Tree Growth and Water-Use Efficiency at the Himalayan Fir Treeline and lower altitudes: Roles of Climate Warming and CO₂ Fertilization

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Abstract. Alpine forests are increasingly exposed to rising temperatures and intensified drought, potentially pushing species beyond their tolerance limits. However, the extent to which rising atmospheric CO_2 (C_a) can mitigate these stressors by enhancing tree intrinsic water-use efficiency (iWUE) remains unclear. We investigated the growth and physiological responses of Himalayan fir (*Abies spectabilis*) using basal area increment (BAI) and $\delta^{13}C$ data to track ecophysiological processes over recent decades along an altitudinal gradient in regions with hydrologically distinct regions on the Tibetan Plateau. Significant growth increases were observed at all altitudes in wet regions, while negative growth trends were noted at lower altitudes in dry regions. Climate–growth correlation analysis revealed that growth is primarily constrained by growing season temperatures and spring moisture availability. Tree iWUE increased over time at all altitudes, with a stronger increase in wet regions. Tree growth at lower altitudes in dry stands was negatively related to iWUE, whereas BAI in wet regions was positively associated with iWUE during the post-1965 period. Structural equation modeling indicated that temperature was a key driver of BAI and iWUE at all altitudes in wet regions, while temperature had negative effects on BAI at lower altitudes in dry regions. These results suggest that elevated C_a and temperature can stimulate tree growth in high-altitude forests in wet regions, but the positive effects do not compensate for the negative impacts of reduced water availability at lower altitudes in dry regions. Warming-induced drought stress may thus emerge as a more significant driver of growth compared to increasing C_a levels in comparable alpine forests. Our findings provide critical insights for refining assumptions about CO_2 fertilization and climate change effects in ecophysiological models.

1 Introduction

Forests play a crucial role in regulating terrestrial carbon fluxes and influencing the rate of atmospheric CO_2 (C_a) increase (Bonan, 2008; Pan et al., 2024), despite facing various climatic and atmospheric changes. Studies have shown that rising C_a has contributed to greater tree growth, driven by the synergistic effects of warming and increased atmospheric CO_2 (Saurer et

al., 2014; Qi et al., 2015; Silva et al., 2016; Martínez-Sancho et al., 2018; Guo et al., 2022). However, this potential growth benefit is often overshadowed by growth declines induced by warming-related stressors, particularly drought, which has overridden the effects of rising CO_2 in the past decade (Peñuelas et al., 2011; Silva and Anand, 2013; Van Der Sleen et al., 2015; Liu et al., 2024; Klesse et al., 2024). Understanding the long-term physiological and growth responses of trees to global changes remains a challenge, especially in climate-sensitive areas (Lindner et al., 2010; Charney et al., 2016; Shestakova et al., 2019; Olano et al., 2023; Sterck et al., 2024).

The Tibetan Plateau, which has experienced a rapid increase in annual mean air temperature at a rate of 0.26°C per decade over the past 40 years, is warming faster than the global average (Du, 2001). The forests of the Tibetan Plateau are particularly vulnerable to warming due to the amplified temperature increases at higher altitudes (Guo et al., 2018; Sigdel et al., 2018; Mu et al., 2021b; Panthi et al., 2020). Although warmer temperatures have been linked to enhanced vegetation productivity (Piao et al., 2014; Silva et al., 2016; Huang et al., 2017), climate warming increases atmospheric water demand, exacerbating drought stress on plants. Water availability may therefore become increasingly critical for Tibetan Plateau forests under continued warming and rising C_a (Liang et al., 2016b; Silva et al., 2016; Zhao et al., 2023). However, the long-term effects of these changes on tree physiology and growth in Tibetan Plateau forests, particularly in relation to the unprecedented rates of modern warming and increasing C_a, have not been adequately addressed (Xu et al., 2013; Wu et al., 2015; Huang et al., 2017; Panthi et al., 2020).

Tree-ring records provide valuable insights into long-term physiological and growth changes (Bräuning and Mantwill, 2004; McCarroll and Loader, 2004). The isotopic discrimination against ¹³C that occurs in leaves (i.e., diffusion and carboxylation fractionations) is reflected in the stable carbon isotope ratios ($\delta^{13}C$) of the organic matter produced in a given year. There is a well-established relationship between carbon isotopic discrimination and leaf physiology, such that $\delta^{13}C$ is directly related to assimilation rates (A) and stomatal conductance (g_s), which together define intrinsic water-use efficiency (iWUE) as the ratio between the two processes (Farquhar et al., 1982; Farquhar et al., 1989). Global studies using tree-ring $\delta^{13}C$ data have shown widespread increases in iWUE due to enhanced photosynthesis and carbon availability in response to rising C_a (Saurer et al., 2004; Wang et al., 2012; Keenan et al., 2013; Peñuelas et al., 2013; Frank et al., 2015). However, climatic factors, such as temperature and precipitation, may also influence iWUE and reduce the potential CO_2 fertilization effects on radial growth (Frank et al., 2015; Guerrieri et al., 2019; Liu et al., 2019; Wang et al., 2020; Zhang et al., 2018). Furthermore, the spatial variability of climate warming and decreasing moisture availability may be more influential in driving tree growth than changes in C_a in cold mountain forests (Salzer et al., 2009). Recent studies have highlighted contrasting physiological strategies among plant species and altitudes in response to environmental changes (Klein, 2014; Garcia-Forner et al., 2016; Martínez-Vilalta and Garcia-Forner, 2017; Fang et al., 2020; Wang et al., 2020). Therefore, differences in water-use efficiency and ecophysiological strategies across species and regions underscore the importance of shifting from global studies to more localized, species-specific approaches for assessing the long-term effects of warming temperatures and rising C_a (Frank et al., 2015; Martínez-Sancho et al., 2018; Voltas et al., 2020).

In this study, we present annually resolved iWUE and BAI data for Himalayan fir (*Abies spectabilis*), a widely distributed conifer species of the Tibetan Plateau. Although some studies have explored the relationship between iWUE and growth of Himalayan fir on the Tibetan Plateau (Huang et al., 2017; Panthi et al., 2020; Wang et al., 2020), they have typically focused on single locations. Here, we examine a broader set of stands distributed along altitudinal gradients and in both wet and dry regions of the Tibetan Plateau, aiming to identify the climatic conditions under which trees exhibit vulnerability. Our specific objectives are: (i) to explore whether rising C_a and climate changes have induced region-specific and altitude-specific changes in tree growth and physiological parameters; (ii) to determine the extent to which changes in climate and iWUE are related to radial growth in the study area; and (iii) to assess the physiological adjustments of trees to rising temperature and increased atmospheric CO_2 over the study period.

