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Research

Diel and seasonal stem growth responses to climatic variation are consistent across species in a subtropical tree community

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Summary

- Understanding how intra-annual stem growth responds to atmospheric and soil conditions is essential for assessing the effects of climate extremes on forest productivity. In species-poor forests, such understanding can be obtained by studying stem growth of the dominant species. Yet, in species-rich (sub-)tropical forests, it is unclear whether these responses are consistent among species.
- We monitored intra-annual stem growth with high-resolution dendrometers for 27 trees belonging to 14 species over 5 yr in a montane subtropical forest. We quantified diel and seasonal stem growth patterns, verified to what extent observed growth patterns coincide across species and analysed their main climatic drivers.
- We found very consistent intra-annual growth patterns across species. Species varied in the rate but little in the timing of growth. Diel growth patterns revealed that – across species – trees mainly grew before dawn when vapour pressure deficit (VPD) was low. Within the year, trees mainly grew between May and August driven by temperature and VPD, but not by soil moisture.
- Our study reveals highly consistent stem growth patterns and climatic drivers at community level. Further studies are needed to verify whether these results hold across climates and forests, and whether they can be scaled up to estimate forest productivity.

Introduction

Understanding how forest dynamics may be altered under changing climate requires detailed information on tree-level growth responses to environmental conditions at various temporal scales (Steppe *et al.*, 2015). At annual level, stem growth responses to climatic conditions have been studied rather intensively using tree ring analyses (Babst *et al.*, 2019; Zuidema *et al.*, 2022). Yet, these studies do not provide insights into environmental factors driving the underlying intra-annual stem growth patterns (Deslauriers *et al.*, 2007; Drew & Downes, 2009; Cuny *et al.*, 2014; Cocozza *et al.*, 2016). Studies measuring intra-annual stem growth patterns using dendrometers have provided insights on the environmental drivers of intra-annual stem growth, in particular vapour pressure deficit (VPD), soil moisture (Etzold *et al.*, 2021) and air temperature (Tumajer *et al.*, 2022). Most dendrometer studies were conducted in temperate forests (Oberhuber *et al.*, 2014; van der Maaten *et al.*, 2018; Etzold *et al.*, 2021; Tumajer *et al.*, 2022), but knowledge on climatic drivers of intra-annual stem growth dynamics for tropical and subtropical climate zones is very poor (Krepkowski *et al.*, 2010; Wagner *et al.*, 2016; Meng *et al.*, 2021; Kaewmano *et al.*, 2022). One of the challenges for dendrometer studies in these species-rich systems is that community-level growth responses cannot be easily estimated by measuring a single or few dominant species, as is usually done in species-poor temperate forests (Oberhuber *et al.*, 2014; van der Maaten *et al.*, 2018; Etzold *et al.*, 2021; Tumajer *et al.*, 2022). Instead, a much larger number of species need to be included to assess community-wide responses, because it is unclear to what extent species growth patterns and climate responses are aligned within a community.

Annual stem growth results from a series of intra-annual cambial processes, including cell division, cell enlargement, cell wall thickening and lignification (Steppe *et al.*, 2015) and their response to atmospheric and soil conditions at scales of days to seasons (Cuny *et al.*, 2015, 2019; Huang *et al.*, 2020). The growth of cambial tissue is limited biophysically by temperature–moisture conditions and therefore assumed to be conserved across species, despite interspecific differences in phenology and physiology (Martin *et al.*, 2017). In temperate and boreal climates, cambial activity of trees starts in spring and ends in autumn following the seasonal pattern in temperature (Deslauriers *et al.*, 2007; Etzold *et al.*, 2021), while it tends to follow rainfall seasonality in tropical and subtropical climates (Volland-Voigt *et al.*, 2010; Meng *et al.*, 2021; Kaewmano *et al.*, 2022). The magnitude of seasonal stem growth in temperate forests is usually favoured by temperatures > 5°C in spring and sufficiently moist conditions during the growing season (Etzold *et al.*, 2021). In tropical and subtropical forests, intra-annual stem growth patterns may be different owing to different seasonal trends in temperature and moisture limitations (Fan *et al.*, 2019; Meng *et al.*, 2021; Kaewmano *et al.*, 2022). For example, compared with most forests in temperate areas (Cocozza *et al.*, 2016; van der Maaten *et al.*, 2018; Etzold *et al.*, 2021), forests in the subtropical monsoon region are characterized by similar seasonal trends in temperature but different seasonal trends of atmospheric and soil moisture (rainfall, VPD and soil moisture). The present study focuses on stem growth responses to seasonal trends in monsoon climate in a montane subtropical forest.

