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Intra-Annual Radial Growth of *Pinus kesiya* var. *langbianensis* Is Mainly Controlled by Moisture Availability in the Ailao Mountains, Southwestern China

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Abstract: Intra-annual monitoring of tree growth dynamics is increasingly applied to disentangle growth-change relationships with local climate conditions. However, such studies are still very limited in subtropical regions which show a wide variety of climate regimes. We monitored stem radius variations (SRV) of *Pinus kesiya* var. *langbianensis* (Szemao pine) over five years (2012–2015 and 2017) in the subtropical monsoon mountain climate of the Ailao Mountains, Yunnan Province, southwest China. On average, the stem radial growth of Szemao pine started in early March and ended in early October, and the highest growth rates occurred during May to June. Stem radius increments were synchronous with precipitation events, while tree water deficit corresponded to the drought periods. Correlation analysis and linear mixed-effects models revealed that precipitation and relative humidity are the most important limiting factors of stem radial increments, whereas air temperature and vapor pressure deficit significantly affected tree water balance and may play an important role in determining the growing season length and seasonality (i.e., duration, start, and cessation). This study reveals that moisture availability plays a major role for tree growth of *P. kesiya* var *langbianensis* in the Ailao Mountains, southwest China.

Keywords: Ailao Mountains; climate response; pine; point dendrometer; stem radius variations; tree water deficit

1. Introduction

Global climate change already affects tree species composition, forest productivity, and ecosystem functioning across biomes [1,2]. Therefore, understanding the possible impact of changing environmental conditions on forest growth and vitality is of crucial importance [3]. Growth–climate relationships are frequently determined by empirically correlating tree-ring parameters (i.e., ring width, maximum latewood density, wood anatomical variables) to monthly climatic variables [4]. However, such empirical approaches may only capture limited information of climatic forcing on tree growth, as similar amounts of radial tree growth can be achieved with different combinations of growth rate and duration under contrasting climatic conditions during the vegetation period [5,6]. Therefore, studies on intra-annual growth dynamics may shed more light on the impact of climatic forcing on tree growth [7,8] and may allow better understanding the response of the forest ecosystem to climatic extreme events.

High-resolution dendrometers continuously measure stem radius variations (SRV), which are composed of (1) irreversible radial expansion of the stem due to newly formed sapwood and bark tissue cells, and (2) water-related contraction and expansion of wood and bark [9,10]. Stem growth is mainly driven by turgor and water potential conditions in the cambium, which triggers cell division and elongation [11]. Water-related processes of the stems are mainly driven by water potential gradients between the different compartments of the soil–tree–atmosphere system, which are mainly induced by transpiration and altered by water availability in the soil [12]. Zweifel et al. [8] proposed a zero-growth concept (ZG model) for separating stem radius fluctuations into growth-induced irreversible expansion of the stem and reversible tree water deficit-related shrinkage of the stem. The ZG model assumes that stem radial growth is restricted to periods of stem water saturation, while stem radius variations below a previous stem radius maximum are induced by changing water status [8].

High-resolution dendrometer measurements were extensively used to analyze tree–water relationships [13], intra-annual growth [6,14], wood formation [15], and carbon fixation [16] in forest ecosystems in different climate zones. For example, moisture availability during the growing season is the most important factor limiting the radial growth of various tree species in semi-arid areas of north China [17–19]. However, only few studies were so far conducted in tropical and subtropical forest ecosystems. For example, precipitation and vapor pressure deficit were attributed to determine tree radial growth and drought responses in tropical dry mountain forests of east Africa [20] and South America [21,22]. High air temperatures have a negative influence on the radial increment of tree species in tropical dry forests in Bolivia, probably caused by increasing vapor pressure deficit and enhancing evapotranspiration rates [23]. Moreover, a combination of intensive monitoring of stem radial variations and quantitative wood anatomy may provide more valuable information on intra-annual growth variability [24].

Pinus kesiya var. *langbianensis* (Szemao pine), a regional subspecies of *Pinus kesiya*, is distributed naturally in the humid and sub-humid areas of Yunnan Province, southwestern China. Due to its rapid growth rate, vigorous germination, and high productivity of quality wood and resins, Szemao pine is one of the main timber plantation species in the tropical and subtropical areas of Yunnan. Despite of its economic and ecological importance, little is known about its intra-annual growth dynamics and responses to climatic factors. This, however, is of great relevance to derive reliable estimates of its productivity and resilience under projected future climate conditions in the study region, where a higher frequency of drought events is expected [25].

This study presents five years of high-resolution dendrometer measurements on *P. kesiya* var. *langbianensis* in the Ailao Mountains, southwestern China. Our specific aims were (i) to describe the inter-annual variability of growth seasonality (i.e., growth onset, cessation, and duration) and xylem anatomical traits under contrasting weather conditions, and (ii) to identify the main meteorological factors that determine daily and seasonal stem radial growth of Szemao pine.