2 Materials and methods

2.1 Site conditions and tree species

The study was conducted in the southern and southeastern regions of the Xizang Province, located on the southern and southeastern Tibetan Plateau, characterized by a typical monsoon climate. The study sites spanned a broad range across the southern and southeastern Tibetan Plateau (Fig. 1). Meteorological data, including mean temperature and precipitation, were obtained from two meteorological stations of the China Meteorological Administration (Fig. 1) for the study period (1950s-2010s). Instrumental records showed a mean annual temperature of 0.23°C and an average total precipitation of 429 mm in Pali (wet region) recent decades, while the mean temperature is 2.7°C and the average total precipitation is only 282 mm in Dingri (dry region) recent decades (Fig. S1). Additionally, we retrieved climate data including monthly mean temperature, monthly precipitation and 3-month Standardized Precipitation-Evapotranspiration Index (SPEI) data from the Climate Research Unit (CRU, University of East Anglia) TS Version 4.01 from the climate explorer (http://climexp.knmi.nl). The SPEI were calculated based on the climate data from the CRU TS Version 4.01 with a spatial resolution of 0.5°× 0.5° over the period from 1900 to 2014. The regional mean values of SPEI were calculated over the grids within the region 27.75°–28.25°N, 88.75°–89.25°E for SYD, and the region 27.95°–28.45°N, 86.75°–87.25°E for DJ, respectively. The regional mean climate data reveal a significant warming trend in the study area over the past century, with the rate of temperature increase accelerating from 0.007 °C/yr (1901–1964) to 0.032 °C/yr (1965–2013) at the drier site (DJ) and from 0.008 °C/yr to 0.023 °C/yr at the wetter site (SYD) (Fig. S2a). In contrast, annual precipitation remained stable since 1901 (Fig. S2b), leading to an overall decline in SPEI at both sites (Fig. S2c).

Himalayan fir (*Abies spectabilis*) is a cold-tolerant species native to the high-altitude montane forests of the Himalayas. It has a wide altitudinal distribution ranging from 2,800 m a.s.l. to the upper treeline. The species is found across the central and western Himalayas, with a significant presence on the southwestern and southern Tibetan Plateau (Panthi et al., 2020).

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2.2 Field Sampling and Tree-Ring Width Chronologies

95   The tree-ring samples used in this study were collected from healthy Himalayan fir trees growing at altitudes ranging from 3,378 m to 4,557 m a.s.l. in the southern and southeastern Tibetan Plateau (Table S1; Fig. 1). These sites were undisturbed by human activities during the study period. Tree-ring increment cores were extracted from trees along an altitudinal gradient in both dry (Dingjie) and wet (Shangyadong) regions. The cores were air-dried indoors, mounted on wooden slats, and polished with progressively finer sandpaper up to 1000 grit until the tree-ring boundaries became clearly visible. Using a

100 microscope, tree rings from each sample were crossdated by comparing ring patterns among samples. We measured tree-ring widths using a LINTAB 6 measuring system, with a resolution of 0.001 mm. Visual crossdating was verified with COFECHA software (Holmes and Kozinn, 1983). All crossdated ring widths were processed using ARSTAN software to standardize the ring-width series, employing a negative exponential or linear growth curve to remove non-climatic signals. The detrended index series were then merged using the biweight robust mean method to create a standard (STD) chronology

105 for each forest stand. For each tree-ring value, tree-ring width was converted into basal area increment (BAI, cm² per year) using the following formula proposed by Phipps and Whiton (1988), assuming balanced growth for each round (1 year = 1 round, early and late): $BAI = \pi \times (R_n^2 - R_{n-1}^2)$. Where R is the radius of the tree, and n is the year of tree-ring formation. The raw basal area increment (BAI) series were used to assess long-term growth trends, as BAI is less susceptible to biological trends and provides a more direct measure of stem biomass compared to tree-ring width data (Franco and Fares,

110 2008; Martinez-Sancho et al., 2018; Yang et al., 2022b). To further minimize age-related effects, we excluded the early growth period from both trend analysis and isotope measurements. For climate-growth relationship analysis, we applied standard detrending procedures to BAI series using either a negative exponential or a linear function. The calculation and detrending of BAI was performed using the R package dplR (Bunn, 2008).

2.3 Stable Carbon Isotope (δ^{13}C) and Intrinsic Water-Use Efficiency (iWUE)

115 Five cores from different trees were selected at each forest stand, ensuring clear and continuous ring boundaries with no missing rings. The annual rings from the five samples were pooled by year to produce a single composite isotope series for each forest stand (Table S2). The wood material was ground using a centrifugal mill to ensure homogeneity and efficiency in α-cellulose extraction. The α-cellulose was extracted from the annual tree rings following standard methods (Loader et al., 1997). To maximize homogeneity, the cellulose was treated in an ultrasound unit in a hot water bath (JY92-2D, Scientz

120 Industry, Ningbo, China) to break down the cellulose (Laumer et al., 2009). The α-cellulose was then freeze-dried for 72 hours using a vacuum freeze dryer (Labconco Corporation, Kansas City, MO, USA) prior to isotope analysis. The δ^{13}C values were determined using an element analyzer (Flash EA 1112; Bremen, Germany) coupled with an isotope-ratio mass spectrometer (Delta-plus, Thermo Electron Corporation, Bremen, Germany) at the State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences. The analytical errors (standard deviations) for

125 the isotope measurements were less than 0.05‰ for δ^{13}C. Calibration was performed using the International Atomic Energy

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Agency (IAEA) standards, USGS-24 (Graphite) and IAEA-CH3 (cellulose). All δ¹³C values are expressed relative to their respective standards (Vienna Pee Dee Belemnite for carbon isotopes and Vienna Standard Mean Ocean Water for oxygen isotopes).

The formula used to calculate δ¹³C is:

$$\delta^{13}C = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000‰ , \tag{1}$$

Where R represents the ratio of ¹³C to ¹²C; R_{sample} and $R_{standard}$ are the R values of the samples and the standard, respectively.

