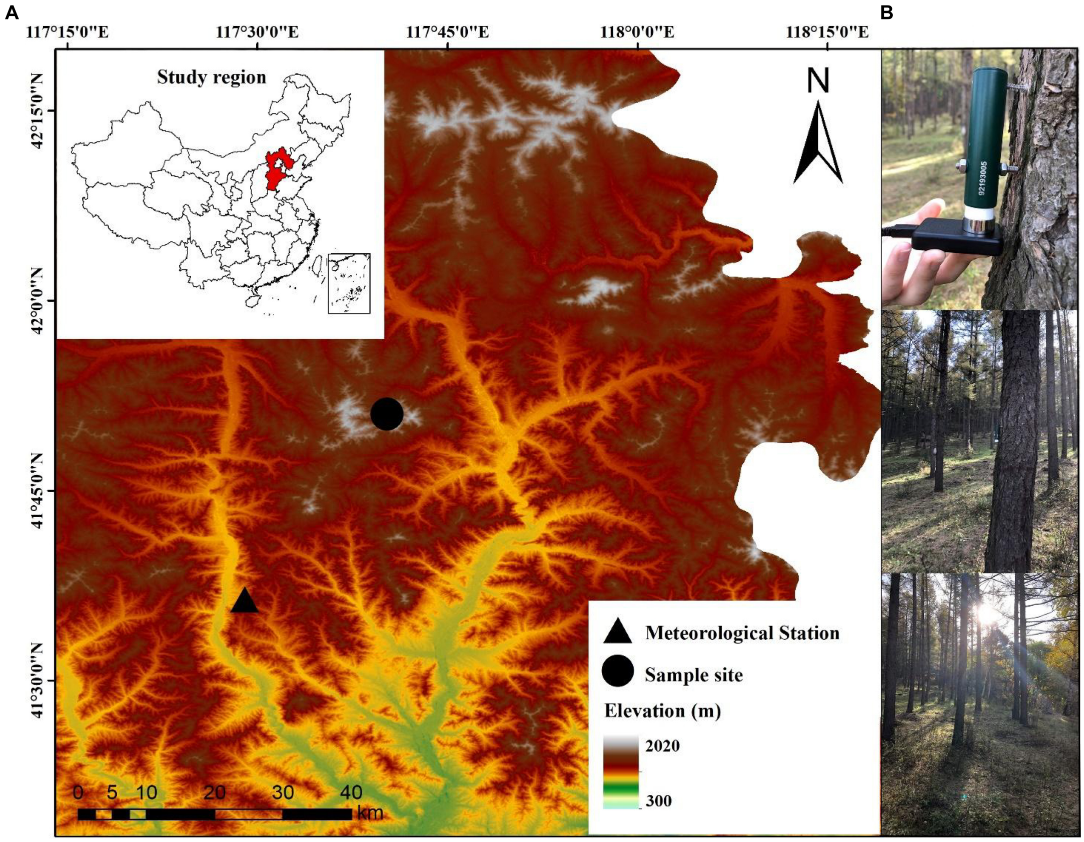

FIGURE 1
(A) Location of the monitoring site (black circle) and the nearest meteorological station (black triangle). **(B)** Pictures show the forest structure and composition of our monitoring site, from top to bottom.

0.27 μm thermal expansion coefficients of < 0.1 μm /K, TMOST, Praha, Czechia). All point densitometers were installed at 1.3 m breast height on each sampled tree. The monitoring period spanned from July 2020 to September 2021. Daily trunk shrinkage and swelling dynamics were recorded at 15-min intervals, with 96 data recorded daily. Considering that transpiration during the daytime causes stems shrinkage (Zweifel et al., 2001), we chose to take readings during the morning hours (7:30 to 8:30 a.m.) to reduce the bias caused by transpiration during the daytime hours.

Climatic data

We obtained daily climate data from the China Meteorological Administration (see text footnote 1) for the WeiChang station (41.58°N, 117.46°E, **Figure 1**), which is 34.7 km far from the study area. Daily precipitation (Pre), air temperature (mean, Tmean; minimum, Tmin; and maximum, Tmax), soil temperature (T), relative humidity (RH), and sunshine duration (SD) were collected. The vapor pressure deficit (VPD) was calculated based on air temperature (T) and relative humidity (RH) using the following equation (Campbell and Norman, 1998):

$$VPD = a \times e^{\left(\frac{bT}{T+c}\right)} (1 - RH) \quad (1)$$

where $a = 0.6108$, $b = 17.27$, $c = 237.3$.

Historical and future monthly temperature and relative humidity data from CMIP 5 Models were downloaded from the following website http://climexp.knmi.nl/selectfield_cmip5.cgi?id=someone@somewhere. The gridded data in the study area were selected from multi-model ensemble simulations to calculate the regional mean temperature and relative humidity. Historical and projected VPD were calculated based on temperature and relative humidity for the RCP26 scenario for the period 1990–2100.