At diel scale, trees are found to grow mainly at night since growth ceases at high VPD levels that occur during daylight hours during summer months in temperate climates (Zweifel *et al.*, 2021). Trees rehydrate during the night and establish the turgor pressures required for cell division and expansion (Hsiao & Acevedo, 1974; Steppe *et al.*, 2015). Such VPD-imposed diel growth constraints can be released during night and early morning (Zweifel *et al.*, 2021). Diel and seasonal growth patterns in temperate forest trees therefore strongly depend on the moisture conditions in atmosphere and soil (Etzold *et al.*, 2021; Zweifel *et al.*, 2021). So far, such patterns have been investigated for a limited number of species from temperate climates (De Swaef *et al.*, 2015; van der Maaten *et al.*, 2018; Etzold *et al.*, 2021; Zweifel *et al.*, 2021; Tumajer *et al.*, 2022). Such diel patterns with strongest growth at night may however vary over seasons and across climate regions due to the variability in growth conditions and forest composition (Aldea *et al.*, 2018; Ziaco & Biondi, 2018; Meng *et al.*, 2021), but remain poorly explored for tropical and subtropical forests.

This study aims to identify the role of atmospheric conditions and soil moisture in driving intra-annual stem growth variation – both timing and magnitude – of a tree community in a montane subtropical forest. We monitored stem growth at 10-min resolution of 27 trees belonging to 14 species. We analysed diel and seasonal growth patterns of these trees, verified to what extent observed growth patterns are consistent across study species and tested underlying climatic drivers. Specifically, we ask three key questions:

(**1**) To what extent are diel and seasonal growth patterns consistent across species?

We predict that diel and seasonal growth patterns are similar across species, but that the achieved stem growth rate (per hour, day or month) varies between species (Poorter *et al.*, 2010; Fan *et al.*, 2012).

(**2**) What climatic factors drive diel stem growth in a subtropical tree community?

We expect that stem growth in this tree community mainly occurs during night and early morning hours with low VPD and with high soil water availability (Zweifel *et al.*, 2021). Yet, we also expect this pattern to differ with seasonal changes in air humidity (Supporting Information Fig. S1).

(**3**) What climatic factors drive seasonal stem growth in this community?

We predict that trees mainly grow during warm and wet months with high soil moisture availability and relatively low VPD.

Materials and Methods

Study site and tree species

The study site is located in a subtropical evergreen broadleaf forest at the Ailao Mt. (24.32°N, 101.01°E, 2505 m above sea level (asl)), Yunnan province, in Southwest China. Mean annual temperature is 11.7°C with January being the coldest month and July the warmest (Fei *et al.*, 2018). The mean annual precipitation is 1728 mm of which *c.* 81% falls in the rainy and warm season from May to October. The dry and cold season lasts from approximately November to April (Fig. S1). The forest is dominated by evergreen broadleaf tree species that account for 76% of all 101 tree species and 96% of all tree individuals in a 20-ha plot at the study site (Wen *et al.*, 2018). We aimed to cover tree species that are common and dominate the local tree community. Our selection of 14 species includes typical tree families in subtropical evergreen forests (*Fagaceae*, *Theaceae*, *Lauraceae* and *Magnoliaceae*) and other common plant families (such as *Aquifoliaceae*, *Araliaceae*, *Ericaceae*, *Sabiaceae* and *Sapindaceae*; Table 1). The availability of equipment and sensor failure limited the level of replication per species, ranging from 1 to 3 trees monitored per species.