To accurately obtain tree-ring δ¹³C, the climate change effect, i.e., the increasing trend of atmospheric CO_2 concentration, was removed. The atmospheric CO_2 concentration data was derived from a combination of the reconstructed values (period 1900-2003) using ice cores (Mccarroll and Loader, 2004; Boucher et al., 2014) and the direct observations of CO2 concentration for the period 2004-2013, which were obtained from the Mauna Loa Observatory of America (http://www.esrl.noaa.gov/gmd/obop/mlo/). The carbon isotope fractionation sequence in the tree rings was then calculated using the following equations (Farquhar et al., 1989):

$$\Delta^{13}C = \frac{\delta^{13}C_a - \delta^{13}C_p}{1 + \frac{\delta^{13}C_p}{1000}} , \tag{2}$$

Where ¹³C_p and ¹³C_a were ¹³C values of plant photosynthetic products and atmospheric CO_2, respectively. The ratio of C_i to C_a was calculated using:

$$\frac{C_i}{C_a} = \frac{\Delta^{13}C - a}{b - a} , \tag{3}$$

Where C_i and C_a represent the concentrations of CO_2 in the leaves and atmosphere, respectively. a and b are constants representing CO_2 isotope fractionation during stomatal diffusion (4.4‰) and RuBP enzyme carboxylation (27‰). iWUE was then estimated using Ci and Ca following Ehleringer (1993):

$$iWUE = \frac{A}{g_s} = \frac{C_a - C_i}{1.6} , \tag{4}$$

Where 1.6 is the ratio of diffusivities of water and CO_2 in air.

2.4 Statistical Analyses

Linear trends for annual climatic variables and tree growth variables were calculated using least-squares regressions. The relationship between the C_i and C_a trends obtained from δ¹³C and the three theoretical gas-exchange scenarios was quantified using root mean square error (RMSE) and mean absolute error (MAE) for each study site. Mann–Kendall trend tests were conducted to identify the most recent significant warming period (1965 to the present).

To quantify the relationships between climatic factors, intrinsic water-use efficiency (iWUE), and basal area increment (BAI) over the past four decades, we implemented a piecewise structural equation modeling (pSEM) approach. The analysis was

performed in R version 4.1 (R Core Team, 2022) using the *pSEM* package (Lefcheck, 2016), which enables the integration of mixed-effects models within an SEM framework. We used a linear mixed-effects modeling approach (Nakagawa and Schielzeth, 2013) to partition variance contributions (R^2) from both fixed effects and random effects on BAI and iWUE. This approach allowed us to assess direct and indirect pathways while accounting for potential hierarchical dependencies in the data. Model adequacy was evaluated using Fisher's C statistic, with a non-significant result ($p > 0.05$) indicating acceptable model fit (Shipley, 2009). This analytical framework provided a robust assessment of how climatic drivers influence tree growth both directly and indirectly through physiological adjustments in iWUE.

3 Results

3.1 Temporal Variability in BAI, iWUE, and Cellulose Stable Carbon Isotopes

The basal area increment (BAI) of Himalayan fir exhibited a significant increasing trend at the treeline in the dry region and at all altitudes in the wet region after 1965 (Fig. 2). In contrast, no significant trend was detected at the middle altitude, and a decreasing growth trend was observed at the lower altitudes in the dry region (Fig. 2b). Similarly, the intrinsic water-use efficiency (iWUE) of Himalayan fir increased significantly, with a steep rise after 1965 (Fig. 3b). The carbon isotopic composition ($\delta^{13}C$) of tree rings showed a clear decreasing trend over recent decades, reflecting the rising atmospheric CO_2 concentration (C_a) across all altitudes in both dry and wet regions (Fig. S3). Our results indicate that tree growth increased with the rising iWUE in wet regions, while the relationship between iWUE and growth shifted from a significant positive correlation to a negative correlation as altitude decreased in the dry regions (Fig. 4).

3.2 Climate Responses of BAI

The BAI of Himalayan fir exhibited region-specific climate sensitivity, with consistent responses observed in the wet region and varying responses along the altitude gradient in the dry region. In the wet region, tree growth showed a significant positive correlation with both the previous autumn temperature and the growing season (June to September) temperature at all altitudes (Fig. 5a). In the dry region, however, tree growth was positively correlated with the previous autumn and growing season temperature at the treeline, while a significant negative correlation was observed at lower altitudes (Fig. 5a). Additionally, tree growth in the wet region was positively correlated with spring precipitation, whereas in the dry region, spring precipitation was negatively correlated with tree growth at lower altitudes (Fig. 5b). The moisture-related variables (relative humidity and SPEI) exhibited generally negative correlations with tree growth in the wet region but positive correlations in the dry region, particularly at mid- and low-altitude stands (Fig. 5c, d). Notably, when BAI chronologies were constructed using all dated core samples, rather than only those selected for isotope analysis, the resulting climate response patterns remained consistent with the above findings (Fig. S4).

3.3 Factors Regulating Changes in BAI

Multiple regression models identified significant contributions of temperature, precipitation/moisture availability, and iWUE to interannual variations in tree growth over the past decades (Fig. 6). In the wet region, regression models identified previous autumn temperature (Tgrs) and growing season temperature (Tpaut) as the dominant explanatory variables for radial growth variability, with supplementary contributions from iWUE and spring precipitation at lower altitude sites (Fig. 6). In the dry region, tree growth was primarily influenced by spring moisture availability and temperature (Fig. 6). Overall, the climatic and physiological factors accounted for 25-58% of the observed growth variation, as quantified through piecewise structural equation modeling (pSEM) (Fig. 7, Table S3). The pSEM framework elucidated distinct mechanistic pathways governing basal area increment (BAI) across climatic zones. In the wet reigon, Tgrs emerged as the principal determinant of BAI (Fig. 7a), while iWUE exerted significant positive direct effects on BAI at lower altitudes (Fig. 7). Notably, Tgrs demonstrated a significant positive relationship with iWUE in these humid forests (Fig. 7). Dry region stands exhibited contrasting responses, with Tgrs and spring temperature (Tspr) showing significant negative associations with BAI at mid- and low-altitude sites. Conversely, positive growth responses to spring moisture availability (RHspr and Pspr) were observed at the treeline and middle altitudes (Fig. 7), highlighting water limitation as the primary growth constraint in these environments.

4 Discussion

4.1 Tree Growth and Its Climatic Responses

Our study reveals a distinct pattern of tree growth across different regions and altitudes on the Tibetan Plateau, with a strong acceleration of growth in the wet region and at higher altitudes in the dry region, contrasting with decreasing growth trends at lower altitudes in the dry region. These results diverge from the widely observed global trend of declining tree growth and increased forest mortality due to high temperatures and drought, particularly in other parts of the world (Allen et al., 2010; Hartmann et al., 2018; Mirabel et al., 2023). While numerous studies have documented the detrimental effects of warming and drought on forest ecosystems, particularly in the northeastern Tibetan Plateau (Liang et al., 2016a; Wang et al., 2018), our findings suggest that the Tibetan Plateau, particularly in its southeastern and southern regions, is undergoing a phase of warming and humidification that has benefited tree growth (Shi et al., 2020; Mu et al., 2021a; Guo et al., 2022).