Extraction of stem radial variation and determination of growing season

We used high-precision dendrometers to monitor the daily stem radial growth variation of *L. principis-rupprechtii*,

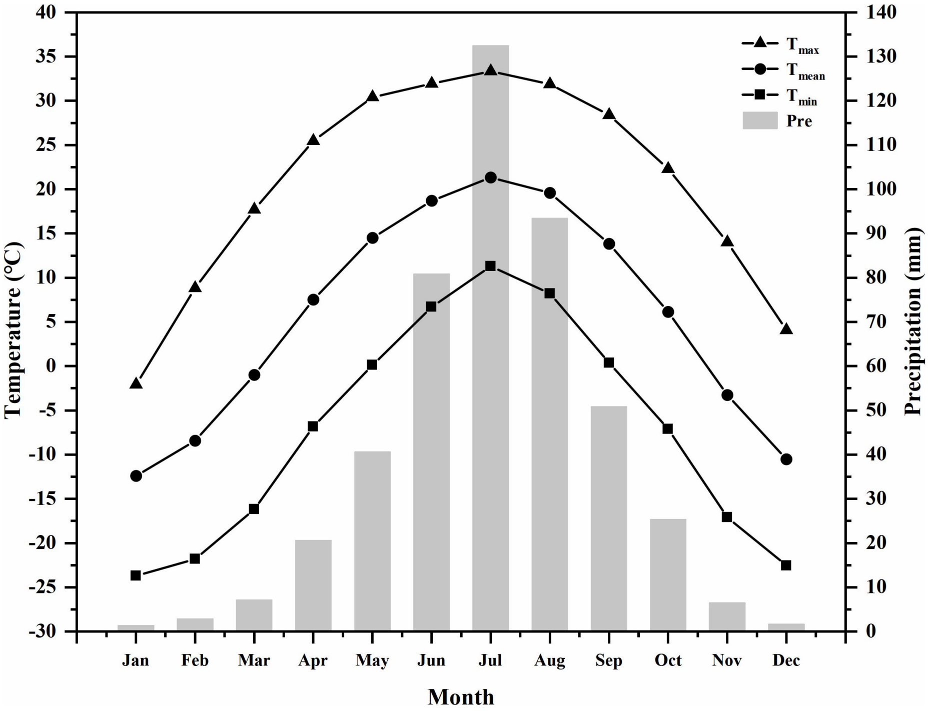

FIGURE 2
Monthly maximum (Tmax), mean (Tmean), and minimum (Tmin) temperatures and monthly precipitation (Pre) for WeiChang county from 1990 to 2021.

recording 96 data per day. The maximum value was defined as the maximum measurement value of the daily cycle in a day (Bouriaud et al., 2005). The daily maximum values from tree stem radius data were extracted by the "dendRoAnalyst" package of the R software (R Core Team, 2010; Aryal et al., 2020) to obtain the maximum daily stem radial variation series for each tree. The data from seven monitored trees were averaged to obtain the average growth condition of the species. The difference between the maximum values for two consecutive days was calculated as the daily radial change (SRC) of tree trunks. The sigmoid Gompertz growth model was used to fit the cumulative daily stem radial growth variation curve to simulate the intra-annual stem radial growth process because of its flexibility and asymmetry (Deslauriers et al., 2003; Duchesne et al., 2012). The function was as follows:

$$y = \mathrm{A} \times exp\left[-exp\left(\beta - \kappa \times t\right)\right] \tag{2}$$

where y is the daily stem radial growth maximum raw measurements; A is the upper asymptote; β is the x-axis placement parameter; k is the rate of change parameter; and t is time (expressed as a day of the year, DOY).

Based on the results of the model, the onset and end days of tree stem radial growth were defined when 5 and 95% of the total cumulative radial variation were reached. The length of the growing season was the difference between the onset and end days (van der Maaten et al., 2018).

A zero-growth model was used to distinguish between tree water deficit-induced reversible stem shrinkage (TWD) and growth-induced irreversible stem expansion (GRO) (Zweifel et al., 2016). The model assumes that cells grow stagnant when the stem radius is less than the previous maximum (saturated state). Under this assumption, the irreversible growth processes and reversible water fluctuations are separated from continuous stem radius fluctuations (**Figure 3**). Stem growth was defined as the process in which the stem radius exceeds the last great value. The daily stem radial increase (SRI) was the difference between the GRO of two consecutive days.

The growth process of the zero model was calculated as follows:

$$GRO = \begin{cases} SR(t) - max\left[SR(<t)\right], \\ SR(t) \geq max\left[SR(<t)\right] \\ 0,\ SR(t) < max\left[SR(<t)\right] \end{cases} \tag{3}$$

where t is the current moment; $< t$ is from the beginning to the current moment; GRO is growth-induced irreversible stem expansion; SR is the stem radius fluctuations.

Statistical analysis

Spearman correlation analysis was used to analyze the relationship between SRI and meteorological factors (e.g.,