2. Material and Methods

2.1. Study Site

The study was conducted in the Ailao Mountains of central Yunnan in southwestern China. The local climate is influenced by the Asian summer monsoon, consisting of the branches of the southwest monsoon crossing the Bay of Bengal and the southeast monsoon originating in the Pacific Ocean [26]. Meteorological data from the Ailaoshan Station for Subtropical Forest Ecosystem Studies (24°31′ north (N), 101°01′ east (E), 2480 m above sea level (a.s.l.), 1982–2015) display an annual mean temperature of 11.6 °C, with monthly minimum temperatures occurring in January (5.8 °C) and maximum temperatures in July (15.8 °C). Mean annual precipitation is 1799 mm, 65% of which (1179 mm) occurs during the summer monsoon season from June to September, and only 14% of which (258 mm) occurs during the pre-monsoon season from March to May (Figures S1 and S2, Supplementary Materials).

Covering an area of 503 km^2, the Ailao Mountains encompass the largest protected area of subtropical evergreen broad-leaved forests in China. *P. kesiya* var. *langbianensis* (Szemao pine) is one of the native species selected for plantations. It was sown by airplane since the 1960s, largely replacing the natural vegetation in the middle mountain regions of Yunnan [27]. Szemao pine covers vast parts of the landscape from 1600 to 2000 m in the Ailao Mountains. Our study site is located in a ~20-year-old secondary forest of Szemao pine (24.50° N, 100.98° E, 1900 m a.s.l.). The investigated trees are characterized by a diameter at breast height (DBH) of around 15–20 cm and a height of 10–15 m. *P. kesiya* is the dominant tree species in the secondary forest, and *Schima noronhae* is the main associated broad-leaved tree species of the mixed forest.

2.2. Meteorological Data

Meteorological data were obtained from the Ailaoshan meteorological station located around 8 km away from the study site. Available climate variables include precipitation (PRE), air temperature (T_a) at 2 m height and soil temperature (T_s) at 10 cm depth, relative humidity (RH), photosynthetic active radiation (PAR), and wind speed (WS). Vapor pressure deficit (VPD) was calculated from the values of T and RH. The hourly measured climate data were averaged to daily means for further analyses.

2.3. Dendrometer Measurements

Stem radius variations (SRV) were monitored for three Szemao pines using electronic point dendrometers (DR type, Ecomatik, Munich, Germany), with a spatial resolution of 2 m. The instruments were installed on the tree trunks at breast height. The dead outmost layers of the bark were removed to reduce the influence of hygroscopic shrinking and swelling of the bark. Stem radius variations were recorded at 10-min intervals by a data logger (DL15, Ecomatik, Munich, Germany) during the period from January 2012 to December 2017. Data were not recorded properly during the growth season of 2016 due to technical problems and were, thus, not included in our analysis. Nevertheless, our data represent the longest continuous stem diameter growth records in the study region.

2.4. Data Analysis

To describe the seasonality of tree growth over years, a Gompertz model [28] was fitted to the daily means of stem radius increment, as shown in Equation (1).

$$Y = Y_0 + A\, exp\left[-e^{(\beta - kt)}\right] \quad (1)$$

where Y represents the daily average stem diameter, Y_0 and A are the lower and upper asymptotes, β is the x-axis placement parameter, k is the rate of change parameter, and t is day of year (DOY). Consequently, $(A - Y_0)$ corresponds to the total seasonal growth whereas $(Y_t - Y_{t-1})$ corresponds to the growth rate (mm·d^{-1}). The parameters were estimated using the ordinary least squares method with the *nsl* function in R software (version 3.5.1) [29]. Days of growth initiation and cessation were determined when 10% and 90% of the total annual growth were attained [14].

The growth line (GRO) was defined by a moving maximum of the current and previous dendrometer measurements, while tree water deficit (TWD) was defined as the deviations of current measured stem radius from the GRO baseline. Thus, GRO covers any increase in stem radius (SR) exceeding a precedent SR maximum. TWD covers any shrinkage of the stem plus the increase in SR during periods with shrunken stems (Figure S3, Supplementary Materials). Daily sums of growth (GRO rate, mm·d^{-1}) and daily minimum tree water deficit (TWD, mm) were calculated for the study period.

The monthly sum of daily precipitation, GRO rate, and monthly average of TWD were compared. Daily and weekly GRO rates and TWD were correlated with corresponding climatic variables for the main vegetation period from 1 March to 31 October for 2012–2017.

