

Article

Inconsistent Growth Responses of Alpine *Rhododendron* Shrubs to Climate Change at Two Sites on the Eastern Tibetan Plateau

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Abstract: Evidence is accumulating that the radial growth of high-elevation *Rhododendron* shrubs has high dendrochronological potential. However, it remains unclear if the growth responses of alpine *Rhododendron* shrubs to climate are contingent on site conditions. Herein, the climate–growth relationships of alpine *Rhododendron przewalskii* Maxim. shrubs were investigated at two sites (NQ, LWQ) at an elevation of 4300 m on the eastern Tibetan Plateau. We collected ring-width data from 53 *Rhododendron* shrubs. Well-replicated 111-year-old and 51-year-old long shrub ring-width chronologies were built for NQ and LWQ, respectively. Mean shrub growth did not differ between the two study sites. Mean maximum temperature in September of the previous year was significantly negatively correlated with shrub ring-width indices in site NQ, whereas the August minimum temperature of the current year showed a strong negative association with shrub growth indices in site LWQ. Random effects with the shrub level condition exerted a certain influence on shrub radial growth. Results of previous studies in other forest regions across the Tibetan Plateau, along with this study, revealed the diverse responses of radial growth of alpine *Rhododendron* shrubs to climate change. Thus, both climatic and local-scale variables should be considered when conducting shrub-based dendrochronological studies. A warmer and drier climate in the future could further reduce *Rhododendron* shrub growth in particular sites and threaten the survival of alpine shrub ecosystems on the eastern Tibetan Plateau.

Keywords: shrub ring; alpine shrub; radial growth; climate change; Tibetan Plateau



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1. Introduction

Shrublands cover ca. 13% of the Earth's land surface area and constitute the dominant vegetation in many treeless areas with harsh environmental conditions, including alpine regions [1]. For instance, nearly 25% of terrestrial ecosystems consist of shrublands in China [2]. It is widely recognized that shrublands provide several key ecosystem services, including carbon uptake, reduction of soil erosion, provision of timber production, and biodiversity maintenance. As a foundation species in alpine ecosystems [3], shrubs play a significant role in the regulation of water cycles and the conservation of soil fertility [4,5]. Since the multiple services provided by alpine shrubs are closely associated with their productivity and growth dynamics [6], it is necessary to assess how their radial growth patterns respond to climate change.

Shrubs in alpine and arctic regions have great dendrochronological potential because their well-defined annual growth rings are sensitive to climate warming [7]. Evergreen alpine shrubs such as *Rhododendron* species can reach ages of more than 100 years [8–10]; thus, they have been frequently used to explore long-term climate–growth relationships [11–16]. For instance, a previous study found that higher minimum winter temperatures have exerted a positive effect on the radial growth of *Rhododendron campanulatum* since 1787 in the central Himalayas [14]. By contrast, high minimum winter temperatures have had a negative effect on alpine *Rhododendron* shrub growth since 1800 in the Baima Snow Mountains of southwest

China [15]. Nevertheless, the growth of alpine *Rhododendron ferrugineum* L. in the northern Alps has mainly been governed by growing season temperature [11]. It was found that the growth-limiting factor of alpine *Rhododendron ferrugineum* shrub in the Alps shifted from the sum of snow-free growing degree days between 1960 and 1988 to the combination of August temperature and drought between 1989 and 2016 [16]. In addition, alpine shrub responses to climate change might be mediated by local-scale variables (e.g., site condition) [17,18]. Given these different and often conflicting results, we argue that thermal and non-thermal climate factors (e.g., drought, site condition) should be carefully considered when performing dendrochronological studies on alpine shrubs.

The Tibetan Plateau (TP), as one of the three core distribution areas of the modern *Rhododendron* species in the Sino-Himalaya flora region, provides an ideal place to study the growth dynamics of alpine *Rhododendron* shrubs under climate change [19,20]. Several studies have revealed the limiting factors for the radial growth of *Rhododendron* shrubs on the TP. For instance, July mean temperatures positively drove the growth of high-elevation *Rhododendron aganniphum* var. *schizopeplum* in the Sygera Mountains on the southeastern TP [12]. It was also reported that high temperatures in the previous winter and current July promoted the growth of alpine *Rhododendron nivale* near the Zuochupu glacier in southeastern TP [13]. By contrast, the growth of *Rhododendron przewalskii* in the Zhegu Mountains of the eastern margin of the TP was negatively affected by the late winter mean temperature [21]. However, it remains unclear how alpine *Rhododendron* shrubs in the eastern TP respond to climate variables in different sites.