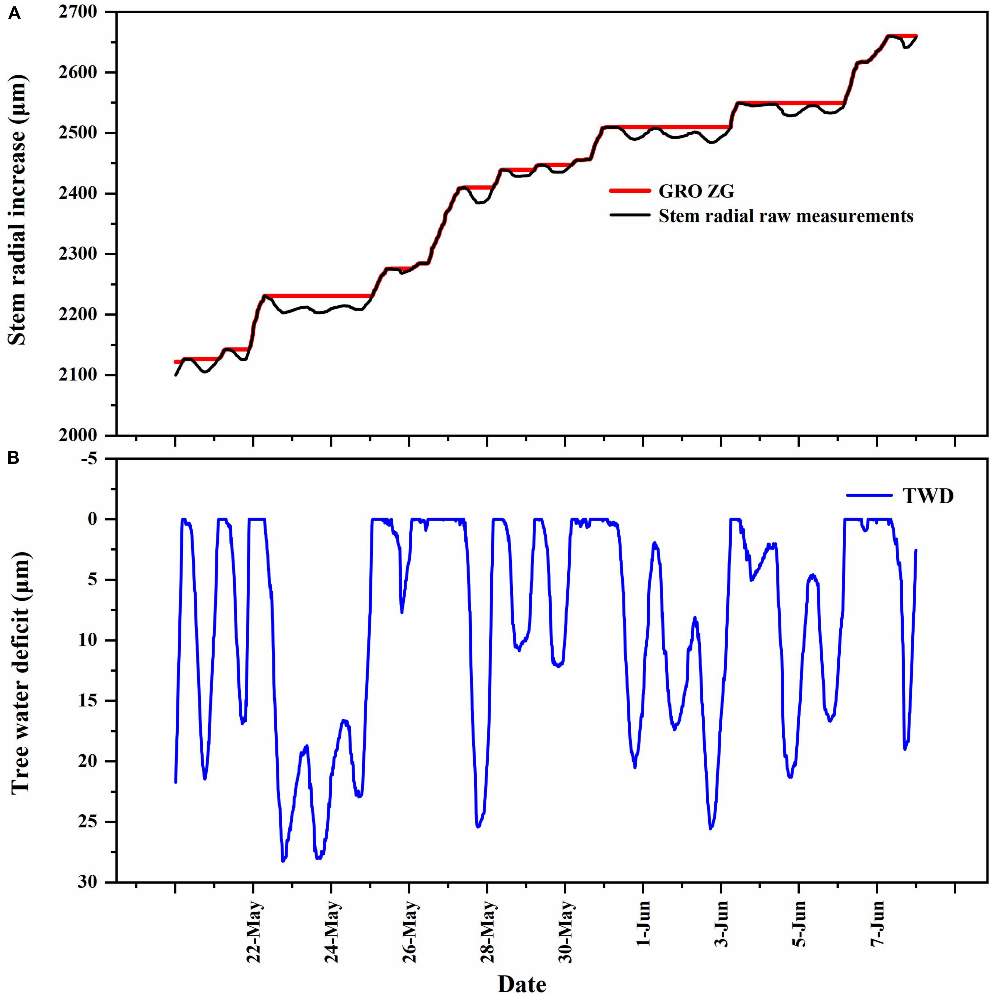

FIGURE 3
Tree stem radial raw measurements (black line, **A**) and the growth-induced irreversible stem expansion (GRO) according to the zero growth concept (red line, **B**). The difference between irreversible growth and stem radial raw measurements is tree water deficit (TWD) (blue line, **B**). Data are for the period from May 21 to June 8 in 2021.

VPD, Air temperature, Precipitation, Relative humidity). A machine learning algorithm, Random Forests, was used to represent variable importance (VIM) and to rank the important variables (Anderegg et al., 2018). The importance of climatic factors on the irreversible growth of *L. principis-rupprechtii* was assessed using Random Forests. Linear mixed models (LMM) were used to analyze the relative contribution of different climate variables to SRI. After excluding the less correlated climatic factors by the model selection, we selected the climatic factors which were significantly correlated to growth as fixed effects. Individual trees and years were set as random effects. The influence of different climate variables on daily stem radial growth was analyzed by assessing standardized regression coefficients to understand the relatively important climatic factors affecting stem radial growth. The model was built using the "nlme" package of the R software (Pinheiro et al., 2015).

To quantify the response of intra-annual stem radial growth of *L. principis-rupprechtii* to climate factors, we grouped Tmean per degree Celsius (°C) and the sunshine duration (SD) per 1 hour within their respective ranges in 2021. The curves were fitted with the parabolic functions. To obtain threshold values of VPD and its relationship with the GRO variation of *L. principis-rupprechtii*, we fitted the logistic curves to assess how *L. principis-rupprechtii* intra-annual growth variation varies with different levels of VPD. VPD was divided into eight different scales on a gradient of 0.1 kPa. Since fewer VPD values lay between 0–0.4 and 1.0–1.5 kPa, we combined these bins. The monitoring period was relatively short, and the data for 2020 was incomplete, so the end time was referenced to the end of stem radial growth in 2021.

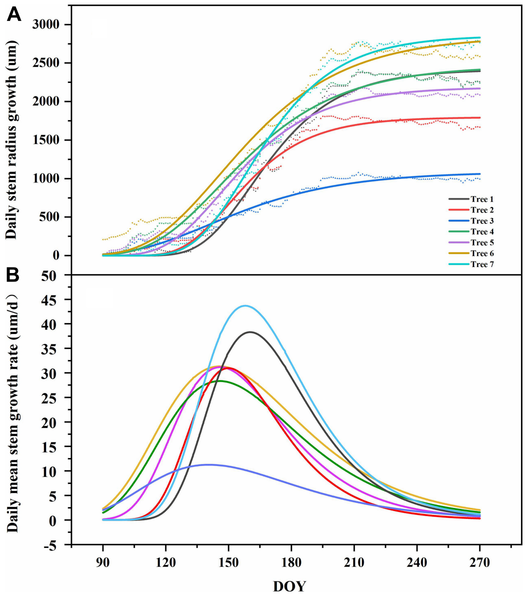

FIGURE 4
Observed and modeled stem radial increment **(A)** and daily growth rates of seven *L. principis-rupprechtii* trees in 2021 **(B)**. The points and lines indicate the daily maximum radius and the original measurements of the sigmoid Gompertz function model curves.

Results

Growth season identification

The Gompertz curves explained 96 and 99% of the change in daily maximum stem radial data for *L. principis-rupprechtii* in 2021 (**Supplementary Table 1**). The stem radial growth curves of *L. principis-rupprechtii* were all "S" shaped (**Figure 4A**). The stem radial growth rate of the tree was single-peaked and showed a slow-fast-slow trend (**Figure 4B**). The onset days of the stem radial growth in *L. principis-rupprechtii* in 2021 ranged from 12 April to 15 May (DOY 102–135), and the cessation of stem growth ranged from 20 July to 4 August (DOY 219–249). The average stem radial growth started on 29 April and stopped on 17 August 2020 (**Table 1**). Consequently, the average growing season lasted 110 days. The average cumulative growth of the seven sample trees was 2.21 mm ± 1.12 mm, and the maximum daily growth rate was 30.7 μm ± 19.4 μm (**Table 1**).