Linear mixed-effects modeling (LMM) was performed in the *nlme* package in the R statistical software [30] to assess the relative importance of different climate factors on GRO rate and TWD. The values of GRO rate, TWD, relative humidity, and precipitation were log-transformed to fit the normal distribution. All dependent and predicted variables were scaled according to their means and standard deviations [30]. We calculated variance inflation factors (VIF) of the models containing all variables to assess collinearity among variables. To reduce the collinearity problem, we excluded those climate variables with high collinearity according to the threshold of VIF values smaller than 2.5, i.e., mean and minimum air temperature and soil temperature. We constructed a full model with T_{max}, WS, PRE, RH, and PAR as fixed factors. LMMs with a random intercept associated with trees nested in years and first-order auto-correlation structures were fitted. Fixed-effects selections were based on Akaike's information criterion (AIC), and the models with the lowest AIC values were selected. We performed the LMM model first for the full available time period and subsequently for each single year separately.

3. Results

3.1. Climate Variability

The climate of the study area is characterized by a distinct seasonality, i.e., pre-monsoon season from March to May, summer monsoon from June to September, and post-monsoon and winter season from October to February (Figure 1, Figure S2, Supplementary Materials). Climatic conditions during the studied period from 2012 to 2017 were generally warmer and drier than the long-term mean from 1982–2011 (Figure S2, Supplementary Materials). During 2012–2017, the pre-monsoon season from March to May showed lower RH and higher VPD compared to the long-term mean (Table S1, Figure S2b,d, Supplementary Materials). In 2017, VPD and RH were generally above the long-term mean, except for a short dry period during May–June. In 2014, pre-monsoon season (March–May) rainfall was only 57 mm, which is only 21.1% of the long-term mean (270 mm) (Figure S2, Supplementary Materials).

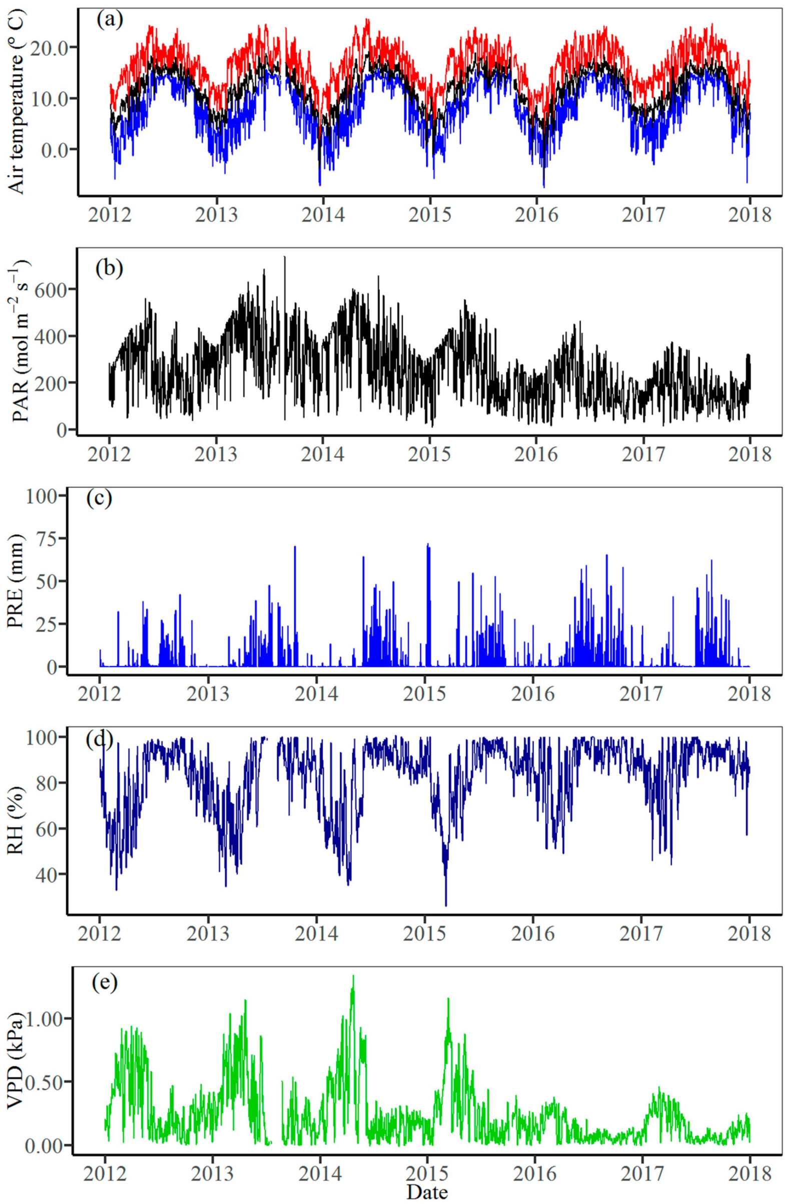

Figure 1. Daily climate conditions from the Ailao meteorological station for the period of January 2012 to December 2017: (**a**) daily minimum (blue), mean (black), and maximum (red) temperature; (**b**) photosynthetic active radiation (PAR); (**c**) precipitation (PRE); (**d**) relative humidity (RH); (**e**) vapor pressure deficit (VPD).