This study aims to: (1) explore the growth–climate relationships of alpine *Rhododendron* shrubs at two sites; (2) compare the difference of *Rhododendron* shrub growth patterns between the two study sites; (3) evaluate the potential effect of ongoing climate warming on *Rhododendron* shrub growth. Given the differences in climatic conditions and inhomogeneous environments at the two sites [22,23], we hypothesize that the growth-limiting factor for alpine *Rhododendron* shrubs would differ between different sites.

2. Materials and Methods

2.1. Study Area and Study Species

The two study sites were located in the Nangqian (NQ, 31°81' N, 96°46' E) and Leiwuqi (LWQ, 31°09' N, 96°93' E) counties on the eastern TP (Figure 1). The elevation of both sites is 4300 m a.s.l. According to meteorological stations located in NQ County (32°12' N, 96°29' E, 3643 m, time period: 1957–2019) and LWQ County (31°13' N, 96°36' E, 3811 m, time period: 1979–2019), the annual mean temperature in NQ and LWQ is 4.4 °C and 3.2 °C, respectively. Notably, the temperature for the sample area is markedly lower than that of the meteorological station due to their elevational differences. The annual precipitation in NQ and LWQ is 535 and 609 mm, respectively; 74% and 78% of annual precipitation in NQ and LWQ occurs during the summer monsoon season (from June to September). Both the mean annual and summer temperatures have shown significant positive trends in these two counties over the past decades ($p < 0.01$), with the summer warming rate being higher in LWQ than NQ. The average summer and annual Palmer Drought Severity Index (hereafter *PDSI*) values in LWQ (mean $\pm$ SD; summer: -0.28 ± 1.64 ; annual: -0.31 ± 1.52) were lower than in NQ (summer: -0.26 ± 1.65 ; annual: -0.28 ± 1.54) between 1901 and 2020, indicating a drier climate in LWQ than NQ (Figure 2).

Monthly minimum, maximum, and mean air temperatures, precipitation, and *PDSI* [24] were used to analyze climate–growth relationships. Temperature data were retrieved from local meteorological stations, whereas *PDSI* data (1901–2020) were downloaded from the Climatic Research Unit (CRU, resolution: $0.5^\circ \times 0.5^\circ$) gridded dataset [25]. CRU climate data showed a high correlation with meteorological station data across the TP [26]; thus, it is considered a reliable source in studies of shrub growth–climate associations.

