Intra-annual stem radial growth of four plantation species with different water use strategies and life types on the Loess Plateau, China postprint

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Abstract

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Full Text

Preamble

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Intra-annual stem radial growth of four plantation species with different water use strategies and life types on the Loess Plateau, China

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Abstract: Tree growth is extremely vulnerable to climate change, especially in semi-arid areas. Although the response of stem radial growth (SRG) to climate change has been extensively studied, the intra-annual regulatory mechanisms of SRG in trees with different water use strategies and life types remain poorly understood. This study calculated the SRG of four native species in the semi-arid area of the Loess Plateau, China, including two isohydric species (*Pinus tabuliformis* Carrière and *Populus* × *hopeiensis* Hu & Chow) and two anisohydric species (*Prunus sibirica* L. and *Platycladus orientalis* (L.) Franco). The results revealed that the intra-annual SRG of all four tree species exhibited a single peak, and greater SRG was found in anisohydric species. Principal component analysis and structural equation model revealed that atmospheric water, particularly relative humidity, was the main factor affecting the SRG of coniferous species (*P. tabuliformis* and *P. orientalis*), whereas the SRG was mainly affected by soil water content in broadleaf species (*P. sibirica* and *P.* × *hopeiensis*). These findings suggested that water use strategies and life types play important roles in SRG and environmental response of trees in semi-arid area. Considering the high climate sensitivity of wood formation in trees, our results highlight the importance of water use strategies and life types of trees in SRG prediction in the context of future climate change in arid and semi-arid areas.

Keywords: semi-arid area; plantations; water use strategy; stem radial growth; tree water deficit; environmental factor

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1 Introduction

The rapid and widespread warming associated with global climate change has profoundly impacted terrestrial ecosystems, particularly in arid and semi-arid areas that encompass more than one-third of Earth’ s total land area (FAO, 2019). These impacts manifest as alterations in species composition, functional diversity, and distribution patterns (Hisano et al., 2018). Dryland forests, which cover approximately 18.0% of the global dryland area, are particularly vulnerable to climate change-induced stresses that threaten productivity and ecological functions (Safriel et al., 2005; Choat et al., 2018). As drought events become more frequent, affected trees exhibit increased sensitivity to water availability (Battipaglia et al., 2014). Therefore, understanding how stem radial growth (SRG) in trees with different water use strategies and life types responds to environmental factors is essential for providing insights into tree growth strategies under future climate change in arid and semi-arid areas.

Tree SRG is driven by the periodic renewal of secondary xylem and phloem in the cambium (Rajput et al., 2018). Tree growth is a complex process involving interactions among nearly all tree parts, including the crown, trunk, and roots. Tree rings alone fail to fully explain how environmental conditions affect growth, often missing seasonal changes and related growth constraints (Rossi et al., 2016). Furthermore, tree-ring data offer insights into long-term patterns but reveal little about intra-annual growth processes (Zhang et al., 2021). Currently, dendrometers have emerged as indispensable tools for studying changes in tree SRG due to their exceptional resolution, operating at scales as fine as daily or even hourly (Szatniewska et al., 2022). Through meticulous monitoring of the formative layer activities, dendrometers can accurately delineate intra-annual SRG characteristics, including the initiation, cessation, and duration of growth, as well as SRG rate and volume (Deslauriers et al., 2003). Integrating meteorological data, Deslauriers et al. (2003) offered insights into temporal effects of environmental factors on tree growth and revealed how climate influences physiological reactions.

Tree SRG is sensitive to various climatic factors, including air temperature, vapor pressure deficit, and photoperiod, which directly influence cambium activities (Rossi et al., 2008; Cuny et al., 2012; Furze et al., 2019; Zweifel et al., 2021). In boreal regions, climatic factors influencing cambium activity consist of air temperature and daylight, resulting in a growth peak near the summer solstice in boreal and montane forests (Duchesne et al., 2012). Conversely, in tropical and Mediterranean regions, tree growth is affected mainly by water availability, leading to bimodal or multimodal patterns linked to alternating dry and wet seasons (Morino et al., 2021; Tumajer et al., 2022). Moreover, air temperature and water availability during the year jointly impact SRG in European broadleaf temperate forests (Duchesne et al., 2012). In arid areas, the intra-annual SRG pattern of *Pinus tabuliformis* Carrière in the Helan Mountains of northern central China also shows a single peak, with daily SRG significantly positively correlated with precipitation and negatively correlated with air temperature (Gao et al., 2019). *Juniperus przewalskii* Kom. and *Picea crassifolia* Kom. in the Qilian Mountains of northwestern China exhibit similar patterns (Zhang et al., 2024). However, it remains unclear whether SRG patterns are unimodal or multimodal during the year and which climatic factors dominantly affect intra-annual SRG in typical arid and semi-arid areas such as the Loess Plateau.