3.2. Seasonal Stem Radius Variations

Stem radius variations showed characteristic seasonal patterns (Figure 2). Tree water deficit (TWD) derived from the ZG model showed substantial stem shrinking during the pre-monsoon seasons of 2012–2015 and during the autumn–winter seasons in 2012 and 2013 (Figure 2b). In all years, irreversible stem expansion (GRO rate) was concentrated during the late pre-monsoon and summer monsoon seasons from DOY 100 to DOY 300 (Figure 2c). Gompertz nonlinear regressions explained more than 99% of the variations in the dendrometer measurements. According to the modeled results, annual cumulative growth ranged from 3.6 mm in 2014 to 6.0 mm in 2017 (Table S1, Supplementary Materials). The beginning of the growing season ranged from 25 March (DOY 85) in 2012 to 1 May (DOY 121) in 2014, while the end of the growing season ranged from 8 October (DOY 281) in 2014 to 17 October (DOY 290) in 2017. The length of the growing season ranged from 160 days in the dry year 2014 to 203 days in the comparatively wet year 2012 (Figure 3, Table S1, Supplementary Materials). The occurrence of maximum growth rates varied from 24 May in 2012 (DOY 145) to 24 June in 2014 (DOY 173).

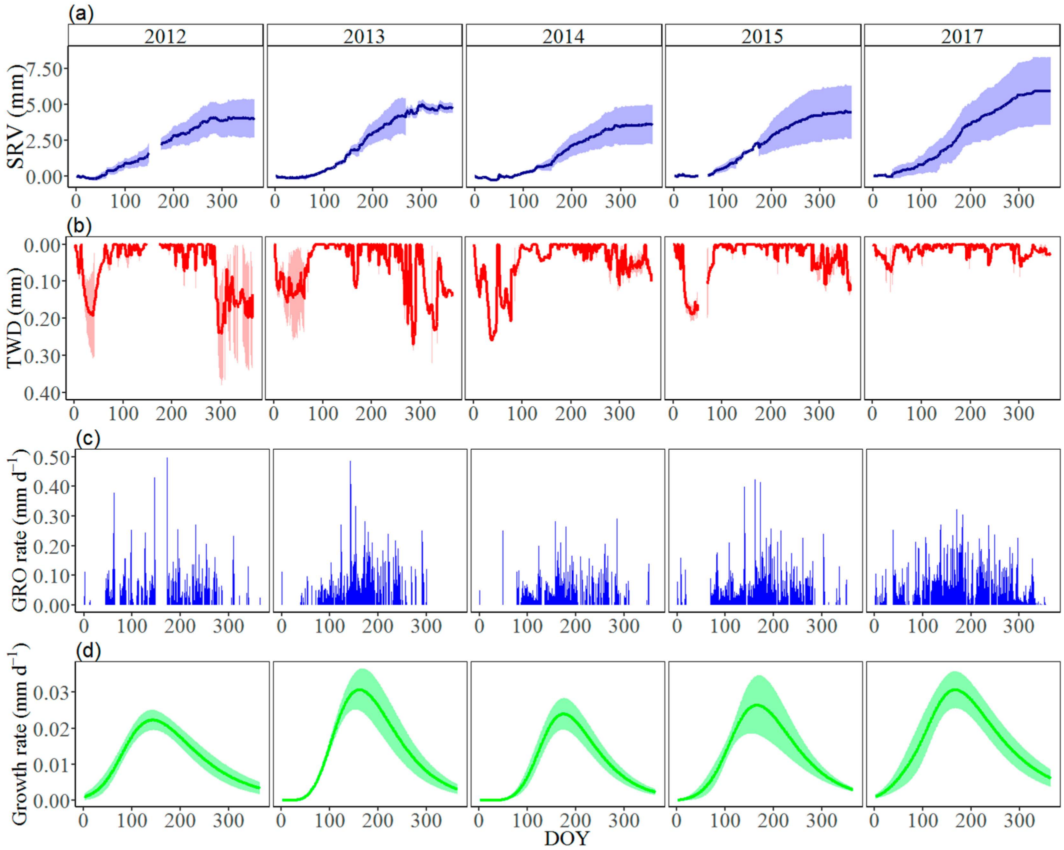

Figure 2. (**a**) Cumulative daily mean stem radius variations (SRV, mm); (**b**) daily minimum tree water deficit (TWD); (**c**) daily sums of growth-induced irreversible stem expansion (GRO rate) calculated from a zero-growth (ZG) model ([8]); (**d**) daily stem growth rates of *Pinus kesiya* var. *langbianensis* trees modeled with a Gompertz function for the years 2012–2015 and 2017. Shaded areas indicate the standard error of the mean.