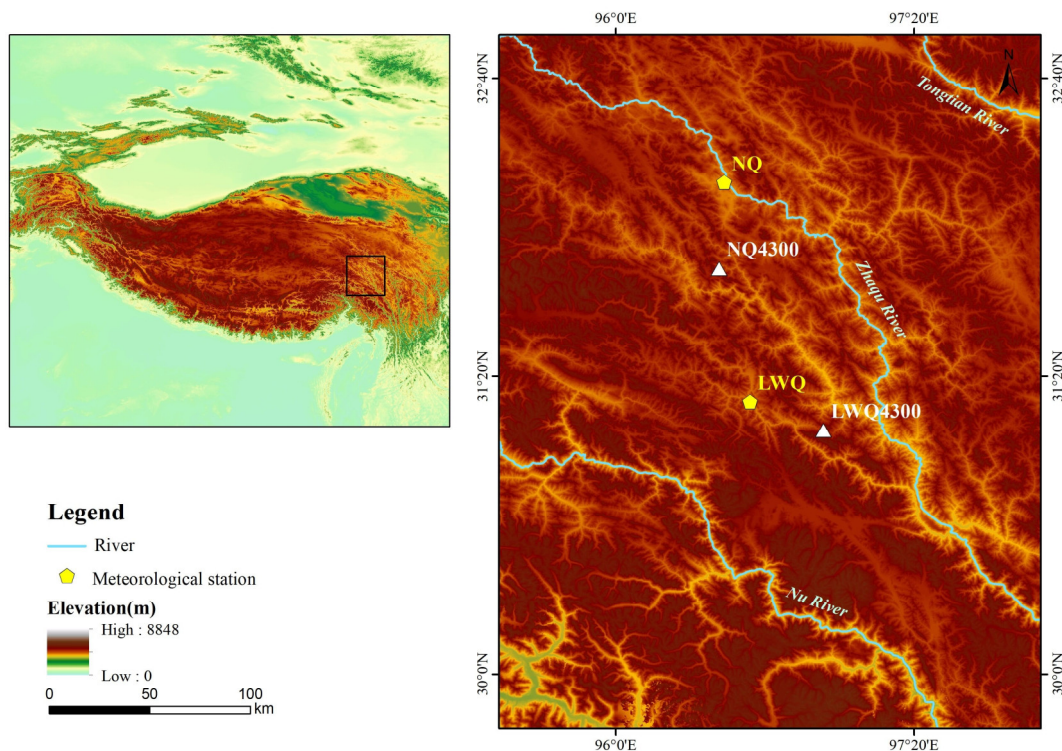


Figure 1. Location of the two study sites (white triangles in the right map) and the meteorological stations (yellow pentagons in the right map) situated on the eastern TP (upper left).

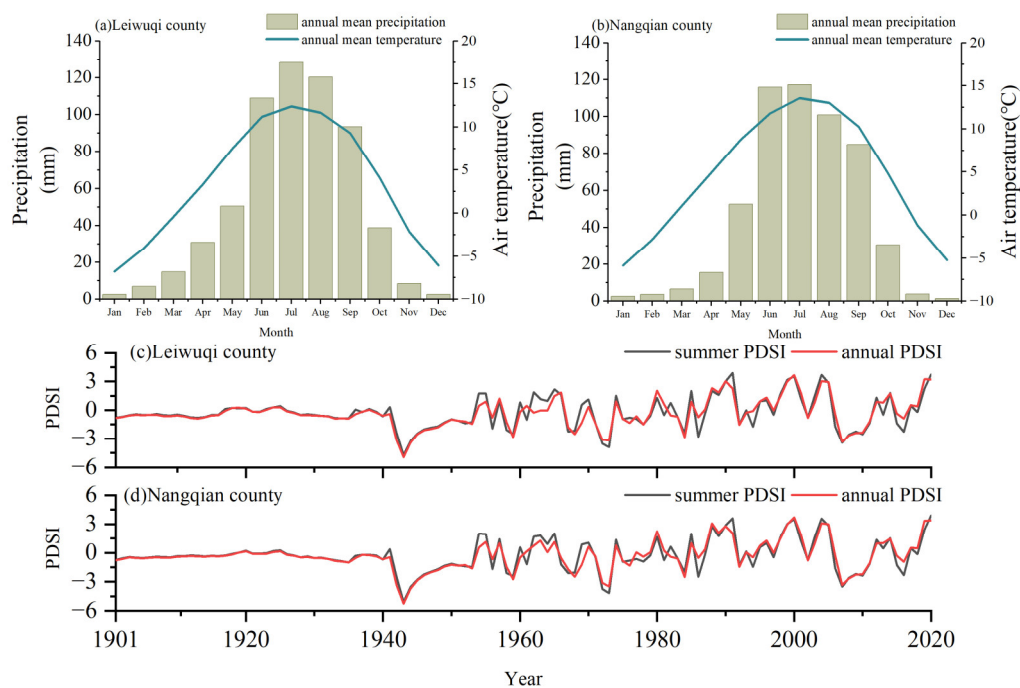


Figure 2. Variations of mean monthly precipitation, mean monthly temperature (a,b), average summer, and annual PDSI (c,d) in the study area on the eastern TP based on data from meteorological stations and the CRU TS gridded data.

We selected high-elevation *Rhododendron przewalskii* Maxim. (hereafter *R. przewalskii*) as the study species. The shrub species is widely distributed on the eastern TP, with the altitudinal range varying from 2900 to 4500 m a.s.l. [27].

2.2. Sample Collection and Chronology Development

In early June of 2021, a total of 53 samples were taken from the stem base of alpine *R. przewalskii* shrubs at two study sites (NQ: $n = 27$; LWQ: $n = 26$). In the case of multi-stemmed *R. przewalskii* individuals, the sample was taken from the stem with the largest basal diameter. All disks were air-dried and sanded and smoothed with sandpapers with different grains. The ring widths were measured along two radii (separated by 90°) per disk using the Lintab 6 system (accuracy: 0.001 mm). Wedging rings were not detected in our samples. The COFECHA program was used to check the quality of the cross-ring dating data [28].