Tree SRG is also influenced by water use strategies and life types due to marked differences in drought susceptibility among species (Zhou et al., 2023). Trees can be classified as either isohydric or anisohydric based on stomatal responses to drought, with corresponding differences in physiological parameters (Meinzer et al., 2016). Anisohydric species, with loose stomatal regulation (stomata remain open even under drought conditions) and high water transfer efficiency in the xylem, have high photosynthetic rates and leaf area indices that enable optimization of light acquisition during the growing season. In contrast, isohydric species, with tight stomatal regulation (stomata close in response to drought conditions) and low water transfer efficiency, may prevent irreversible xylem damage caused by water imbalance at the expense of photosynthesis (Cuny et al., 2012; Wang et al., 2021).

Regarding life types, ring-porous broadleaf species with large differences in wood anatomy between earlywood and latewood experience longer growing seasons, allowing them to form earlywood in early spring with low drought stress probability (Pérez-de-Lis et al., 2016). In contrast, the annual SRG rate of diffuse-porous species with homogeneous wood structure is more dependent on the summer dry season due to delayed cambial activity onset (Prislan et al., 2013). Photosynthesis is directly associated with xylem and tree growth (Hari and Nöjd, 2009). On a subdaily scale, ring-porous broadleaf species with large conduits are more prone to cavitation-induced embolism, which might limit SRG during days with strong negative water potential (Sperry et al., 2008). Diffuse-porous species prevent cavitation by closing stomata early, which might also restrict SRG during dry periods via decreased photosynthetic rates or even carbon starvation (Walthert et al., 2021). In arid and semi-arid areas, water plays an important role in tree SRG, creating an urgent need to understand how water use strategies and life types affect tree SRG responses to environmental factors.

This study aims to reveal growth patterns of trees (*P. tabuliformis*, *Prunus sibirica* L., *Platycladus orientalis* (L.) Franco, and *Populus* × *hopeiensis* Hu & Chow) and how environmental factors affect intra-annual SRG in trees with different water use strategies (isohydric or anisohydric) and life types (evergreen coniferous or deciduous broadleaf). We analyzed tree SRG patterns and potential environmental drivers via Gompertz growth function modeling using dendrometer records integrated with meteorological and soil data. Research was conducted in a semi-arid area of the Loess Plateau, China, which stands as one of the world’ s largest loess repositories and has long experienced severe soil erosion (Zhang et al., 2008). The species *P. tabuliformis*, *P. sibirica*, *P. orientalis*, and *P.* × *hopeiensis* are native plantation species on the Loess Plateau, planted as part of the Grain-for-Green Project to prevent soil erosion (Shi et al., 2020). Furthermore, different water use strategies have been identified in these species: *P. tabuliformis* (evergreen coniferous) and *P.* × *hopeiensis* (deciduous broadleaf) are isohydric, while *P. sibirica* (deciduous broadleaf) and *P. orientalis* (evergreen coniferous) are anisohydric (Cuny et al., 2012), allowing us to evaluate connections between tree growth and water use strategies.

2.1 Study area

This research was conducted at the Gongjing Observation Site (35°58 20 N, 104°20 06 E) within the Yuzhong Mountain Ecosystem Scientific Observation and Research Station, affiliated with Lanzhou University and situated in Yuzhong County, Lanzhou City, Gansu Province, China. The observatory lies within the scenic loess hills and gullies area at the confluence of the Loess Plateau, Qinghai-Xizang Plateau, and Mongolian Plateau. This location falls within the semi-arid area of the Loess Plateau, characterized by an average elevation of approximately 2067.17 m a.s.l. and a climate typified by arid grasslands. With an average air temperature of 7.0°C, the area receives annual precipitation of approximately 300.0–350.0 mm, whereas potential evaporation reaches approximately 1500.0 mm. The region experiences a distinct rainy season from July to September, contributing 70.0%–80.0% of total annual precipitation, with monthly mean maximum air temperatures ranging from 17.9°C to 25.4°C. Frost prevails from mid-September to mid-April of the following year. The growing season spans approximately 140–160 days annually from May to mid-September. Since the 1950s, extensive afforestation efforts have transformed vast swathes of barren land in this region, with prominent species including *P. tabuliformis*, *P. sibirica*, *P. orientalis*, *Caragana korshinskii* Kom., *Tamarix chinensis* Lour., and *P.* × *hopeiensis*.