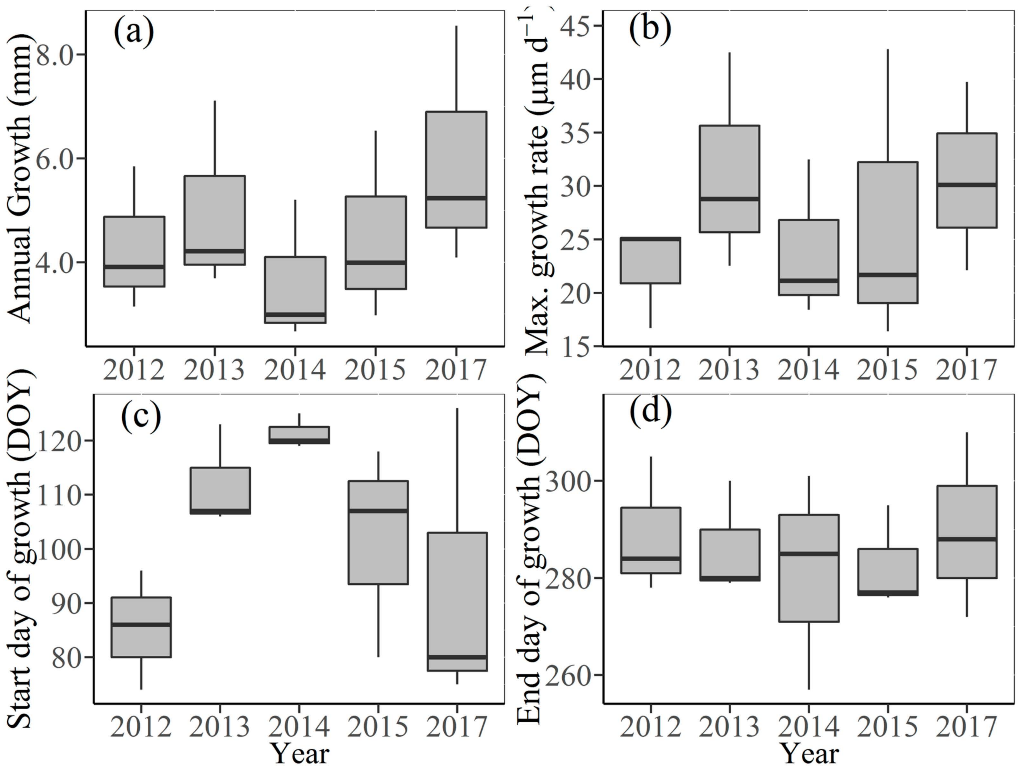

Figure 3. (**a**) Total annual growth (mm); (**b**) maximum growth rate (μm·d^{-1}); (**c**) starting day of year (DOY) of growth; (**d**) cessation day of year (DOY) of growth, predicted by a Gompertz model fitted on daily mean stem radius variations (SRV). The boxplots show medians, the 25th and 75th quartiles, and minimum–maximum values.

3.3. Effects of Climate Factors on Stem Growth

Monthly summed radial increments (GRO rate) were highly synchronous with rainfall events during the main growing season, whereas periods with tree water deficit (TWD) were synchronous with drought periods during the pre-monsoon and post-monsoon seasons (Figure 4). Based on the linear mixed-effect model, precipitation and relative humidity had strong positive effects on stem radial growth (Table 1, Tables S2 and S3, Supplementary Materials). Tree water deficit (TWD) was mainly affected by daily vapor pressure deficit (VPD) (Table 1, Table S4, Supplementary Materials). Correlation analyses confirmed that daily stem radius increments (GRO rates) were highly correlated with precipitation and relatively humidity (Figure 5a), indicating that radial growth of Szemao pine is mainly limited by moisture availability during the pre-monsoon and summer monsoon season. The correlations between weekly averaged GRO rates and corresponding precipitation and RH were consistent with results from daily data; however, negative correlations between weekly GRO rates and VPD and PAR increased (Figure 5b). Correlations between monthly GRO rates and climatic variables generally were higher with precipitation and relative humidity during the early and late growing seasons (Figure 6a). Tree water deficit (TWD) correlated positively with maximum temperature and relative humidity (Figure 6b), which is related to higher water consumption and canopy transpiration under warmer and drier conditions.