Since shrub ring widths tended to decrease with increasing age, negative exponential curves were used to remove the biological growth trend in individual shrub ring-width series using ARSTAN software [29]. Ring-width values were divided by fitted values to obtain ring-width indices. Then, autoregressive models were fitted to obtain standard ring-width indices, which were averaged using bi-weight robust means to obtain two standard site chronologies. The expressed population signal (EPS) and mean series inter-correlations (R_{bar}) were also calculated to check the reliability and signal strength of standardized mean series or chronologies. We also calculated the mean sensitivity (MS), which is a measure of the mean relative change between adjacent ring widths.

To compare *R. przewalskii* shrub growth patterns between the study sites, Pearson correlations were calculated between the shrub chronology of the two sites. One-way ANOVA was employed to test if mean shrub growth differs significantly between the two study sites.

2.3. Analysis of Climate–Growth Relationships

Monthly climate data (minimum, maximum, and mean temperature, precipitation, $PDSI$) from September of the previous year to the current October were used in the analysis of climate–growth relationships.

Pearson correlation analysis was used to determine the potential climatic drivers of shrub growth. However, the significant factors could be correlated with each other. The inter-correlations between them were eliminated using partial correlation analysis by controlling other potentially correlated factors over the same time interval [30]. Then, a linear mixed model (LMM) was used to reveal the best predictor of individual ring-width indices. Significant ($p < 0.05$) factors revealed by the partial correlation analysis were used in the LMMs. Firstly, individual shrubs were set as a random effect in the LMM for each study site. Then, the data for the two sites were mixed up to explore the relationships between shrub growth and random factors (e.g., site condition or shrub age). Climatic factors were set as fixed effects in these models. The LMMs with the lowest Akaike Information Criterion (AIC) and higher R^2 values were selected [31]. R software (V4.1.2) and the nlme package were used to fit the LMMs [32]. Site conditions were described because they might disturb shrub growth–climate relationships. Despite the same elevation, the two study sites differed in slope and aspect (NQ: slope: 18° , aspect: 351° ; LWQ: slope: 25° , aspect: 326°). Our results were compared to the results of previous *Rhododendron* shrub studies in other forest regions of the TP. These forest regions include the Sygera Mountains and the Hengduan Mountains on the southeastern margin of the TP [12,15], the Zhegu Mountains on the eastern margin of the TP [21], and the central Himalaya on the southern margin of the TP [14].

3. Results

3.1. Characteristics of Shrub Chronologies

We were able to build well-replicated 111-year-old and 51-year-old long shrub chronologies with $EPS > 0.85$ for the NQ and LWQ sites, respectively (Table 1, Figure 3). The mean ring widths in two sites (NQ: 1855–2020; LWQ: 1913–2020) were 0.21 mm. However, the mean ring width for NQ and LWQ during the common period (1970–2020) was 0.23 and 0.22 mm, respectively. The correlation between the two chronologies during the common

period (1970–2020) was insignificant ($r = 0.17$, $p > 0.05$). An insignificant difference was detected between the two sites according to one-way ANOVA ($p > 0.05$).

Table 1. Statistics of ring-width chronologies for the *R. przewalskii* shrub on the eastern TP. Abbreviations: R_{bar} (mean inter-series correlation), MS (mean sensitivity), EPS (expressed population signal).

Site	Time Span	No. Individuals (No. Radii)	Mean Ring Width in the Total Time Span (mm)	Mean Ring Width since 1970 (mm)	R_{bar}	MS	$EPS > 0.85$ since
NQ	1855–2020	27 (54)	0.21 ± 0.07	0.23 ± 0.04	0.61	0.42	1910
LWQ	1913–2020	26 (52)	0.21 ± 0.06	0.22 ± 0.05	0.28	0.33	1970