This study focused on native plantations of *P. tabuliformis*, *P. sibirica*, *P. orientalis*, and *P.* × *hopeiensis* established in 1970. The planting methodology involved digging horizontal ditches along contour lines spaced approximately 2.00 m apart, with trees planted at 2-m intervals within these ditches. Afforestation density averaged approximately 2500 plants/hm^2. Further details regarding the sample plots are provided in Table 1 and Figure 1 [Figure 1: see original paper].

2.2 Sample setup

Six trees were selected from each of the *P. tabuliformis*, *P. sibirica*, and *P. orientalis* plantation plots, while three trees were selected from the *P.* × *hopeiensis* plot for monitoring. A DC4 dendrometer (Ecomatik, Munich, Germany) was installed 1.30 m above the land surface to collect SRG data, recorded at 30-min intervals using a CR1000X data collector (Campbell Scientific, Logan, USA). Monitoring of *P. tabuliformis*, *P. sibirica*, and *P. orientalis* began in June 2021, whereas monitoring of *P.* × *hopeiensis* commenced in June 2022, with all monitoring for the four species still ongoing. Additionally, TEROS 12 probes (ME-

TER Group, Pullman, USA) were installed at each sample site at depths of 10.00, 20.00, 40.00, 60.00, 80.00, and 160.00 cm above the ground surface since 2020 to automatically monitor soil water content and soil temperature. Meteorological data—including precipitation, net radiation, photosynthetically active radiation, air temperature, and relative humidity—were measured at 15-min intervals using the automated monitoring probe of the Dynamet research-grade automated weather station (Campbell Scientific, Logan, USA). All meteorological data were recorded on a CR1000X data collector. Saturated vapor pressure deficit (VPD; kPa) was calculated from air temperature and relative humidity (Yang et al., 2015):

$$VPD = 0.6108 \times e^{\frac{17.27T}{T+237.3}} \times (1 - \frac{RH}{100})$$

where RH is the relative humidity of air (%); e is the base of the natural logarithm; and T is the air temperature (°C).

2.3.1 SRG data extraction

We processed raw data collected from the data collector for 2022 and 2023 for *P. tabuliformis*, *P. sibirica*, and *P. orientalis*, and for 2023 for *P.* × *hopeiensis*. The raw data were cleaned at 30-min intervals using the R v.4.1.1 (R Core Team, Auckland, New Zealand) package "treenetproc" (Knüsel et al., 2021). Following data cleaning, we extracted daily mean values from the raw SRG data via the daily mean method to derive daily mean stem radius variation series for each tree (Bouriaud et al., 2005). Subsequently, SRG data for each of the four monitored tree species were averaged to represent their mean growth conditions. To facilitate comparisons of intra-annual SRG between years, we utilized daily cumulative SRG, setting the first measurement value of radial variation data for all monitored trees on January 1 of each year as the reference value of 0. We employed a "zero-growth model" to discern between reversible and irreversible processes of stem radius change (Zweifel et al., 2016).

In the zero-growth model, all changes in stem radius below the previous maximum are attributed to reversible shrinkage and expansion due to water deficit, whereas changes above the previous maximum are considered irreversible growth processes driven by vascular cambium activity. Using the "treenetproc" package in R v.4.1.1, we separated these two components and calculated tree water deficit (TWD) resulting from water deficit by removing growth tendency (Knüsel et al., 2021). The formula for calculating TWD is as follows (Zweifel et al., 2016):

$$TWD(t) = \max[SR(< t)] - SR(t)$$

where SRG(t) is the stem radial growth (m); t is the current record; $<t$ is the historical record; SR(t) is the tree stem radius (m); max[SR($<t$)] is the

historical maximum tree stem radius (m); and TWD(t) is the stem water deficit caused by water deficit in trees (m).