Relationship between stem radial growth and climatic factors

Precipitation in July–August 2020 was significantly less than the same period in 2021. Mean VPD in July–August 2021 was 0.42 kPa, with a maximum of 0.82 kPa, while mean VPD in the same period was 0.54 kPa with a maximum of 1.27 kPa in 2020, the average VPD was 0.12 kPa higher compared to 2021.

Stem radial increase had significant differences between the 2 years (**Figure 5**). SRC ranged from -24 to 97 μm in July–August of 2021, compared to a maximum of 120 μm and a minimum of -97 μm in July–August of 2020. SRC and VPD showed a significant negative correlation during the growing season ($p < 0.001$, **Supplementary Table 2**).

Stem radial increase of *L. principis-rupprechtii* was significantly and positively correlated with precipitation and relative humidity (RH). Mean soil temperature (ST), maximum air temperature (Tmax), vapor pressure deficit (VPD), and sunshine duration (SD) had negative influences on daily stem radial growth during the growing season (**Figure 6**).

The results from Random Forests showed that VPD had the highest value of the increase in mean squared error (%IncMSE), indicating that VPD mainly influenced the SRI in both 2020 and 2021 (**Supplementary Figure 1**). LMM analyzed the contribution of each climatic factor to the SRI in *L. principis-rupprechtii*. The results of LMM confirmed that the absolute value of the standardized regression coefficient for VPD was the largest one (**Table 2** and **Supplementary Figure 2**). The intra-annual stem radial growth of *L. principis-rupprechtii* was relatively more influenced by VPD.

TABLE 1 Parameters estimated from the Gompertz functions.

Trees	Onset of growth (DOY)	Ending of growth (DOY)	Cumulative seasonal growth (mm)	Growing season length (Days)	Max rate (um/day)
Trees1	135	224	2.38	89	38.3
Trees2	127	219	1.81	92	31.0
Trees3	102	249	1.09	147	11.3
Trees4	111	232	2.42	121	28.3
Trees5	118	223	2.19	105	31.1
Trees6	109	236	2.80	127	31.3
Trees7	132	222	2.79	90	43.7
Mean	119	229	2.21	110	30.7

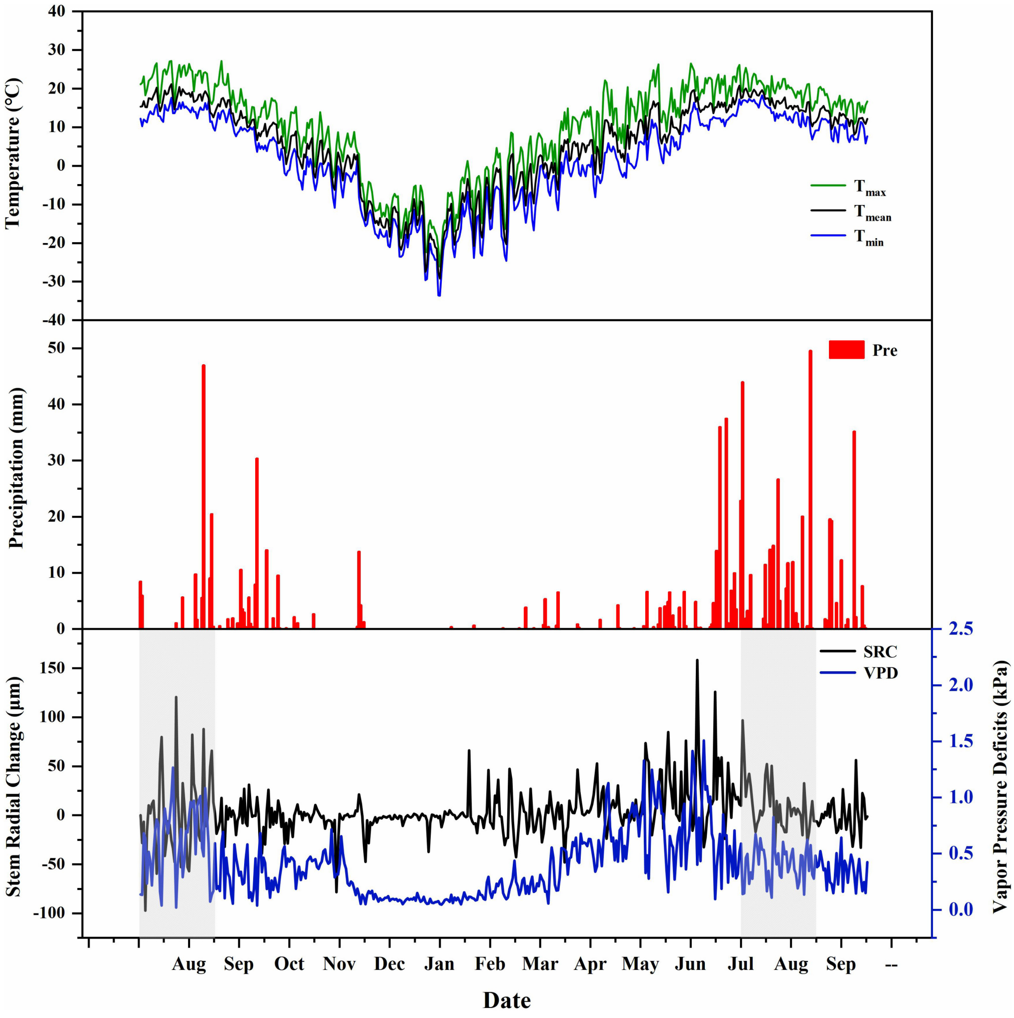

FIGURE 5

Daily climatic conditions at the meteorological stations in WeiChang station during the monitoring period from July 2020 to September 2021. From top to bottom: daily minimum (blue), average (black), and maximum (green) temperature; precipitation (red); changes in stem radial change (black line: SRC) of mean trees and vapor pressure deficits (blue line: VPD). The shaded part is the comparison of SRC and VPD in the same period in 2 years.