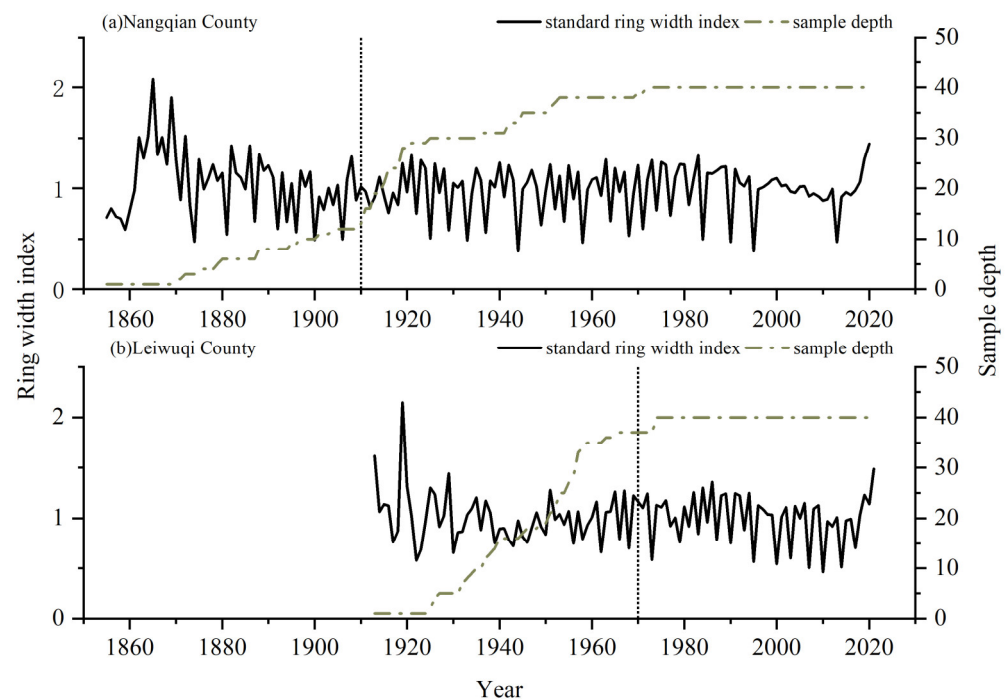


Figure 3. Variations of the standard ring-width index (solid lines) of *R. przewalskii* shrubs at the two study sites ((a) NQ; (b) LWQ). The sampled depth (dashed lines) is shown in the right y-axis. Vertical dashed lines denote the year with $EPS > 0.85$.

3.2. Climate–Growth Relationships

The mean maximum temperature in September of the previous year was negatively associated with standard shrub ring-width indices in NQ ($r = -0.31$, $p < 0.05$) (Figure 4). In LWQ, both mean and minimum temperatures in August showed negative correlations with shrub ring-width indices (August mean temperature: $r = -0.32$, $p < 0.05$; August minimum temperature: $r = -0.46$, $p < 0.01$). The growing-season (May to September) minimum temperature was negatively correlated with shrub ring-width indices ($r = -0.38$, $p < 0.05$). In contrast, $PDSI$ in October and November of the previous year was positively correlated with shrub ring-width indices in site NQ (previous year's October: $r = 0.16$; previous year's November: $r = 0.19$; $p < 0.05$ in both cases). However, $PDSI$ in September and October of the previous year was positively associated with shrub ring-width indices in site LWQ (previous year's September: $r = 0.27$, $p < 0.01$; previous year's October: $r = 0.23$, $p < 0.05$). To sum up, the mean maximum temperature in September of the prior year was significantly and negatively correlated with shrub ring-width indices in site NQ, while the minimum temperature in the current August was the most significant factor negatively associated with shrub growth in site LWQ. Insignificant correlations were detected between precipitation factors and shrub growth.