We employed a Gompertz growth function to model daily cumulative SRG dynamics throughout the growing season and estimate daily SRG rate, determined by calculating the first derivative of the fitted curve (Zweifel et al., 2001). Moreover, we identified instances when daily SRG rate exceeded or fell below 2.0 m/d. Through these steps, we delineated SRG onset and cessation, enabling computation of daily SRG. Daily TWD was also derived from SRG onset and cessation. The Gompertz growth function is expressed as follows (Zweifel et al., 2001):

$$Y = A \times e^{-e^{-\kappa(d-\beta)}}$$

where Y is the daily cumulative SRG of tree (m); A is the asymptote of the function; β is the intercept parameter of the x-axis; is the parameter determining SRG rate; and d is time expressed in yearly cumulative days (d).

To compare daily-scale SRG and TWD of each species throughout the growing season, we normalized daily SRG and TWD for each of the four species for each year to the initial stem radius observed that year. This normalization yielded relative daily SRG and TWD values, allowing us to account for variations in tree size and directly compare relative growth and water deficit patterns across species and years.

2.3.2 SRG response to environmental factors

We conducted Spearman correlation analysis to assess relationships between daily SRG and TWD of the four tree species and meteorological and soil factors. Covariant environmental factors were identified and subsequently removed. To discern the importance of environmental factors for daily SRG, we employed an interpretable machine learning model—specifically Shapley Additive Explanations (SHAP)—which facilitates ranking of meteorological and soil factor effects on daily SRG, pinpointing key influencing factors. Moreover, we utilized principal component analysis (PCA) to explore daily SRG response to combinations of environmental factors, excluding covariants. Finally, to construct and evaluate relationships between environmental factors and daily SRG, we employed a structural equation model (SEM). Data preprocessing and analysis were conducted using Excel 2019 (Microsoft Corporation, Redmond, USA) and R v.4.1.1, with image mapping performed using R v.4.1.1 and Origin 2022 (OriginLab Corporation, Northampton, USA).

3.1 Environmental situation of sample plots

Figure 2 [Figure 2: see original paper] depicts temporal variations in environmental factors in the study area for 2022 and 2023. Trends in maximum, mean, and minimum air temperatures exhibited consistent patterns across both years, characterized by seasonal fluctuations with temperatures rising in spring, peaking in summer, and subsequently declining annually. Mean annual air temperatures were 8.9°C and 9.1°C in 2022 and 2023, respectively. Similarly, radiation factors—including photosynthetically active radiation and net radiation—mirrored air temperature trends, with peak levels coinciding with summer months and highest mean air temperatures. Precipitation events occurred primarily during the growing season, with cumulative precipitation at the Gongjing Observation Site totaling 197.7 mm and 175.2 mm in 2022 and 2023, respectively—notably lower than historical regional levels. Soil water content for the four tree species remained relatively low and stable during the first half of 2022 (January–June), increased during the concentrated precipitation period from July to September, then decreased toward the end of the growing season in September. Even with concentrated precipitation in October 2023, soil water content returned to pre-growing season levels, suggesting inadequate soil water replenishment. Notably, *P. tabuliformis* showed the highest soil water content and post-precipitation water replenishment in both years, indicating the lowest retention effect on precipitation. In summary, environmental factor values at sample sites in 2022 and 2023 remained relatively consistent and stable, albeit drier than historical records, indicating a consistently arid microclimate over the two years.

3.2.1 Dynamic of intra-annual SRG

Gompertz growth function equations modeled SRG of the four tree species with goodness of fit exceeding 96.0% over two years. The resulting growth curves exhibited characteristic "S" shapes (Fig. 3 [Figure 3: see original paper]). Analyzing first-order derivatives provided insights into daily SRG rates, which displayed a slow-to-fast-to-slow growth trend during the active growing season for all four species. Specifically, *P. orientalis* had the earliest average SRG initiation (day of year (DOY) 172), latest cessation (DOY 270), and longest growth duration (99 d) (Table 2), with the highest average daily SRG observed in 2022 (Fig. 3). Annual SRG patterns of *P. tabuliformis*, *P. sibirica*, and *P. orientalis* exhibited single-peak patterns in both 2022 and 2023 (Fig. 3). Average daily SRG rates of *P. sibirica* and *P. orientalis* surpassed those of *P. tabuliformis* (in 2022 and 2023) and *P.* × *hopeiensis* (in 2023) (Table 2). *P. tabuliformis* showed lower average daily SRG rate but longer growth duration, whereas *P. sibirica* and *P. orientalis* showed higher rates but shorter durations (Table 2). These findings underscore distinct growth dynamics among the four species, highlighting variations in rates, durations, and seasonal patterns captured by the Gompertz growth function.