The acceleration of growth in the wet regions aligns with the well-established finding that increased temperature can enhance tree productivity in humid climates (Liang et al., 2016b; Silva et al., 2016; Wang et al., 2023), which is further confirmed by our results showing a positive correlation between growth and growing season temperature. However, this contrasts with the negative or stable growth trends observed in the dry region, particularly at lower altitudes, where warming-induced drought stress appears to inhibit growth. Our study extends existing research by highlighting that tree growth in moisture-limited ecosystems (such as the dry regions) is more constrained by water availability than by warming.

This reinforces the growing body of literature suggesting that CO_2 fertilization effects are more likely to occur in temperature-limited ecosystems (Körner, 2015), whereas moisture-limited regions are less responsive to increased C_a (Wu et al., 2015).

This research provides novel insights into how specific regional climatic shifts may lead to divergent growth responses in montane forests. In contrast to the increasing mortality rates and growth decline observed in other high-altitude forest systems (Linares and Camarero, 2012; Lévesque et al., 2014), our study suggests that areas undergoing warming and increased moisture availability could experience enhanced tree growth, provided drought stress remains manageable.

4.2 Spatial heterogeneity of tree growth-iWUE relationships

Our findings reveal a consistent decline in $\delta^{13}C$ values in Himalayan fir, corresponding to a marked increase in intrinsic water-use efficiency (iWUE), particularly in mesic regions and at treeline sites in arid zones. This trend aligns with global observations of enhanced iWUE under rising atmospheric CO_2 (C_a) (Frank et al., 2015; Huang et al., 2017; Guerrieri et al., 2019). However, our results demonstrate greater complexity in the iWUE response of Himalayan fir than previously documented, with pronounced site- and altitude-specific variability. Specifically, at the mid- and low-altitude sites in arid region, limited moisture availability appears to constrain iWUE gains despite rising C_a, whereas the forest stands with more moisture availability, including wet sites and the treeline site of the drier region, exhibit more pronounced iWUE increases. These findings provide a physiological framework for understanding how trees adjust water-use strategies under concurrent increases in CO_2 and temperature.

While elevated C_a is frequently associated with enhanced photosynthesis and iWUE (Cole et al., 2020; Brienen et al., 2011; Saurer et al., 2014), the observed increase in intrinsic water-use efficiency (iWUE) does not necessarily correspond to enhanced radial growth, as evidenced by the non-significant relationship between basal area increment (BAI) and iWUE (Andreu-Hayles et al., 2011; Girardin et al., 2016; Reed et al., 2018), particularly in the dry regions (Peñuelas et al., 2011; Franks et al., 2013; Silva and Anand, 2013; Peters et al., 2018). This pattern suggests a drought-tolerance strategy that optimizes the trade-off between transpiration and carbon assimilation, highlighting the importance of local-scale ecophysiological adaptations to climate change (Aranda et al., 2000; Hereș etal., 2014; Panthi et al., 2020). The negative correlation between BAI and iWUE at the low-altitude stands in the dry region supports the idea that drought stress can offset the benefits of CO_2 fertilization (Granda et al., 2014; Fang et al., 2020). Moreover, previous investigations have revealed altitudinal divergence in the physiological mechanisms driving iWUE enhancement: while treeline populations primarily achieved increased iWUE through photosynthetic enhancement, populations at lower elevations predominantly relied on stomatal conductance reduction (Pu and Lyu, 2023). In this study, divergent intercellular CO_2 concentrations (C_i) across sites suggest plasticity in leaf gas exchange (Fig. S5), demonstrating that trees actively regulate physiological traits in response to rising C_a, rather than responding passively (Ainsworth and Rogers, 2007; Walker et al., 2015; Voelker et al., 2016). These adjustments reflect an adaptive capacity to balance carbon gain with water conservation under changing climatic conditions.

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These findings emphasize the need for meso- to local-scale investigations to unravel the interactive effects of C_a, temperature, and moisture on tree physiology. This is particularly critical in high-altitude ecosystems like the Himalayas, where climatic gradients create complex, non-linear responses in tree growth and iWUE (Körner, 2003; Salzer et al., 2009). Future research should prioritize mechanistic models that integrate these spatial and temporal variations to improve predictions of forest dynamics under climate change.

5 Conclusions

In summary, our study provides novel insights into the ecophysiological and growth responses of Himalayan fir to climate change on the Tibetan Plateau. By examining the effects of rising atmospheric CO_2, temperature, and drought across different regions and altitudes, we have shown that climate change has diverse effects on tree growth, with moisture availability being a critical limiting factor at lower altitudes. Our findings underscore the importance of considering spatial and regional differences when assessing the impacts of climate change on forest ecosystems, and highlight the complex interactions between temperature, moisture, and CO_2 in shaping tree growth patterns. These insights are crucial for refining our understanding of forest dynamics and carbon cycling in montane ecosystems, and for predicting the future trajectory of high-altitude forests under climate change.

Author contribution

L.L. acquired the funding and designed the study. X.P. processed the tree-ring samples, conducted the analysis and wrote the first draft. L.L. and X.P. interpreted the results, revised the manuscript, and contributed to writing. Both authors reviewed and approved the final submission.

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Declaration of competing interest

The authors declare no competing interests.

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Data availability

Data will be made available on request.