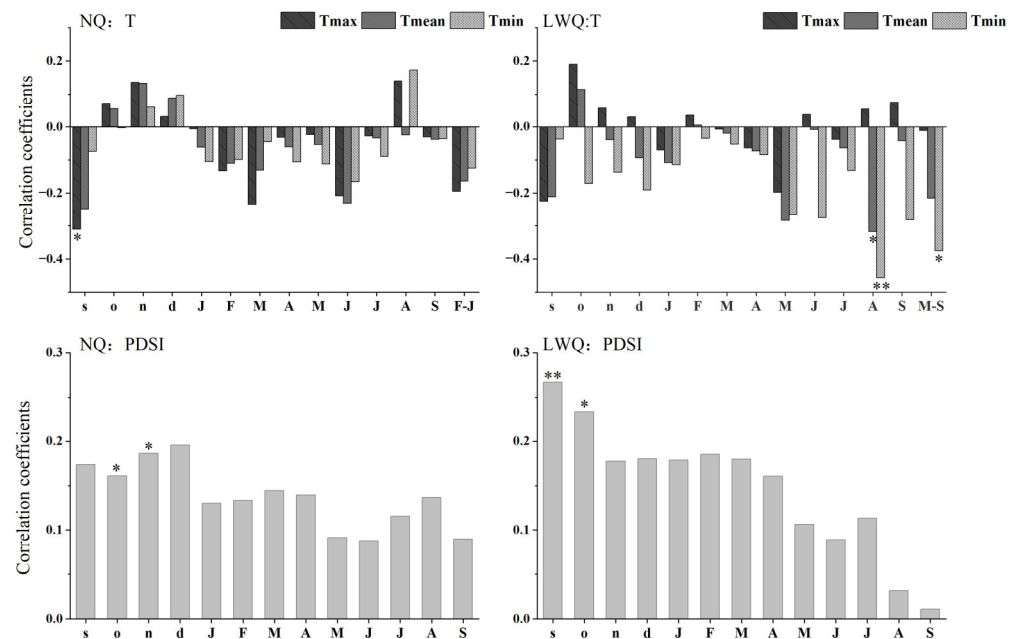


Figure 4. Correlation coefficients of shrub chronologies and climatic variables (T , temperature variables, $PDSI$, drought index) from September of the previous year (lowercase letters: e.g., s, o, n, d) to September of the current year (uppercase letters: e.g., J, F, M). Abbreviations: F–J, February to June; M–S, May to September; T_{max} , mean maximum monthly temperature; T_{mean} , mean monthly temperature; T_{min} , mean minimum monthly temperature; $PDSI$, Palmer Drought Severity Index. Significance levels: *, $p < 0.05$; **, $p < 0.01$.

3.3. Partial Correlation Analysis

In NQ, the partial correlation between the mean maximum temperatures of September of the previous year and the shrub ring-width index was significant when controlling for the $PDSI$ of September of the previous year (Table 2). The partial correlation between $PDSI$ in November and December of the previous year and the shrub ring-width index was insignificant when controlling for the mean maximum temperature of November and December of the previous year.

Table 2. Partial correlations between shrub ring-width indices and climatic factors at the two sites. Abbreviations: T_{max} , mean maximum temperature; $PDSI$, Palmer Drought Severity Index; p_9 (p_{10} , etc.), previous September (October, etc.); c_8 , current August. Significance levels: *, $p < 0.05$; **, $p < 0.01$.

Site	Climatic Variables/Month	Controlled Climatic Variable	Partial Correlation
NQ	T_{max}/p_9	$PDSI_p_9$	−0.27 *
	$PDSI/p_{11}$	$T_{max_p_{11}}$	0.18
	$PDSI/p_{12}$	$T_{max_p_{12}}$	0.20
LWQ	T_{min}/c_8	$PDSI_c_8$	−0.53 **
	T_{mean}/c_8	$PDSI_c_8$	−0.32 *
	$PDSI/p_9$	$T_{max_p_9}$	0.20
	$PDSI/p_{10}$	$T_{max_p_{10}}$	0.31

In LWQ, the partial correlation between the minimum temperature and mean temperature in the current August and the shrub ring-width index was significant and increased when $PDSI$ of the current August was controlled. However, when controlling for maximum temperature in September and October of the previous year, the partial correlation between the shrub ring-width index and $PDSI$ in September or October of the previous year was insignificant.

Thus, the maximum temperature in September of the previous year and the current August's minimum temperature were the most significant climatic factors relating to shrub growth for NQ and LWQ, respectively.

3.4. Predictors of Shrub Growth

Based on the results of the LMMs, the fixed effect with one variable (maximum September temperature of the previous year) explained 10% of the variance of shrub ring-width indices in the NQ site, while the explained variance for the random effect associated with individual shrubs tended to be zero (Table 3). In LWQ, the fixed effect with one variable (August minimum temperature) accounted for 18% of the variance of ring-width indices, while the random effect associated with individual shrubs accounted for 12% of the variance (Table 3). Thus, climate factors well predicted the shrub growth in both sites.

Table 3. Summary of the linear mixed-effects models (LMMs) fitted to shrub ring-width indices at the two sites. Abbreviations: LWQ + NQ (LN), LMM model for the mixed data of two sites; T_{mean} , mean temperature; T_{min} , mean minimum temperature; T_{max} , mean maximum temperature; $PDSI$, Palmer Drought Severity Index; $c8$ ($c9$), current August (September); $p9$ ($p10$, etc.), previous September (October etc.); SV , seven variables ($PDSI$ in previous September to December, mean and minimum temperature in current August, maximum temperature in previous September); R^2_m , marginal R^2 ; R^2_c , conditional R^2 ; AIC, Akaike Information Criterion.