The results of the parabolic fit between the intra-annual stem radial growth in 2021 and climate factors of *L. principis-rupprechtii* showed that the highest growth increase occurred at an optimum sunshine duration of about 7 h (**Figure 7A**). *L. principis-rupprechtii* grew most rapidly when the temperature at approximately 18°C (**Figure 7B**).

Threshold values of vapor pressure deficits on the stem radial growth

Logistic models explained 98% (2020) and 99% (2021) of the total variation between GRO and VPD in *L. principis-rupprechtii* (**Supplementary Table 3**). The intra-annual stem radial growth (2020–2021) comparison demonstrated that the intra-annual stem growth of *L. principis-rupprechtii* showed different sensitivity to changes in VPD ranges (**Figure 8**). When VPD < 0.5 kPa, GRO was less influenced by VPD, and tree stem growth reached a maximum value. Radial stem growth was significantly reduced when VPD ranged at 0.5 kPa $<$ VPD < 0.6 kPa. The GRO of *L. principis-rupprechtii* was severely restricted when VPD was above the range of 0.8–0.9 kPa.

Future changes in vapor pressure deficits

From 1990 to 2020, the mean vapor pressure deficit (MVPD) in May–July showed an increasing trend, and VPD

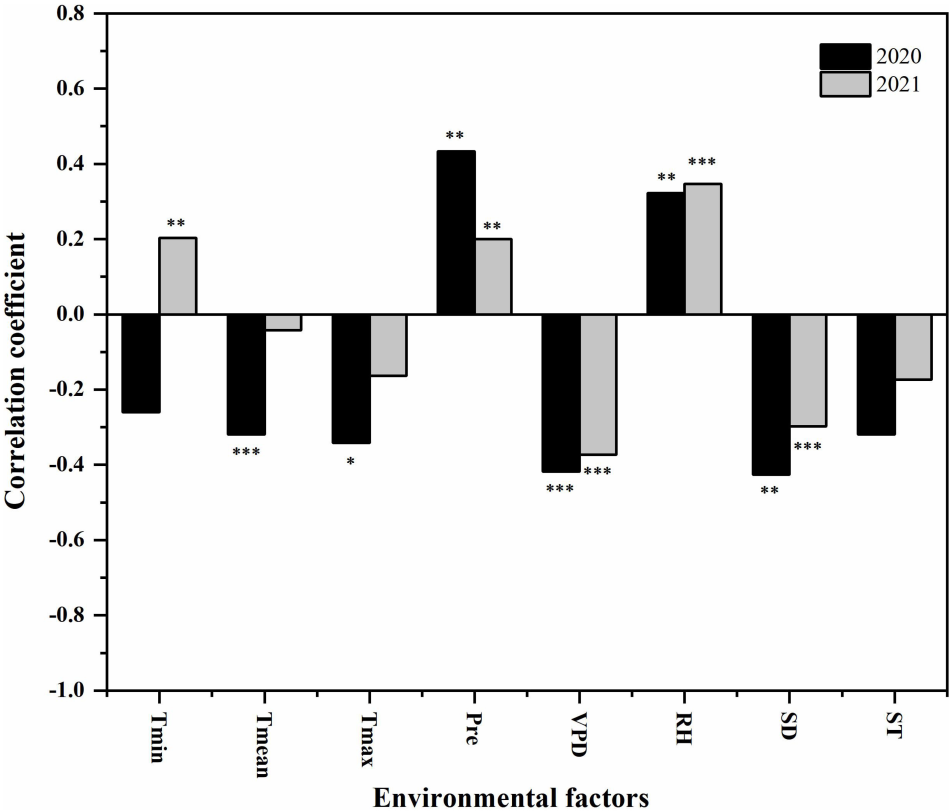

FIGURE 6

Spearman correlations of SRI and air temperature (mean, Tmean; minimum, Tmin; and maximum, Tmax), precipitation (Pre), relative humidity (RH), vapor pressure deficit (VPD), sunshine duration (SD), and soil temperature (ST) in 2020 and 2021. Significance levels (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

already exceeded 0.8 kPa in 2020 (**Figure 9A**). In the future, VPD may continue to rise in our study area. MVPD will increase significantly during 2021–2050 (**Figure 9B**). From 2051 to 2100, MVPD will fluctuate horizontally with no clear trend. It is worth noting that MVPD values will always be above the 0.8 kPa level from 2051 to 2100 (**Figure 9C**).

Discussion

Impact of environmental factors on intra-annual stem radial growth

Tree growth was influenced by multiple climatic factors (Zhang et al., 2019; Zhang X. et al., 2022). Temperature affected the transport and distribution of the products of photosynthesis (Rossi et al., 2008; Deslauriers et al., 2016). In general, the positive effect of temperature on stem radial growth may be associated with the optimum temperature (Buras et al., 2017; Oladi et al., 2017). The maximum stem radial growth of *L. principis-rupprechtii* roughly corresponded to an average temperature of 18°C during the growing season (**Figure 7B**). However, higher temperatures and longer sunshine durations (> 7 h, **Figure 7A**) led to a decrease in relative humidity and an increase in VPD, which increased water stress in *L. principis-rupprechtii* (Zhang Q. et al., 2022). By contrast, the positive effect of precipitation and relative humidity on tree stem radial growth may be explained by swelling trunk hydrological processes (**Supplementary Figure 3**). Rainfall events can alleviate water deficit in tree trunks by increasing soil moisture and promote trunk cell expansion and growth (Steppe et al., 2006; Urrutia-Jalabert et al., 2015). The effects of moist atmospheric conditions on stem radial growth were manifest in short time scales (Oberhuber et al., 2014). In addition, rainfall events can reduce the demand for internal plant water, and rainwater intercepted by tree branches can be used to meet the transpiration demand of canopy (Katz et al., 1989; Deslauriers et al., 2007).