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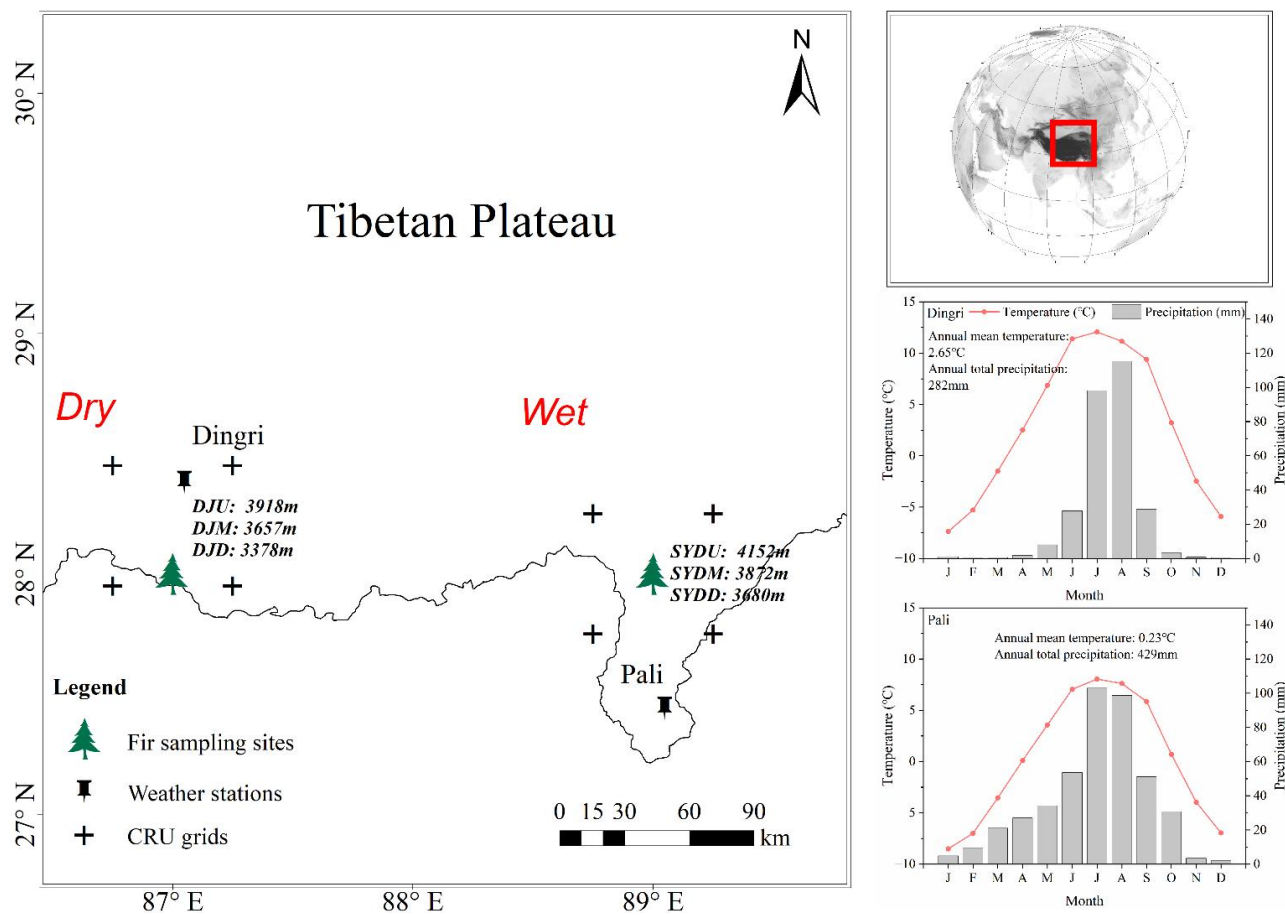
525 **Figure 1. Location of the study sites and weather stations for Himalayan fir on the Tibetan Plateau. Climate diagrams are based on meteorological records from the Dingri (28°38' N, 87°5' E, 4300 m) and Pali (27°44' N, 89°5' E, 4300 m) weather stations for the period 1965–2013.**
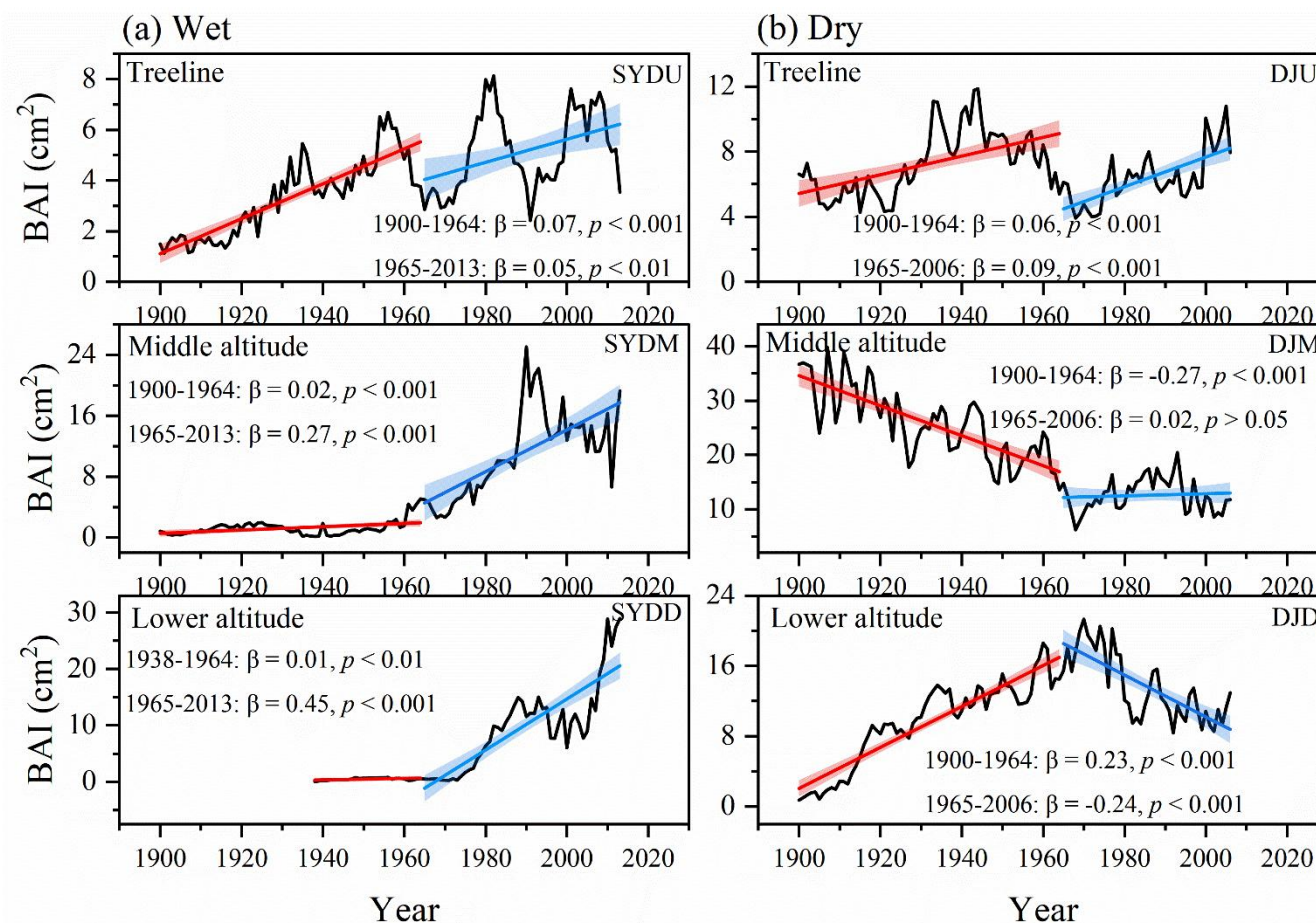
Figure 2. Temporal trends of basal area increment (BAI) for Himalayan fir at different altitudes during the period 1900−2010s.
The solid lines depict piecewise linear regression models, with a breakpoint at 1965. The model statistics include the slope of BAI (β, cm² year⁻¹), coefficient of determination (R^2) and associated p-values. The shaded regions denote 95% confidence intervals for the regression fits.