Name	Climate Variable/Month	R^2_m	R^2_c	p	AIC
LN	SV	0.12	0.14	<0.01	72.21
LWQ	$T_{mean}/c8$	0.09	0.22	<0.05	12.03
	$T_{min}/c8$	0.18	0.30	<0.01	8.19
	$PDSI/p9$	0.12	0.24	<0.05	12.56
	$PDSI/p10$	0.09	0.22	<0.05	14.35
NQ	$T_{max}/p9$	0.10	0.10	<0.05	36.40
	$PDSI/p11$	0.03	0.03	>0.05	41.90
	$PDSI/p12$	0.03	0.03	>0.05	41.68

When the data of the two sites were put together, the fixed effect with seven climatic variables ($PDSI$ in the previous September to December, mean and minimum temperature in the current August, maximum temperature in the previous September) explained 12% of the total variance of shrub ring-width indices at the two sites, while the random effect associated with shrub age only accounted for 2% of the variance (Table 3). No significant effect associated with site factors (slope, aspect) to shrub growth was observed in the model.

4. Discussion

4.1. Growth-Limiting Factor for *Rhododendron przewalskii* Shrubs

Mean shrub growth over the common period (1970–2020) did not differ significantly between the two study sites on the eastern TP. However, the growth-limiting factor for the radial growth of *R. przewalskii* differed in the two study sites.

Radial growth of *R. przewalskii* in site NQ was mainly limited by maximum temperature in September of the previous year. A similar result was also reported in the alpine *Wilson juniper* shrub study on the central TP [33]. It was observed that the end of xylogenesis for high-elevation *Rhododendron* shrubs appeared in late September [34], when late-season photosynthesis could influence the next year's growth through organic storage processes [35], implying that the autumn temperature is of importance for the radial growth of alpine shrub. Nevertheless, higher temperatures during the autumn season would amplify transpiration and respiration rates and increase the evaporative water demand by rising the vapor pressure deficit, thus reducing the carbohydrates available for growth in the following year [36]. Climatic data in NQ County show warmer and drier autumn seasons in the past decades [37]. Such a warm–dry autumn climate would negatively affect the current year's shrub growth by reducing the carbon storage in the late growing

season of the following year [38–40]. Furthermore, the random effect associated with individual shrubs did not have a significant impact on shrub growth in NQ, suggesting that shrub-level conditions did not distort growth–climate associations.

Shrub growth in site LWQ was primarily limited by the August minimum temperature of the current year. Additionally, this negative effect could last the whole growing season. It is possible that a steady increase in summer temperature induced water stress [41] and reduced the accumulation of organic matter, thus depleting the water and nutrient available for shrubs [42]. Such a negative response of ring formation to high temperature was also founded in several timberline sites [36,43,44].

When the data from the two sites were mixed together, the insignificant effect of site conditions on shrub growth was not detected; it may be attributed to data limitation (e.g., only two levels for the site factor). Generally, LMMs with random effects with a factor of less than 5 levels may not be able to estimate the among-population variance accurately [45–47]. In such cases, further investigation is needed to clarify the relationships between the microsite conditions and *R. przewalskii* shrub growth on the eastern TP. In particular, studies on shrub-ring isotopes (i.e., ^{13}C or ^{18}O) are required to test if there is a stomatal adjustment depending on climate fluctuations at the microclimate level at each site [48]. Random effects associated with shrub age also partly affect shrub growth, which may be related to the strategy of plant biomass allocation. For alpine shrubs, biomass allocated to stem growth decreases with age [49], suggesting that shrub age could disturb shrub growth responses.

The negative temperature–growth correlations at the two study sites revealed the adverse influences of a warm–dry climate on alpine shrub growth in the eastern TP. In general, rapid warming would release alpine shrubs from cold stress but also induce water deficiency [50]. Random effects with individual shrub partly disturb shrub growth, while climatic factors mainly drive shrub growth dynamics, further revealing that the growth responses of alpine *Rhododendron* shrubs to climate could be contingent on shrub-level conditions, thus supporting our hypothesis.

4.2. Comparison between the Results of Previous Studies and this Study

The length of shrub chronology, mean shrub growth, and growth-limiting factors in existing research differ among the different forest regions on the TP (Table 4). Specifically, the length of well-replicated shrub chronologies of different *Rhododendron* species ($EPS > 0.85$) range from 61 to 342 years. The mean ring width of *Rhododendron* shrub species in these studies, combined with our results, varies between 0.18 and 0.50 mm.