3.2.2 Dynamic of daily relative SRG and TWD

As illustrated in Figure 4 [Figure 4: see original paper], daily relative SRG of *P. sibirica* and *P. orientalis* consistently surpassed that of *P. tabuliformis* and *P.* × *hopeiensis* over the two-year period. This trend aligned with findings from daily SRG rates obtained through fitted Gompertz growth functions and with daily relative TWD results for the four species. This comprehensive analysis highlighted consistently greater daily SRG rates in *P. sibirica* and *P. orientalis* compared to *P. tabuliformis* and *P.* × *hopeiensis* throughout observed growing seasons, underscoring potential species-specific growth dynamics and responses to environmental factors such as low precipitation or high vapor pressure deficit.

3.3.1 Response of daily SRG to environmental factors

PCA results revealed that daily SRG tended to increase with precipitation, relative humidity, and soil water content, but decreased with vapor pressure deficit, photosynthetically active radiation, and mean air temperature for all four species (Figs. 5 and 6). Soil water content emerged as the most influential factor affecting daily SRG of *P. sibirica*, whereas precipitation was most influential for *P. tabuliformis* and *P. orientalis*, and photosynthetically active radiation was most influential for *P.* × *hopeiensis* (Fig. 7 [Figure 7: see original paper]). Overall, evergreen coniferous species (*P. tabuliformis* and *P. orientalis*) appeared primarily influenced by atmospheric water, particularly relative humidity, whereas deciduous broadleaf species (*P. sibirica* and *P.* × *hopeiensis*) were more influenced by soil water content.

Additionally, we examined correlations between daily TWD of the four species and environmental factors (Fig. 8 [Figure 8: see original paper]). Analysis revealed significant positive correlations between daily TWD and photosynthetically active radiation and negative correlations with water factors such as relative humidity, precipitation, and soil water content. Specifically, coniferous species *P. tabuliformis* and *P. orientalis* showed significant negative correlations with precipitation and relative humidity, whereas broadleaf species *P. sibirica* showed significant negative correlation with relative humidity and *P.* × *hopeiensis* showed significant negative correlation only with soil water content.

3.3.2 Environmental factors drive SRG

SEM revealed that 68.5%, 44.1%, 30.1%, and 27.8% of SRG in *P. sibirica*, *P.* × *hopeiensis*, *P. tabuliformis*, and *P. orientalis*, respectively, could be explained (Fig. 9 [Figure 9: see original paper]). Despite shared environmental factors impacting *P. tabuliformis* and *P. orientalis*, differences in effect pathways on SRG were evident. For *P. orientalis*, mean air temperature, relative humidity, soil temperature, and precipitation significantly influenced SRG through the TWD pathway, except precipitation, which also had a direct effect. In contrast, for *P. tabuliformis*, mean air temperature and soil temperature indirectly affected SRG by influencing TWD; mean air temperature, relative humidity, and precipitation ultimately impacted SRG through effects on soil temperature and subsequently TWD; while relative humidity also had a direct significant effect on SRG. Furthermore, for *P. orientalis*, the path coefficient from mean air temperature to TWD was negative, whereas that from soil temperature to TWD was positive—

the opposite pattern observed in *P. tabuliformis*. For *P. sibirica*, mean air temperature, soil water content, and photosynthetically active radiation drove SRG by influencing TWD, while precipitation affected SRG through its effect on photosynthetically active radiation and subsequently TWD. Additionally, soil water content also exerted a direct effect on SRG. For *P. × hopeiensis*, precipitation and photosynthetically active radiation had direct effects on growth, whereas soil temperature and soil water content influenced SRG by affecting TWD.