The influences of VPD on intra-annual stem radial growth of *L. principis-rupprechtii* was relatively stronger than other climatic factors, which indicated that moisture

TABLE 2 The standardized regression coefficient estimated from linear mixed-effects models.

Fixed effects			
Variable	**Estimate**	**Standard error**	***P*-value**
Intercept	0.419	0.072	3.30e-10***
T_{max}	−0.11	0.065	0.106
T_{mean}	−0.19	0.064	0.127
T_{min}	0.173	0.066	0.00934**
SD	−0.115	0.021	5.75e-08***
VPD	−0.571	0.103	5.75e-08***
ST	−0.013	0.041	0.740
Pre	0.133	0.023	2.42e-08***
RH	0.439	0.054	2.11e-15***

***$p < 0.001$; ns: $p > 0.05$; I, Intercept.

played a significant role in stem radial growth (**Figure 6** and **Table 2**). Water deficiency directly affected cell differentiation in the xylem-forming layer (Rossi et al., 2013). Stomata partially close with increasing VPD, which reduces cell expansion pressure in the forming layer region of the tree (Kocher et al., 2012) and ultimately results in a decrease in radial stem growth (Cornic, 2000; Lawlor and Cornic, 2002). Higher temperatures negatively affected stem radial increment rates, probably due to increased water VPD and increased evaporative dissipation in dry forests (Mendivelso et al., 2016).

L. principis-rupprechtii mainly depended on deep soil moisture during the growing season (Zhang et al., 2018). The effect of soil moisture on tree root uptake was the dominant cause of cell division in tree forming layer, but the restriction of water conditions within the plant on tree stem radial growth began manifest before soil moisture was restricted (de Carcer et al., 2018; Xue et al., 2022). In addition, the diurnal trend of trunk shrinkage and expansion in the growing season of *L. principis-rupprechtii* (**Supplementary Figure 4**) was caused by the strong coupling between water potential gradient and transpiration process (Zweifel and Hasler, 2000). Transpiration came from water stored in the stems of the trees rather than soil moisture (Cermak et al., 2007; Betsch et al., 2011). A correlation between diurnal stem radial variation curve of trees and tree transpiration has

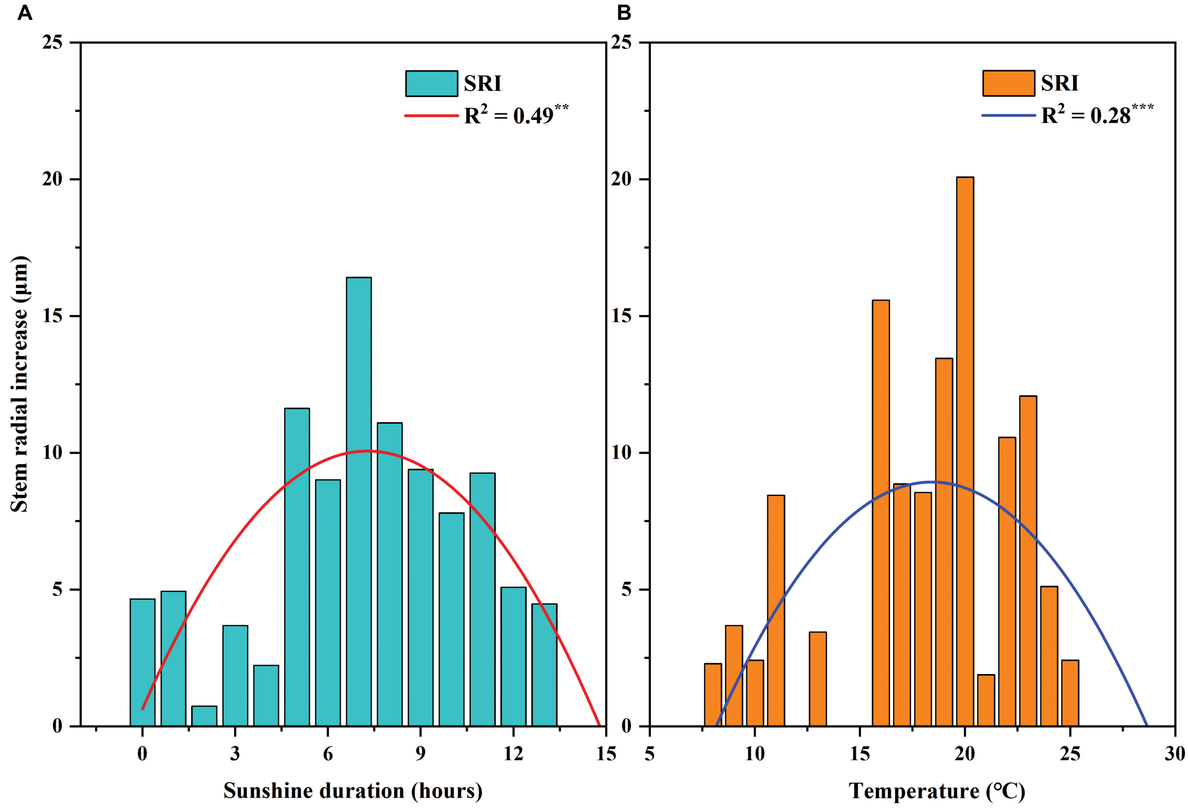

FIGURE 7
Changes in the intra-annual stem radial growth with sunshine duration **(A)** and temperature **(B)** of *L. principis-rupprechtii*. The bars represent the variation of *L. principis-rupprechtii* on different gradients of climate factors. The blue and red parabolas are fitted curves of the trends in 2021. Significance levels (***$p < 0.001$, **$p < 0.01$).