A consistent growth-limiting factor for alpine *Rhododendron* shrubs was not found across the different forest regions of the TP (Table 4). In the Sygera Mountains of the south-eastern TP, characterized by a mild, moist climate, cold July mean temperatures limited the radial growth of alpine *Rhododendron* shrubs [12]. By contrast, the winter minimum temperature showed a strong negative correlation with *Rhododendron* shrub growth in the Hengduan mountains of the southeastern TP, indicating that rapid winter warming may exert detrimental effects on growth due to reduced snow cover under climate warming [15]. The contrasting results in these two studies also suggest that site conditions may play a major role in driving shrub growth, in addition to regional climate [12,15]. In the Zhegu Mountains of the eastern margin of the TP, the late winter mean temperature negatively drove *Rhododendron* shrub growth, also implying the adverse effects of a warm winter on the growth processes of alpine shrubs [21]. In central Himalaya, characterized by a warm climate, the winter minimum temperature positively drove *Rhododendron* shrub growth, suggesting that winter warming contributed to an increase in soil moisture availability through enhanced snowmelt and soil thawing, therefore promoting shrub radial growth in the next year [51,52]. In strong contrast to the results of the aforementioned studies, we found negative temperature–growth correlations during the growing season, dominating *Rhododendron* shrub growth on the eastern TP, where climate is relatively dry. Collectively,

the growth-limiting factors for *Rhododendron* shrubs on the TP are highly dependent on regional climates but partly affected by local-scale factors (e.g., site conditions).

Table 4. Information for the existing *Rhododendron* shrub chronologies in previous studies on the TP. *Rhododendron* shrub species included *Rhododendron aganniphum* var. *schizopeplum* (A), *Rhododendron phaeochrysum* (B), *Rhododendron. traillianum* (C), *Rhododendron przewalskii* (D), *Rhododendron alutace* (E), and *Rhododendron campanulatum* (F). The sign “/” indicates no data. Abbreviations: shrub species (Species), length of chronology with $EPS > 0.85$ (Length), ring width (RW), growth-limiting factor (GLF).

Forest Region	Species	Length (years)	RW (mm)	GLF
Sygera Mts, southeastern TP, China [12]	A	342	0.20	Low July mean temperature
		272	0.20	
		282	0.21	
		117	0.18	
Hengduan Mts, southeastern TP [15]	B	196	/	High December–February mean minimum temperature
	C	212	/	
	D	67	/	
	E	77	/	
	C	142	/	
Zhegu Mts, eastern margin of the TP [21]	D	61	0.5	High January–February mean temperature
Central Himalaya, southern margin of the TP [14]	F	227	/	Low December–February minimum temperature

4.3. Potential Influence of Climate Warming on Alpine Shrubs

According to the sixth IPCC report, increases of +1.5 and +2.5 °C in global temperature are forecasted for the mid and late 21st century, respectively [53]. Such accelerated warming in the future may increase the mortality rate of temperature-sensitive tree and shrub species [54,55]. Given that the TP is likely to face significantly reduced rainfall and enhanced drought in the future [56], the radial growth of alpine shrubs may experience increased drought stress, as found in the growth of *Juniperus indica* shrub in central Himalaya [57]. In this study, negative temperature–growth correlations were detected for *R. przewalskii* on the eastern TP, indicating the negative impacts of climate warming on the radial growth of *R. przewalskii*. Therefore, a warmer and drier climate could threaten the survival and stability of alpine shrub ecosystems on the eastern TP [50,58].

5. Conclusions

We explored the radial growth dynamics of alpine *R. przewalskii* and their responses to climate change on the eastern TP. Mean shrub growth differed insignificantly between the two study sites. Based on the Pearson and partial correlations, the most important predictors of shrub radial growth in the NQ and LWQ sites were the maximum temperature in September of the previous year and the minimum temperature in the current August, respectively. However, linear mixed-effect models indicate that shrub-level conditions could exert a certain influence on shrub growth. Results of previous studies in other TP regions, combined with this study, indicated that growth-limiting factors for *Rhododendron* shrubs are highly dependent on regional climates but mediated by local-scale variables (e.g., site conditions). Thus, climatic and other environmental conditions should be considered with caution when performing shrub-based dendrochronological studies at multi-sites. Cambial phenology and microenvironmental conditions (e.g., soil properties and moisture, understory vegetation) for alpine shrubs are required to clarify the driving mechanism for the growth–climate linkages of *Rhododendron* shrub.

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