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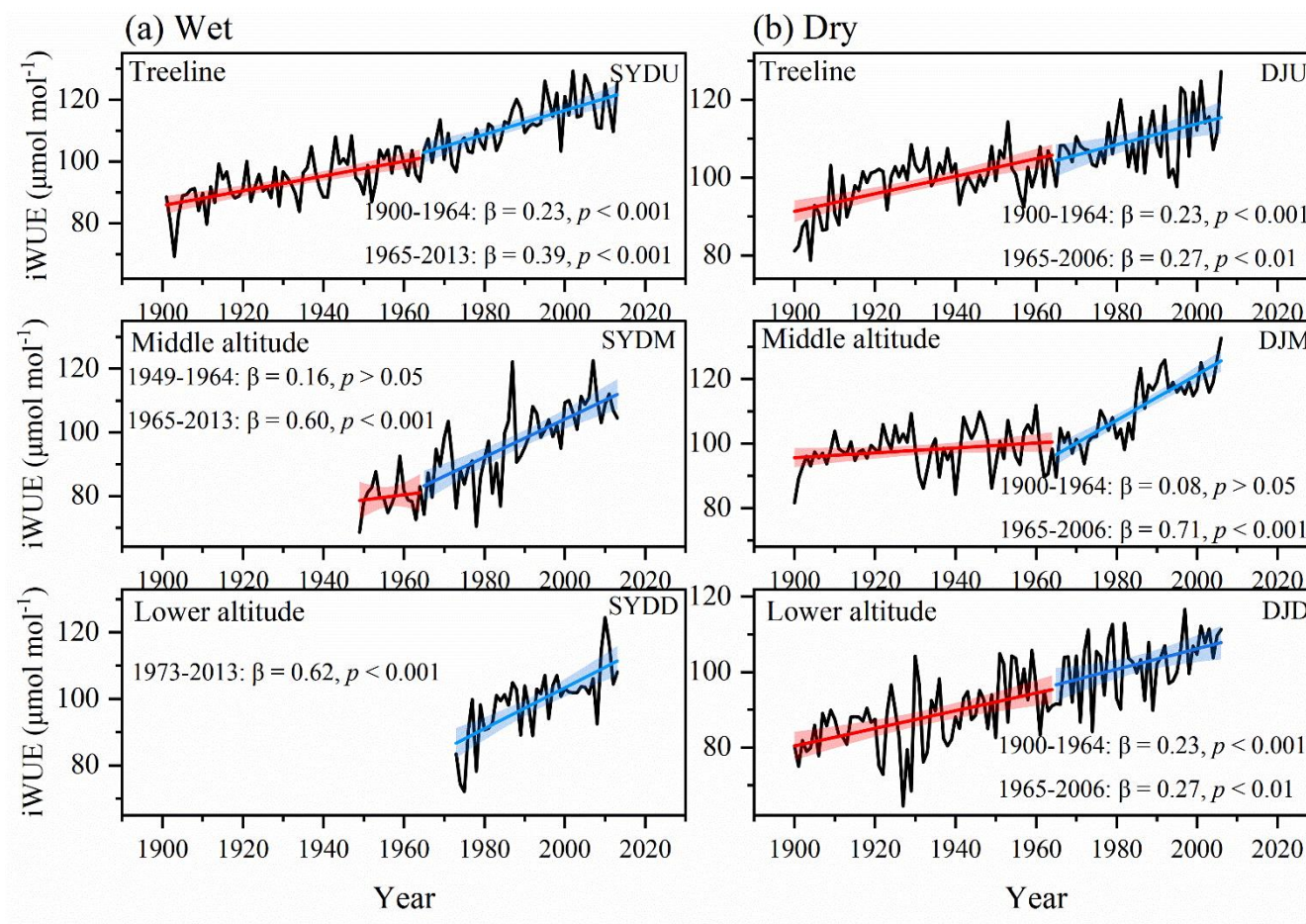
Figure 3. Temporal trends of intrinsic water-use efficiency (iWUE) during 1900-2010s for Himalayan fir at different altitudes. The solid lines depict piecewise linear regression models, with a breakpoint at 1965. The model statistics include the slope of BAI (β, cm² year⁻¹), coefficient of determination (R2) and associated p-values. The shaded regions denote 95% confidence intervals for the regression fits.
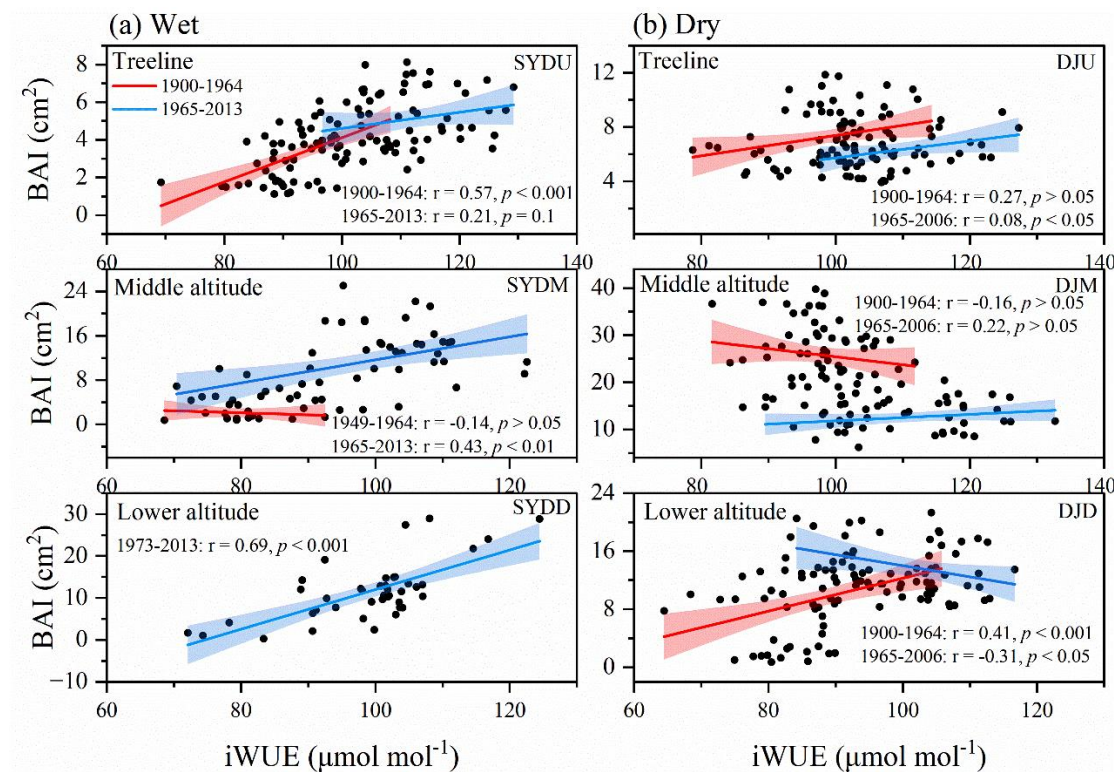
Figure 4. Long-term relationships between intrinsic water-use efficiency (iWUE) and basal area increment (BAI) of Himalayan fir at different altitudes across two hydrologically distinct sites. Linear regression results for each period are shown, along with the explained variance (R^2) and significance levels (p-values). Shaded areas represent 95% confidence intervals.