Stem growth measurements

We equipped 27 broadleaf trees with dendrometers (DR1 and DC2; Ecomatik, Germany) and monitored their radial growth from 2017 to 2021. Dendrometers had a measuring resolution of 2 μm. Dendrometers were mounted at breast height on each tree stem. Before installing, we carefully removed the outer bark to reduce the effect of bark shrinking and swelling. Continuous stem radius change was measured every 10 min during the entire 5-yr period. Trees with data gaps > 50% of the year were excluded from the analysis.

Calculation of stem growth

Raw dendrometer data were checked and processed to extract radial growth with packages DATACLEANR (Hurley, 2022), TREENETPROC (Knüsel *et al.*, 2021) and DENDRoANALYST (Aryal *et al.*, 2020) in R software (R Core Team, 2020) and were then aggregated to hourly, daily and monthly scales (Kaewmano *et al.*, 2022). We applied the zero-growth approach to identify periods of stem growth from raw measurements (Fig. 1a). This approach assumes no growth occurs until the change in stem radius exceeds the previous maximum (Zweifel *et al.*, 2016). We used this growth dataset to quantify stem growth at diel and

Table 1 Study species in the subtropical montane tree community, Ailao Mountain, China.

Species	Phenology	Dominance	No. of trees	DBH (cm)	BA (%)	BA 1-ha (%)
Acer campbellii	Deciduous	Nondominant	2	23.0	1.5	0.3
Castanopsis wattii	Evergreen	Dominant	1	38.5	1.9	21.1
Ilex corallina	Evergreen	Nondominant	2	30.9	2.7	< 0.1
Ilex gintungensis	Evergreen	Nondominant	1	14.4	0.3	1.6
Machilus gamblei	Evergreen	Dominant	2	28.3	2.3	9.8
Machilus yunnanensis	Evergreen	Dominant	3	32.9	4.4	4.1
Manglietia insignis	Evergreen	Dominant	3	23.7	2.2	3.4
Neolitsea chui	Evergreen	Nondominant	2	27.6	2.0	3.0
Schima noronhae	Evergreen	Dominant	2	46.6	5.7	18.3
Stewartia pteropetiolata	Evergreen	Dominant	3	29.6	3.5	1.7
Vaccinium duclouxii	Evergreen	Dominant	1	20.8	0.6	< 0.1
Gamblea ciliata var. evodiifolia	Deciduous	Nondominant	2	47.8	6.0	–
Lyonia ovalifolia	Deciduous	Nondominant	1	26.1	0.9	–
Meliosma arnottiana	Evergreen	Nondominant	2	50.7	6.8	–
Total: 14 broadleaf species, 27 trees, 27.1% BA						

Listed are mean diameter at breast height (DBH) of measured trees, basal area (BA) of measured trees (%) relative to total basal area of 1-ha plot, species-specific basal area (%) for 1-ha plot relative to the total basal area (BA 1-ha), based on plot inventory near our study site in 2015. The number of trees reflects this at the start of the study and has decreased due to sensor failure in some cases. All study species are broadleaved.