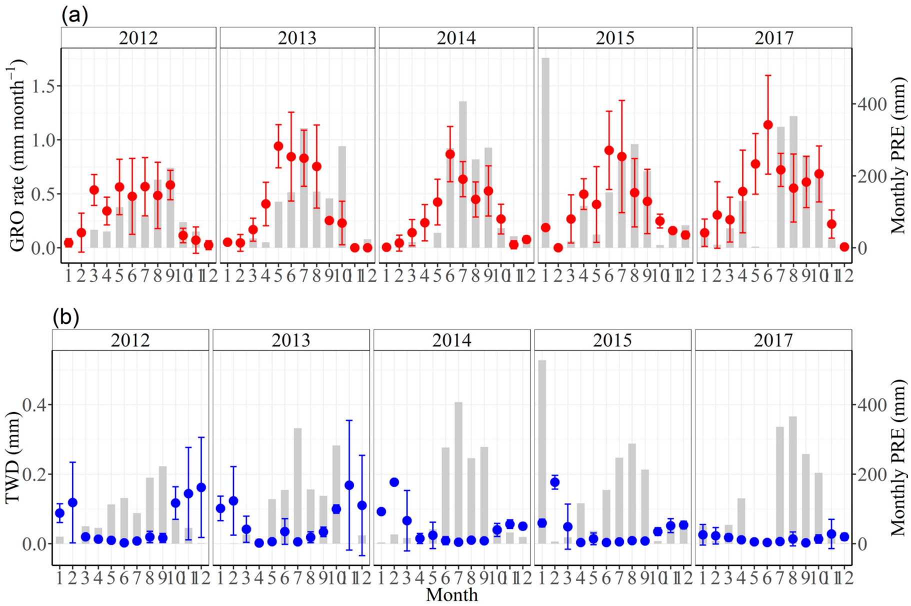

Figure 4. Comparison between monthly sums of precipitation (mm, gray bars) and (**a**) monthly sums of daily growth-induced irreversible stem expansion (GRO rate, mm·month^{-1}, red points), and (**b**) monthly means of daily minimum tree water deficit (TWD, mm, blue points). Standard deviations of three individuals are also shown.

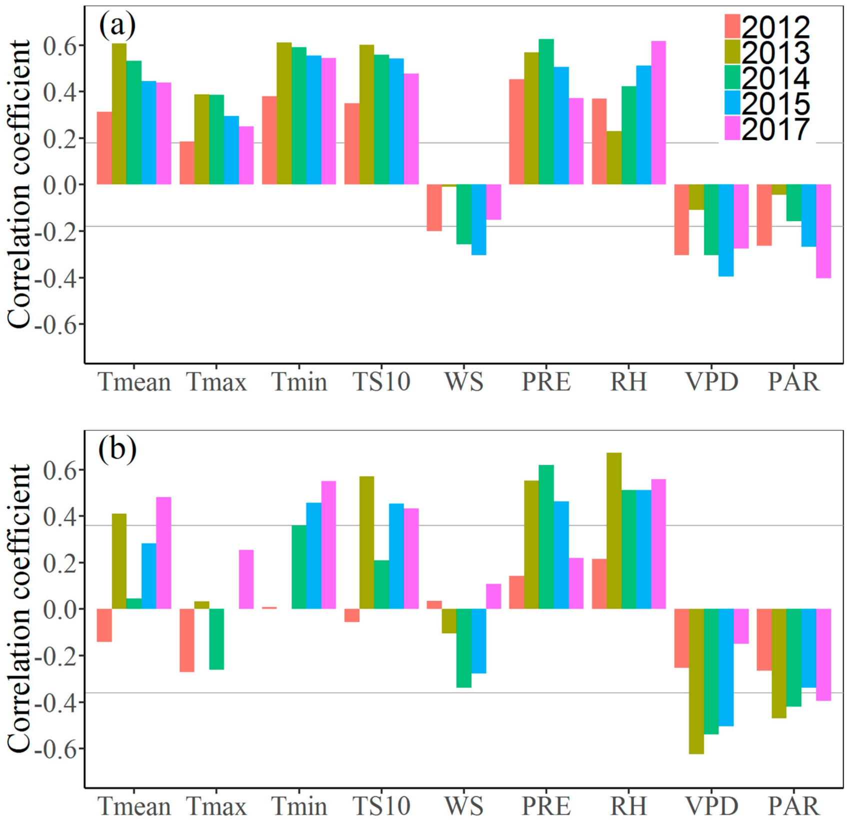

Figure 5. Correlation coefficients between daily (**a**) and weekly (**b**) means of growth-induced irreversible stem expansion (GRO rate) and corresponding climate variables for the years 2012–2015 and 2017. Gray lines indicate correlations significant at the $p \leq 0.01$ level. T_{mean}: mean air temperature; T_{max}: maximum air temperature; T_{min}: minimum air temperature; TS10: mean soil temperature at 10 cm depth; WS: wind speed; PRE: precipitation; RH: relative humidity; VPD: vapor pressure deficit; PAR: photosynthetic active radiation.