4.1 Dynamics of intra-annual SRG in trees with different water use strategies and life types

This study detected single-peak patterns in daily SRG rate of the four plantation trees in a semi-arid area. Similar patterns have been reported in *Tamarix ramosissima* Ledeb. within desert riparian forests (Xiao et al., 2014). Water availability is widely acknowledged as a significant constraint on tree SRG (Churkina and Running, 1998), with drought impacts anticipated to intensify under global warming (Babst et al., 2019). Water limitation was also observed in our study, wherein daily SRG patterns aligned with precipitation patterns (Figs. 2 and 3). When trees maintain optimal water status, photosynthetic organs receive adequate water supply through trunk transport, facilitating optimization of carbon assimilation and growth (Niccoli et al., 2024). Studies across regions have confirmed that on annual time scales, SRG is explained by intermittent temporal windows favorable for growth rather than total growing season length (Etzold et al., 2022). For trees in boreal and temperate forests, SRG is typically unimodal, with peaks occurring around the summer solstice when environmental conditions (air temperature and photoperiod) are optimal (Etzold et al., 2022; Zhou et al., 2023). In contrast, bimodal patterns with two growth peaks in spring and autumn have been observed in Mediterranean region trees (Campelo et al., 2018; Tumajer et al., 2022; Valeriano et al., 2023), where hot, dry summers are followed by mild, wet autumns, permitting reduced SRG rates during summer and enabling bimodal patterns in more favorable spring and autumn seasons when xylem activity peaks (Campelo et al., 2018). In our study, tree SRG was similarly limited by drought, but this limitation was alleviated by the onset of the summer rainy season, which—coupled with sparse precipitation in spring and autumn—ultimately resulted in a single growth peak in summer.

Variations in daily SRG rates among the four plantation species were revealed in our study (Fig. 3). In 2023, SRG rates of two anisohydric species (*P. sibirica* and *P. orientalis*) exceeded those of two isohydric species (*P. tabuliformis* and *P. × hopeiensis*). This variation may be attributed to trees assimilating carbon primarily through photosynthesis, a process significantly influenced by stomatal activity (Zweifel et al., 2021). In *P. tabuliformis*, stomatal regulation involves isohydric behavior, whereby stomata close in response to elevated air temperatures and vapor pressure deficit to mitigate transpiration and prevent water loss (Cuny et al., 2012), reducing gas exchange and consequently decreasing photosynthesis. In contrast, *P. sibirica* and *P. orientalis* display anisohydric behavior, maintaining open stomata even under unfavorable conditions to sustain gas exchange (Tumajer et al., 2022). Similar results were reported for *J. przewalskii* and *P. crassifolia* with different water use strategies in the Qilian Mountains (Zhang et al., 2024). Increased xylem hydraulic conductivity enables more rapid gas exchange during photosynthesis. However, under drought conditions, increased canopy transpiration can exceed root system water absorption capacity, leading to xylem embolism formation that impedes water transport and consequently carbon assimilation (Qian et al., 2023). A study in arid areas revealed that *P.* × *hopeiensis* exhibits reduced resilience to xylem embolism during drought, likely impeding its growth (Hao et al., 2021). Additionally, our study revealed reduced cumulative precipitation during the 2023 growing season, leading to declined SRG for both *P. sibirica* and *P. orientalis*, while SRG of *P. tabuliformis* increased. This result can be attributed to the strong correlation between *P. tabuliformis* SRG and both current-year precipitation and precipitation at the end of the previous year (Wang et al., 2022). Cumulative precipitation in September was greater at the end of the 2022 growing season than in 2023 (Fig. 2), providing water reserves for subsequent year SRG. Furthermore, nonstructural carbohydrates synthesized through carbon assimilation in the previous year are stored in trunks (Furze et al., 2019), contributing to subsequent year growth of *P. tabuliformis*.

Indicators such as SRG start time, end time, and duration in the four plantation trees differed significantly between years, likely influenced by sample site microenvironment. The 2023 microenvironment was drier than 2022 because mean air temperature was higher and precipitation was lower during the same period, resulting in a shorter growing season in 2023 (Fig. 2; Table 2). The 2022 growing season commenced slightly later than in 2023, potentially due to persistent precipitation in late May 2022 and imminent onset of vascular cambium cell activity. In contrast, precipitation began at the end of April 2023, with relatively high air temperatures in both periods. However, following precipitation cessation from mid- to late-August 2023, drought stress effects on vascular cambium cell expansion and division intensified, resulting in earlier 2023 growing season cessation than in 2022. Similar results were reported for *P. tabuliformis* in the Helan Mountains across various altitudes and for *J. przewalskii* and *P. crassifolia* in the Qilian Mountains under different water conditions (Gao et al., 2019; Zhang et al., 2024). Trees in drier environments are characterized by earlier cessation, shorter growing seasons, and lower SRG rates, resulting in less annual growth (Gao et al., 2019). Compared with those study areas, climatic conditions in our study area are more arid with lower annual precipitation, rendering intra-annual SRG patterns more reliant on growing season precipitation dynamics. As mentioned above, alleviation of tree water deficit by precipitation plays a more important role in SRG in semi-arid areas. Our results suggest that despite optimal thermal conditions at the beginning of the growing season, drought may impede cambial activity initiation on the Loess Plateau, potentially resulting in early SRG cessation (Ziaco et al., 2018).