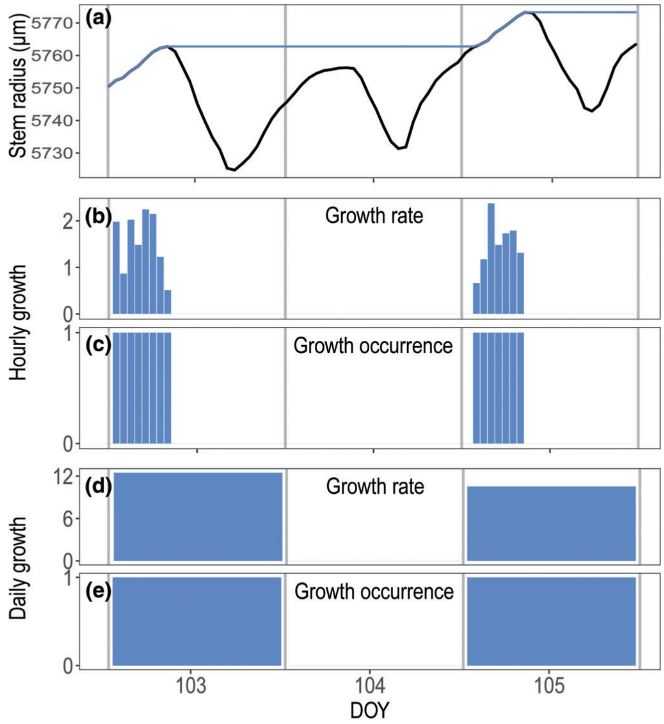


Fig. 1 Schematic figure to illustrate the zero-growth model used to extract net stem growth from dendrometer measurements of tree stem radius during 13–15 April 2019. (a) Measurement of stem radius change (black line) and the net stem growth (blue line) based on the zero-growth model (Zweifel *et al*., 2016). (b–e) Resulting values of growth rates (b, d) and occurrence (c, e) at hourly (b, c) and daily (d, e) level. DOY, Day of the Year.

seasonal scales. For simplicity, we use 'growth hours' to refer to the number of hours with growth and 'growth days' to refer to the number of days with growth. At the diel scale, we first quantified the stem growth for each hour (hourly growth rate, Fig. 1b). Second, we identified hours with and without growth via 1–0 binomial scores (growth occurrence, Fig. 1c). From these two measures, we calculated hour-specific: relative contributions to the total annual stem growth (growth contribution (%)), growth hours relative to the total annual growth hours (growth occurrence (%)) and mean growth rate ($\mu m\ h^{-1}$) for those hours with growth occurrence.

For seasonal stem growth analyses, we first aggregated hourly stem growth to daily stem growth (daily growth rate, Fig. 1d) and identified days with growth (growth occurrence, Fig. 1e). For the sake of convenience, we present these metrics per month, taking the average to get mean daily growth rates ($\mu m\ d^{-1}$) and taking the sum to get monthly growth rate and probability of growth (growth occurrence). Next, we calculated the contribution of each month's growth to total annual growth rate (growth contribution).

Statistical analyses

All analyses were performed in R software (R Core Team, 2020). We restrict our analysis to the growing season, from March to October. Following recent studies of intra-annual stem growth data from dendrometers (Etzold *et al.*, 2021; Tumajer *et al.*, 2022), we limit our analyses of environmental drivers to effects of atmospheric and soil conditions. As stem growth has a higher correlation with VPD compared with radiation, we chose three key climatic variables – air temperature, soil moisture and VPD – as explanatory variables for further analyses (Tumajer *et al.*, 2022). Hourly air temperature, relative humidity and soil moisture were obtained from the meteorological station (M520; Vaisala, Finland), and VPD was calculated from air temperature and relative humidity. Hourly values of these climatic variables were averaged to obtain daily and monthly values.

At the diel scale, generalized linear mixed-effects models (GLMM with binomial link function) were applied to test the effects of the three climatic variables on diel growth occurrence, using the LME4 package (Bates *et al*., 2015). Random variables 'tree' and 'DOY' (day of the year) were used to account for repeated measurements. Linear mixed-effects models (LMM) were used to test the relationships between hourly growth rate and the three climatic variables with 'tree' and 'DOY' as random variables. We also compared diel stem growth patterns and their climatic drivers between the months of May and July, because these months represent similar temperatures and solar position but largely differ in VPD, with potential implications for diel growth trends.

To analyse climatic drivers of seasonal stem growth, GLMM and LMM were conducted for the three selected environmental factors at daily scale with random variable 'tree'. Additionally, another set of GLMM and LMM was conducted based on monthly totals, because these are less affected by daily stem shrinkage and thus less strongly depend on the assumptions of the zero-growth model.

For all analyses, we checked the collinearity (variance inflation factor ≤ 5) between test variables before fitting a model. Fixed effects were scaled and the values of growth rate were log-transformed before analysis. We calculated marginal and conditional pseudo-R^2 for model assessment (Nakagawa *et al*., 2013). All plots were made with the GGPLOT2 package (Wickham, 2016).

Additionally, we provide an overview of studies on seasonal-level climate–growth relations to put our findings in context. We collected scientific publications via Web of Science using the following search string: TITLE-ABS-KEY ("stem growth" OR "tree growth" OR "stem variation" OR "radial growth" OR "radial tree growth" OR "radius change" OR "diameter change" OR "diameter increment") AND ("dendrometer" OR "Dendrometer") AND ("forest" OR "tree"). Two other dendrometer publications known to us were added to increase sample size.