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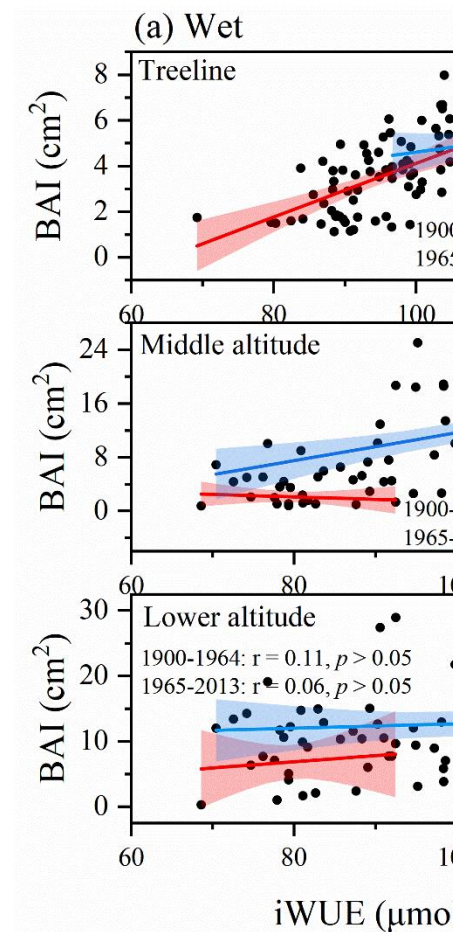
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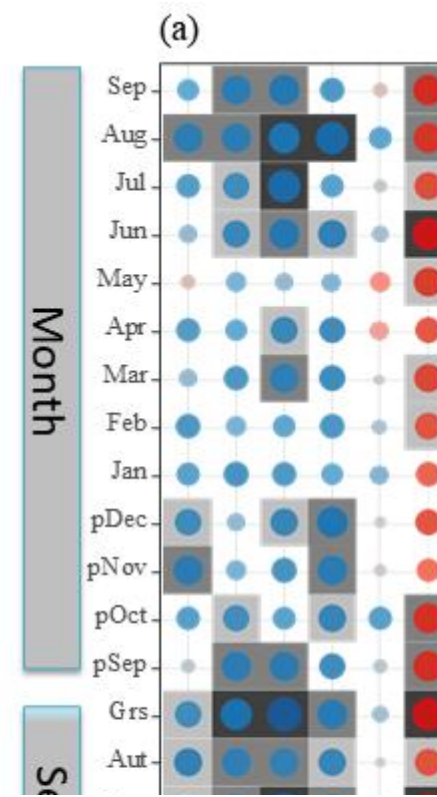
Figure 5. Pearson correlation coefficients between basal area increment (BAI) and climatic variables, including (a) mean temperature, (b) total precipitation, (c) relative humidity and (d) standardized precipitation-evapotranspiration index (SPEI) on both monthly and seasonal scales for Himalayan fir during the period 1965–2013. It should be noted that the BAI chronologies were derived exclusively from samples used for isotope measurements. "Grs" denotes the growing season (June to September). "Cor_value" and "abs_value" represent the correlation coefficient value and the absolute value of the correlation, respectively.
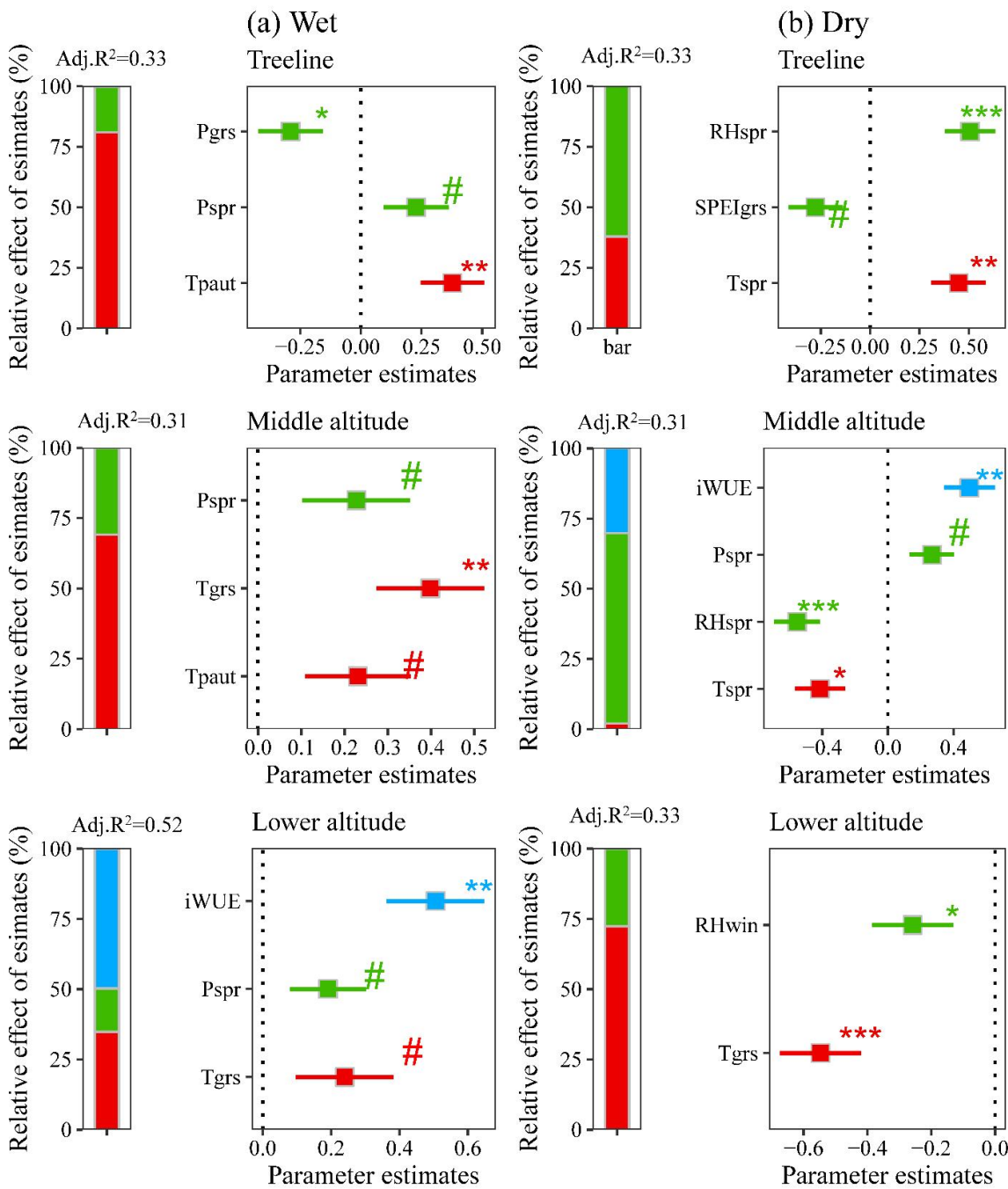
Figure 6. Effects of multiple environmental factors on fir growth at different altitudes. The symbols #, *, **, and *** denote significance levels at p<0.1p<0.1, p<0.05p<0.05, p<0.01p<0.01, and p<0.001p<0.001, respectively. Abbreviations: Tspr = spring mean temperature; Tgrs = growing season mean temperature (June to September); RHspr = spring relative humidity; RHgrs = growing season relative humidity (June to September); RHwin = winter relative humidity; SPEIspr = spring standardized precipitation-evapotranspiration index; SPEIgrs = growing season standardized precipitation-evapotranspiration index (June to September).