4.2 Environmental driving mechanisms of daily SRG in trees with different water use strategies and life types

Results demonstrated consistent correlation between daily SRG and environmental factors for all four species, with significant negative correlations observed with drought factors and significant positive correlations with water factors. Furthermore, correlations between TWD and climatic factors were inverse to those observed for SRG. Alteration of tree radius is attributable predominantly to imbalances in water distribution within the trunk, contingent upon tree transpiration and water uptake from soil through root systems (Bouriaud et al., 2005). Temperature is affected by radiation and exerts multifaceted influence on daily stem changes, impacting tree water status indirectly through vapor pressure deficit and directly governing processes such as respiration and assimilation (van der Maaten et al., 2018). Notably, temperature constraints on SRG are often evident in temperate and cold climates, particularly affecting growth initiation and cessation phases (Rossi et al., 2008). Once a certain threshold temperature is surpassed and the growing season commences, SRG tends to be limited more by other climatic factors than temperature alone (Duchesne et al., 2012). In initial growing season stages when water is not limiting, positive correlation exists between SRG and temperature, but this later diminishes and becomes negative during summer months (Gao et al., 2019). Man et al. (2024) observed similar daily SRG responses to temperature and water in *P. tabuliformis* in the Qilian Mountains based on the Vaganov-Shashkin model. Elevated temperatures can also negatively impact SRG in forests experiencing seasonal drought, potentially due to increased vapor pressure deficit and evaporative loss (Grossiord et al., 2020). Our findings indicated negative air temperature impact on SRG of all species, potentially due to accelerated transpiration and respiration rates at relatively high temperatures, leading to increased water loss and reduced carbohydrate availability for SRG (Liu et al., 2018). Moreover, soil temperature affects root water uptake capacity, trunk substance transport, and accumulation (Gruber et al., 2009). Soil temperature fluctuated above and below 10.0°C from May onward, with gradual increase thereafter. Optimal soil temperature facilitated increased root water transport and vascular cambium cellular activity in *P. tabuliformis*, thus promoting SRG. Research in Luya Mountain, Shanxi Province, China, also revealed that soil temperature has a threshold value for initiating SRG in *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilg (Cui et al., 2025). Moreover, soil temperature contributed more to annual increase and maximum radial growth rate than air temperature. However, for *P. sibirica* and *P.* × *hopeiensis*, increased root water transport intensified evapotranspiration, exacerbating water deficit scenarios, causing SRG activity to demonstrate negative response to soil temperature throughout the growing season.

SRG of the four plantation trees responded positively to water conditions and varied by life type: coniferous species were affected mainly by atmospheric water factors (relative humidity and precipitation), whereas broadleaf species were affected mainly by soil water content. Previous studies of *J. przewalskii* and