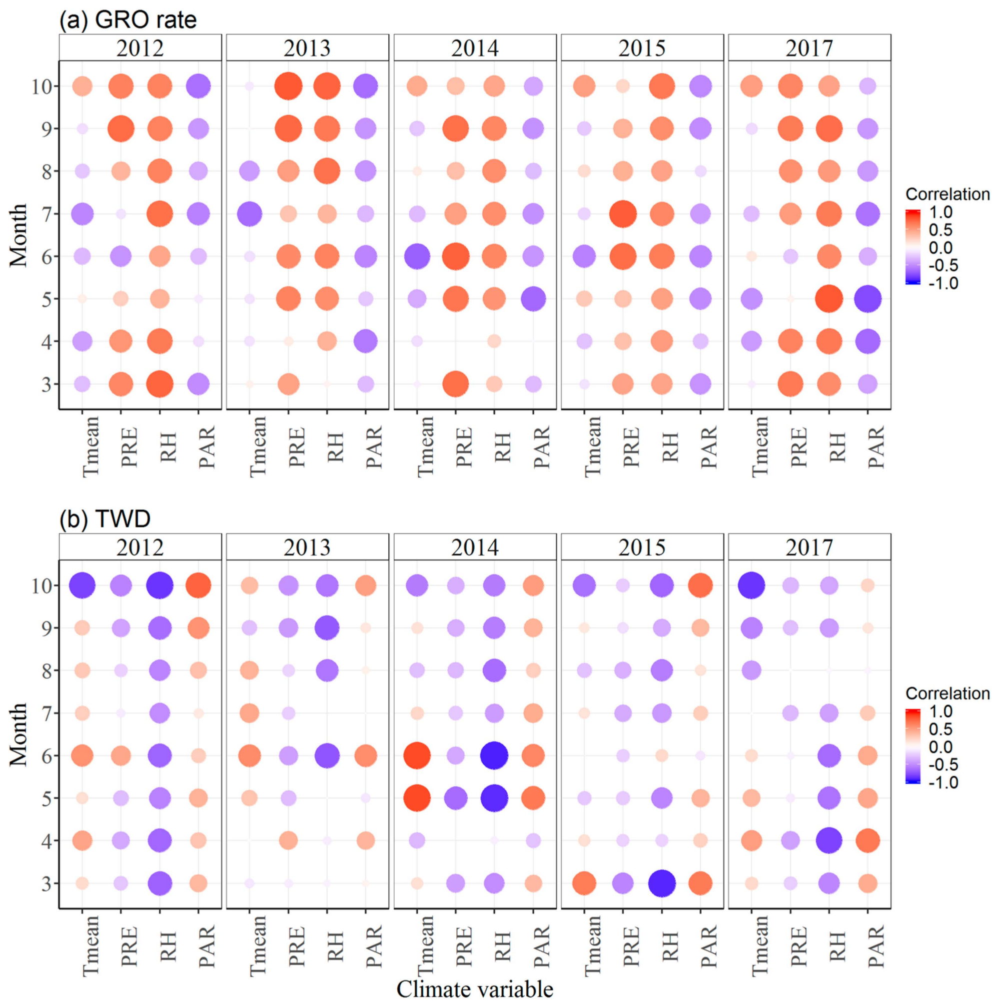

Figure 6. Correlation coefficients between monthly stem growth rate (GRO rate, **a**) and tree water deficit (TWD, **b**) and climatic variables from March to October for the years 2012–2015 and 2017. T_{mean}: mean air temperature; PRE: precipitation; RH: relative humidity; PAR: photosynthetic active radiation. *N* ranges from 289 to 358, and all correlations with a coefficient above 0.18 are significant at the $p < 0.01$ level.

Table 1. Parameter estimates for the selected linear mixed-effects models fitted to explain the variations of daily sums of growth-induced irreversible stem expansion (GRO rate) and daily minimum tree water deficit (TWD). Mixed-effects models were performed separately for GRO rate and TWD, with climate variables as fixed factors and individual trees nested in years and a first-order auto-correlation structure as random factor. PRE: precipitation; RH: relative humidity; WS: wind speed; vapor pressure deficit (VPD); SE: standard error; df: degrees of freedom.