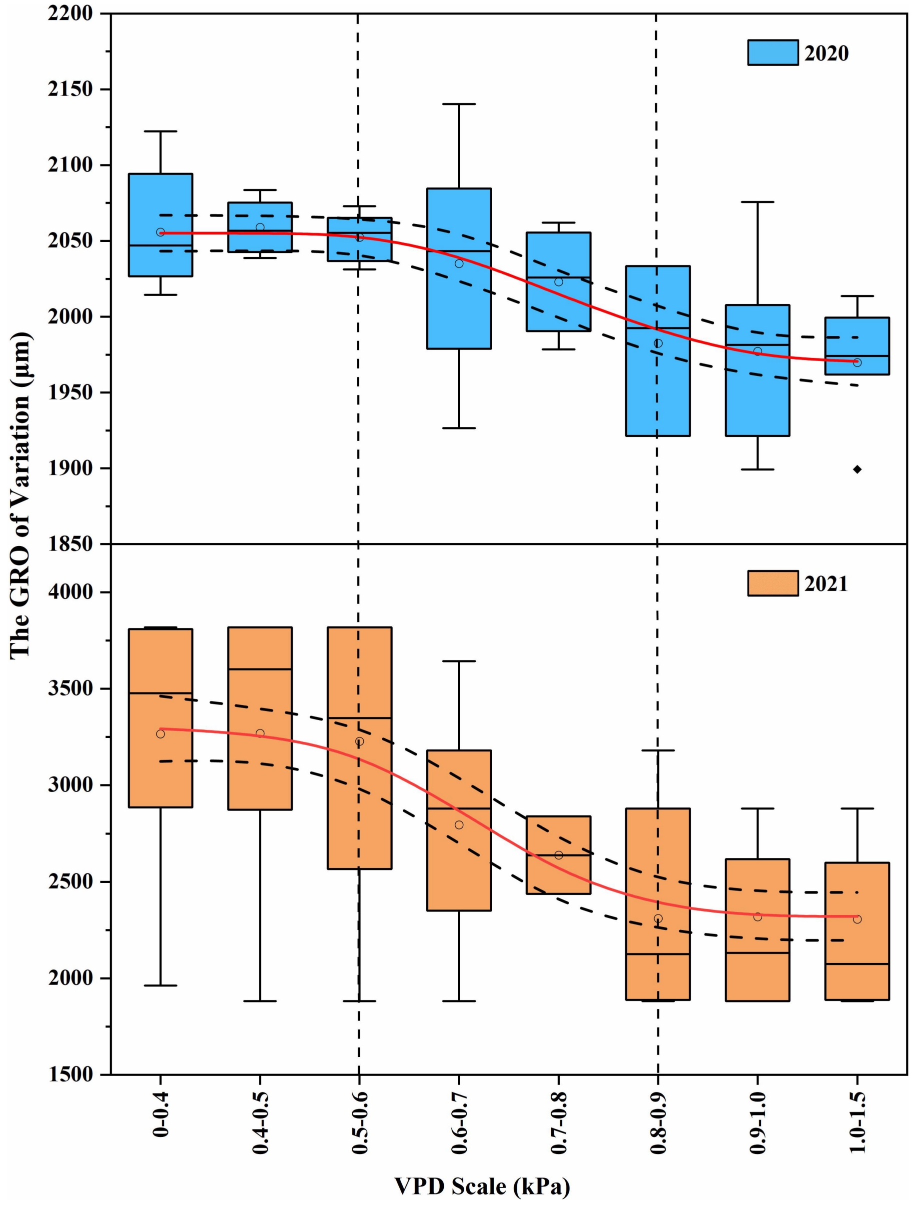

FIGURE 8
The boxplot of the GRO variation of trees for different VPD threshold ranges in 2020 and 2021. The stem radial growth decreases with increasing VPD. The dashed part is the confidence interval obtained with the Logistic models.

been found in semi-arid forests of northern China (Ji et al., 2020).

Threshold effects of vapor pressure deficits on the GRO variation of *Larix principis-rupprechtii*

Our results demonstrate that VPD has threshold effects on the GRO variation of *L. principis-rupprechtii*. Water storage capacity can provide a significant proportion of daily and seasonal water consumption (Cermak et al., 2007). As VPD rises, trees face higher evapotranspiration demands and more severe soil water deficits. Trees had to draw on internal water storage to maintain transpiration demand (Zweifel et al., 2001; De Schepper and Steppe, 2010). When VPD reaches a certain high threshold, there is not enough water inside trees to replenish the stem from daytime losses, which can turn into strong plant water stress. Tree stems may experience more intense shrinkage in this case, which eventually affects the stem radial growth by reducing cell expansion pressure (Dai, 2013). That is why stem radial growth was