P. crassifolia (both coniferous) in the Qilian Mountains reported similar results (Zhang et al., 2024). Precipitation may reach roots of *P. tabuliformis* and *P. orientalis* faster than in broadleaf species such as *P. sibirica* and *P.* × *hopeiensis*, which are more effective at intercepting rainwater. Both broadleaf species are highly dependent on soil water content during the growing season, which influences vascular cambium cell expansion and division by affecting root uptake (Zhang et al., 2018). Research on *Populus euphratica* Oliv. and *T. ramosissima* (both broadleaf) in desert riparian areas revealed that groundwater depth is the major limiting factor for SRG, as precipitation alone is insufficient to meet growth requirements (Xiao et al., 2014; Peng et al., 2022). Precipitation events can alleviate TWD by increasing soil water, thereby promoting cambial cell expansion and growth (Katz et al., 1989; Zhang et al., 2008). Moreover, limitation of SRG by water conditions within the plant manifests before soil water content becomes limiting, as confirmed in *L. principis-rupprechtii* (Xue et al., 2022). As mentioned above, stomatal activity is the initial tree response to drought, with stomatal conductance in *P. tabuliformis* decreasing or even closing with increasing vapor pressure deficit, resulting in reduced photosynthesis and ultimately affecting SRG (Lawlor and Cornic, 2002). In contrast, stomata of *P. sibirica* and *P. orientalis* do not significantly decrease with increasing vapor pressure deficit. Loss of internal water stored in phloem and elastic tissues due to transpiration leads to stem shrinkage and reduced turgor tension, negatively affecting vascular cambium cell division and expansion (Zweifel et al., 2021). When xylem conduits are insufficiently replenished with water and become embolized, water flow is restricted, resulting in "hydraulic failure" (McDowell et al., 2008), which is more likely to occur in ring-porous wood of *P. sibirica* and *P.* × *hopeiensis* and has been implicated as a key mechanism of tree mortality (Choat et al., 2018). In contrast, the xylem tubular structure of *P. tabuliformis* and *P. orientalis*, which have diffuse-porous wood, is less susceptible to embolism, supporting the efficient hypothesis of xylem water transport (McDowell et al., 2008). In summary, daily SRG of the four plantation trees demonstrated relatively stronger response to ambient water conditions than to other climatic factors, underscoring the crucial role of water in tree SRG. Notably, as atmospheric drought intensifies, SRG of trees in arid and semi-arid areas will continue to be limited, and tree mortality may occur (Breshears et al., 2013; Zweifel et al., 2021).

4.3 Recommendations

Since the 1970s, many native tree species naturally growing on the Loess Plateau have been artificially cultivated and extensively planted to control local soil erosion (Shi et al., 2020). This vegetation restoration measure has yielded dual outcomes. On one hand, afforestation has been the primary driver behind increased vegetation cover and reduced soil erosion on the Loess Plateau (Wu et al., 2019). On the other hand, afforestation has been implemented without accounting for local environmental carrying capacity in some regions, leading to soil water depletion and decline or mortality of planted trees (He et al., 2022). Given these conflicting outcomes, our study investigated intra-annual SRG dynamics and environmental drivers of four well-growing plantation species in the semi-arid Loess Plateau to provide a scientific basis for local vegetation restoration and sustainable forestry development. *P. tabuliformis* appears more suitable for planting in this region because it has a more conservative water use strategy and greater drought tolerance. This study also revealed that drought has relatively low negative impact on intra-annual SRG of *P. tabuliformis*, increasing its adaptability to future climate change. However, constrained by monitoring equipment and data limitations, long-term observations should continue. Our study did not further elucidate how water limitation (or drought) affects SRG of each species. As discussed above, drought limits SRG by restricting cambial cell turgor pressure. Subsequent studies should integrate SRG monitoring with assessments of cambial cell formation dynamics and stem water potential to elucidate mechanisms underlying water limitation on tree SRG. Furthermore, expanding research to include other common afforestation species (e.g., *Robinia pseudoacacia* L.) would yield more generalizable findings.

5 Conclusions

By examining daily SRG of four plantation trees (*P. tabuliformis*, *P. sibirica*, *P. orientalis*, and *P.* × *hopeiensis*) in the semi-arid Loess Plateau across a two-year span, we discovered that these species presented a single peak in intra-annual SRG. This growth pattern was influenced by water use strategies: species favoring anisohydric regulation with greater xylem water transfer efficiency (*P. sibirica* and *P. orientalis*) tended to grow faster but faced greater hydraulic failure risk, whereas species employing isohydric regulation with lower water transfer efficiency (*P. tabuliformis* and *P.* × *hopeiensis*) grew slower. Moreover, SRG of coniferous species (*P. tabuliformis* and *P. orientalis*) was influenced mainly by atmospheric water, particularly relative humidity, whereas that of broadleaf species (*P. sibirica* and *P.* × *hopeiensis*) was influenced mainly by soil water content. *P. tabuliformis* should be more suitable for planting in this region due to its conservative water use strategy. In summary, our research offers valuable insights into climatological patterns of intra-annual SRG among trees in semi-arid areas and enhances understanding of how plantation forests in these regions respond to climate change through their growth patterns.

Conflict of interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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