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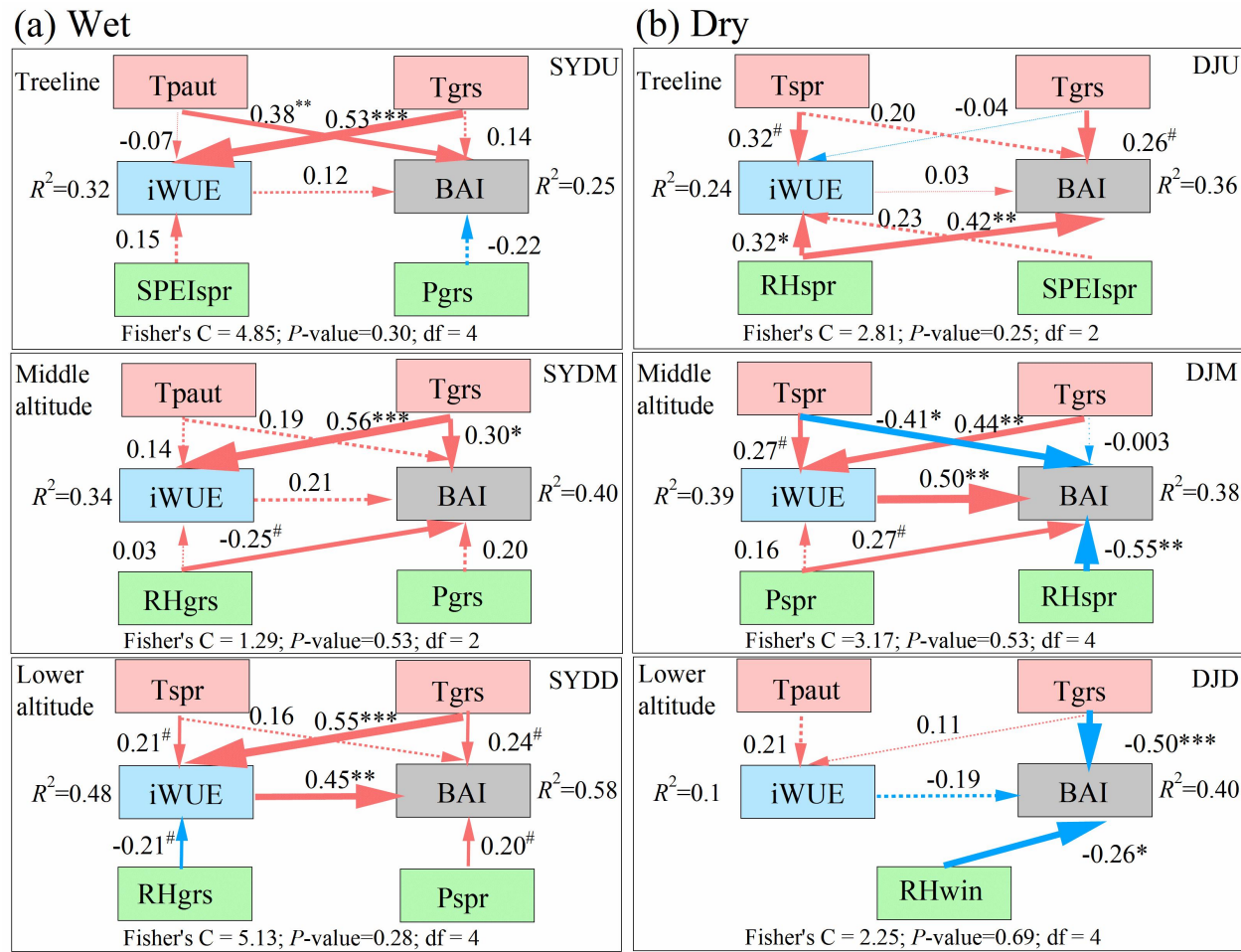
Figure 7. Piecewise structural equation meta-model (pSEM) used to assess the influences of climatic factors on basal area increment (BAI) and intrinsic water-use efficiency (iWUE) of Himalayan fir during the period 1965–2010s at different altitudes. Numbers adjacent to each arrow indicate the standardized regression coefficients for each path. Arrow thickness represents the strength of the effect, while color indicates the direction (red = positive, blue = negative). Solid arrows denote significant effects, whereas dashed arrows denote nonsignificant effects. Symbols #, *, **, and *** indicate significance levels at p < 0.1, p < 0.05, p < 0.01, and p < 0.001, respectively. Abbreviations: Tpaut = previous autumn mean temperature; Tsum = summer mean temperature; Tspr = spring mean temperature; Tgrs = growing season mean temperature (June to September); RHspr = spring relative humidity; RHgrs = growing season relative humidity (June to September); RHwin = winter relative humidity; SPEIspr = spring standardized precipitation-evapotranspiration index; SPEIgrs = growing season standardized precipitation-evapotranspiration index (June to September).