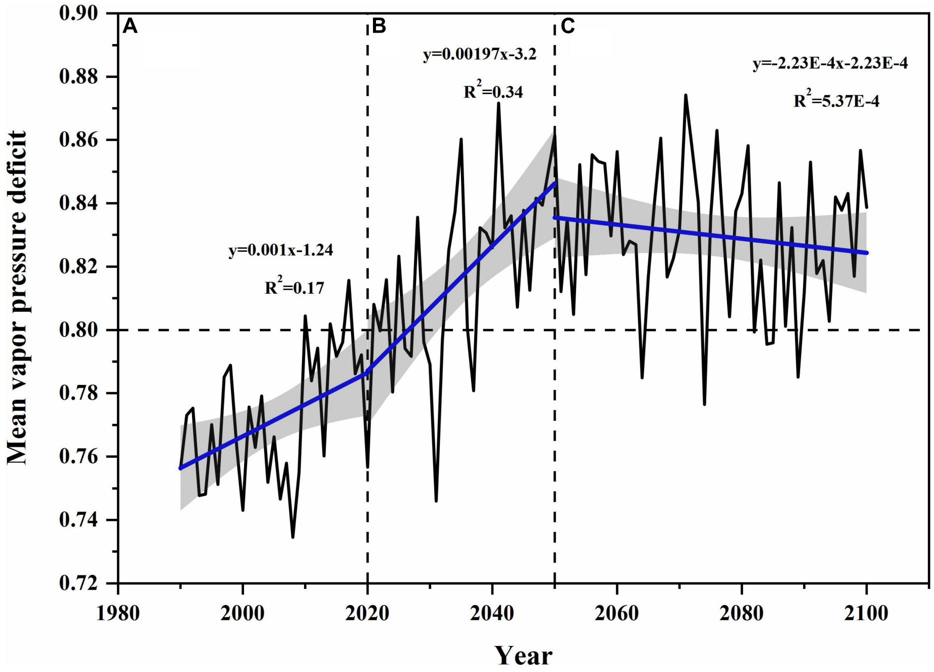

FIGURE 9
Trends of mean vapor pressure deficit (MVPD) in May–July during the period 1990–2020 **(A)** and future projections of VPD for 2020–2050 **(B)** and 2051–2100 **(C)**. The gray shaded areas are the confidence interval obtained with the linear fit.

strongly reduced when VPD exceeded a specific threshold range (0.5 kPa < VPD < 0.6 kPa), and the stem radial growth of *L. principis-rupprechtii* was severely limited when VPD > 0.8 kPa (**Figure 8**). These results are consistent with the results that the effect of drought on radial growth had been the most dominant for larch species in semi-arid regions in recent years. For example, the radial growth of *L. principis-rupprechtii* reduced by 62% at PDSI < -4.5 (Zhang et al., 2021). High VPD was found to be detrimental to stem radial growth in all species during the main growing season in drought-prone mixed conifer forests in high mountains (Oberhuber et al., 2014).

The intra-annual radial growth of trees responded differently to different VPD thresholds. Trees can control stomata to regulate water loss in transpiration (Brodribb and Holbrook, 2003; Zweifel et al., 2006). Stomata of most tree species began to respond at VPD > 0.5 kPa (Oren et al., 1999; Grossiord et al., 2020; Zweifel et al., 2021), and stomata can only respond at VPD > 2 kPa for more drought-tolerant species (Gil-Pelegrin et al., 2017). Norway spruce stomata in European Slovakia closed above a certain VPD threshold (VPD > 1.5 kPa), which greatly limited the growth of trees (Kurjak et al., 2012). Similarly, biomass production of young European beech trees significantly reduced under a specific VPD range (0.05 kPa < VPD < 1.4 kPa), and almost all new shoots died in the driest treatment (VPD = 1.4 kPa) (Lendzion and Leuschner, 2008).

Trees under water stress and those growing in arid areas were more sensitive to VPD (Addington et al., 2004; Aasamaa and Sober, 2011). Above the maximum VPD threshold for tree stem radial growth, stomata did not suddenly close completely, but photosynthesis was inhibited and affected CO_2 uptake (Hetherington and Woodward, 2003). Stem radial growth is influenced by water potential thresholds and growth occurs mainly at night (**Supplementary Figure 4**). There is evidence that low VPD (VPD < 0.4 kPa) conditions at night improved the water status of trees, thus providing favorable conditions for growth. In contrast, high VPD (VPD > 0.4 kPa) during the day reduced the water potential and swelling pressure of the forming layer, which led to inhibition of cell division and growth (Zweifel et al., 2021).

Future implication of elevated vapor pressure deficits on *Larix principis-rupprechtii*

GRO of *L. principis-rupprechtii* had similar responses to VPD in different years, which justifies the comparisons of the reactions of trees to VPD thresholds in future monitoring. Our results indicate that VPD will continue to increase in the future (**Figure 9**), which is consistent with global VPD trend (Liu and Sun, 2017; Yuan et al., 2019; McDowell et al., 2022). Water deficits will become more severe in the context of continuously increasing VPD, as larch trees consume water more rapidly than many other tree species (Zhang et al., 2018). More severe droughts may reach the threshold of lethal plant dehydration and highly restrict stem radial growth in the future (Brodribb et al., 2020). The growth of *L. principis-rupprechtii* reduced significantly in extreme drought years (Zhang et al., 2021). Although it is difficult to make a causal link between drought injury and tree mortality, the results are consistent with other studies that stem radial growth was severely inhibited by high VPD due to the effects of rising VPD (Rowland et al., 2015; Wolf et al., 2016). VPD above 0.8 kPa did not frequently occur in the study region and may not lead to large-scale tree mortality in the past 2 years. However, stem radial growth may face more severe water stress in the context of regional aridification. Therefore, our findings are expected to be useful to predict stem radial growth based on VPD changes in semi-arid regions of northern China.

Conclusion

The average stem radial growth of *L. principis-rupprechtii* started on 29 April and stopped on 17 August. The stem of the *L. principis-rupprechtii* showed optimal growth when temperature was about 18°C and sunshine duration was about 7 h. VPD had threshold effects on stem radial growth of *L. principis-rupprechtii* during the growing season. Maximum stem radial growth occurred at VPD below 0.5 kPa. Stem radial growth had a linear response to elevated VPD when VPD ranges from 0.5 to 0.8 kPa. Considering VPD values will always be above the 0.8 kPa level from 2051 to 2100, stem radial growth will be more limited by water deficits in the future.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

XZ conceive the idea. WL, FY, CW, and JL collected tree cores. WL performed most analysis and wrote the manuscript. XZ provided valuable suggestions and co-wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.948022/full#supplementary-material

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