#	Variable	Estimate	SE	df	*t*-Value	*p*-Value
GRO rate	Intercept	−4.05	0.09	1307	−44.90	<0.001
	PRE	0.266	0.025	1307	10.64	<0.001
	RH	0.401	0.0072	1307	5.54	<0.001
TWD	Intercept	−3.65	0.155	642	−23.59	<0.001
	WS	0.097	0.046	642	2.102	0.036
	PRE	−0.126	0.049	642	−2.586	0.009
	VPD	0.299	0.104	642	2.891	0.004

4. Discussion

Our results revealed that stem radial growth of *Pinus kesiya* var. *langbianensis* mainly occurs during early March to October, with highest growth rates during May to June (Figures 2–4). These results are in good accordance with seasonal domains of cambial activity of *P. kesiya* and *P. merkusii* based on wood anatomy analysis in northern Thailand [31]. Due to inter-annual climate variability, the length of the growing period varied substantially between years, which can strongly affect tree growth performance and forest carbon fixation [32].

Previous studies showed that the maximum growth rates of conifers in cold environments at high latitudes coincide with maximum day length [5,33]. In our subtropical study region, intra-annual radial growth of *P. kesiya* var. *langbianensis* was positively correlated to precipitation and humidity (Table 1, Figure 5), indicating that radial growth of Szemao pine is mainly limited by moisture availability. In a subtropical monsoon climate regime in northwestern Thailand, tree-ring widths of *Pinus kesiya* were significantly correlated with moisture availability during the pre-monsoon season from March to May [34]. Tree water deficit (TWD) was synchronous with drought periods during spring and autumn and correlated positively with air temperatures and VPD, indicating that water consumption through canopy transpiration increased during sunnier, warmer, and less humid conditions [12,13]. During the pre-monsoon season (March–May), relative high amplitudes and duration of stem contraction phases indicated a shortage of stem water supply (Figure 4). These results are consistent with the finding of pre-monsoon moisture limitation of stem radial growth of *Pinus kesiya* in northwestern Thailand [34] and in northeast India [35]. Our results underline the critical importance of this warm but dry season for the whole annual tree growth performance and carbon uptake by monsoonal forest ecosystems [32].

Precipitation and humidity were found as main limiting factors of stem growth for coniferous and broad-leaved tree species in temperate ecosystems, as well as in semi-arid regions of China [5,18,19,36,37]. The daily increment of *Pinus cembra* (L.) at the alpine treeline ecotone was positively correlated with changes in the tree water status controlled by relative humidity and precipitation [38]. As sufficient soil moisture availability is crucial for maintaining stem water status, cell turgor pressure and, thus, cell enlargement [9,39]. Stem hydrological processes, i.e., stem swelling, might also partially explain the strong positive effect of precipitation on stem increment [10]. The negative effect of current-day solar radiation on growth is assumed to be associated with reversible stem shrinkage rather than with irreversible stem growth alone [6].

The seasonal distribution of precipitation and water availability may have influenced the seasonal water budget and growth of the studied pine species. For example, pre-monsoon precipitation and humidity in 2014 were considerably lower than normal (Figure S2, Supplementary Materials). This resulted in a strong stem shrinkage and tree water deficit (TWD), and delayed the start of xylem growth, leading to a shorter duration of the growth period and reduced annual growth rates (Figures 2 and 3). Increased transpiration leads to increasing leaf water demand, resulting in a decline in stem water potential and stomata closure, if soil water availability is low [40]. This may induce carbon starvation and negative consequences for tree growth [41,42]. During prolonged dry periods like in March–June 2014, low soil moisture availability and high evaporation demand cause a negative water budget of the trees, thereby reducing carbon supply for cambial cell production [40]. Thus, a change in the precipitation regime may substantially affect the diel phases of stem hydrological status and influence the dynamics of water depletion and replenishment, as already been observed in single-leaf pinyon pine (*Pinus monophylla*) in North America [43].

5. Conclusions

We studied seasonal dynamics and climatic determinants of stem radius changes of *Pinus kesiya* var. *langbianensis* in the Ailao Mountains, southwestern China. Based on five-year high-resolution dendrometer data, we demonstrated that stem increment of *P. kesiya* var. *lanbianensis* was primarily related to precipitation and humidity, and confirmed that sufficient water supply, especially during the early growing season, is crucial for maintaining tree water status, as well as xylem cell production and cell enlargement. Our results are fundamental to better understand the growth performance and carbon sequestration capacity of this economically important species under future climate change. Further simultaneous measurements of carbon storage, sap flow, and stem diameter variations will allow assessing the potential risk of drought-related growth decline or mortality of tree species from subtropical mountainous environments [44] under expected climate change.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/10/899/s1.

Author Contributions: Z.-X.F. and A.B. conceived and designed the experiments. Z.X.F, P.-L.F., R.-Q.Y. and J.-H.Q. performed the experiments. Z.-X.F. and P.-L.F. analyzed the data and wrote the paper. A.B., J.G., and A.G. reviewed and edited the draft.

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