Results

Diel and seasonal growth patterns across species

All species follow similar median trends for their diel pattern in growth contribution and growth occurrence (coloured lines in Fig. 2a,b) and are thus close to diel trends quantified by the median for the whole sampled tree community (black line, Fig. 2a,b). Across species, stem growth mainly occurred between 21:00 and 08:00 h with growth contribution and growth occurrence ranging from 59% to 85% and 63% to 84%, respectively. The effects of species on these diel trends were inferior, as shown by the lower among-species coefficient of variation (CV) for all hours during the 24 h cycle (median CV of contribution: 0.29; median CV of occurrence: 0.24, Fig. 2d,e) compared with the among-hours CV (contribution: 0.53; occurrence: 0.50). These differences in CV were significant ($P < 0.001$). In contrast to the findings for growth occurrence and contribution, we found large variation among species in the diel pattern of stem growth rate (Fig. 2c). Some species showed a diel pattern with lower values during the day, but others did not. The corresponding comparison of coefficients of variation also showed considerably (and significantly, $P < 0.001$) larger values among species (median CV = 0.54) than over time (median CV = 0.22; Fig. 2f).

The seasonal trends in growth contribution and occurrence were also similar across species and closely matched the seasonal trends of the tree community (Fig. 2g,h). Across species, 80–97% of the growth contribution and 72–93% of the growth occurrence were achieved between May and August (Fig. 2g,h). The significantly lower CV ($P < 0.001$) quantifying species differences in growth contribution and occurrence (CV = 0.51 and 0.37, Fig. 2j,k) relative to that in seasonal variation (CV = 0.93 and 0.66) support this convergence across species. Yet, the temporal variation of stem growth rate substantially varied across species (Fig. 2i), as illustrated by a large CV across species (0.64 and 0.56, Fig. 2l).

Climate drivers of diel stem growth

At community level, 72% of the annual growth occurred before dawn (Fig. 3a). This was mainly due to the high growth occurrence before dawn: 71% of hours during which growth took place correspond to night hours (Fig. 3b). A close correspondence between hourly contributions to annual stem growth and hourly growth occurrence was also supported by a high correlation between these variables (Fig. S2a). By contrast, the correlation between hourly growth contribution and hourly growth rate was very weak (Fig. S2b). This is likely caused by rather stable values of hourly growth over the day (Fig. 3c). Temperature and VPD peaked during the daytime and were rather low during night hours (Fig. 3d,f), whereas soil moisture hardly showed a diel pattern (Fig. 3e). The diel pattern of growth contribution shifted somewhat during the growing season. During the moist month of July, the contribution of day hours to monthly growth was higher (*c*. 33%) than that during the drier month of May (*c*. 23%, Fig. S3).

A mixed-effects model (Fig. 4a) showed that the probability of hourly growth increased at low VPD and, less importantly, at lower temperature (marginal $R^2 = 0.36$). The effect of soil moisture on growth occurrence was weak. Thus, the high growth occurrence during night-time hours was tightly associated with low VPD (Figs 2, 4a). The dominant role of VPD in explaining variation in hourly growth occurrence was consistently found for a drier (May) and more moist (July) month (Fig. S4). Contrasting with the strong climatic associations of growth occurrence, we found very weak associations for hourly growth rate (marginal $R^2 = 0.01$, Fig. 4a), with positive effects of temperature. When plotting the distribution of explained variance across fixed effects, temporal variation (i.e. DOY) and among-tree variation, we found temporal variation to be a larger source of variation for hourly growth occurrence and among-tree variation for hourly growth rate (Figs 4a, S5). Thus, in short, hourly growth varies largely across individuals in terms of magnitude, but is highly consistent in timing.

Climate drivers of seasonal stem growth

At community level, *c*. 88% of annual stem growth was achieved from May to August (Fig. 3g). During the same months, *c*. 80% of days with growth occurred (Fig. 3h). Daily growth rate slightly differed between months (Fig. 3i), while monthly growth

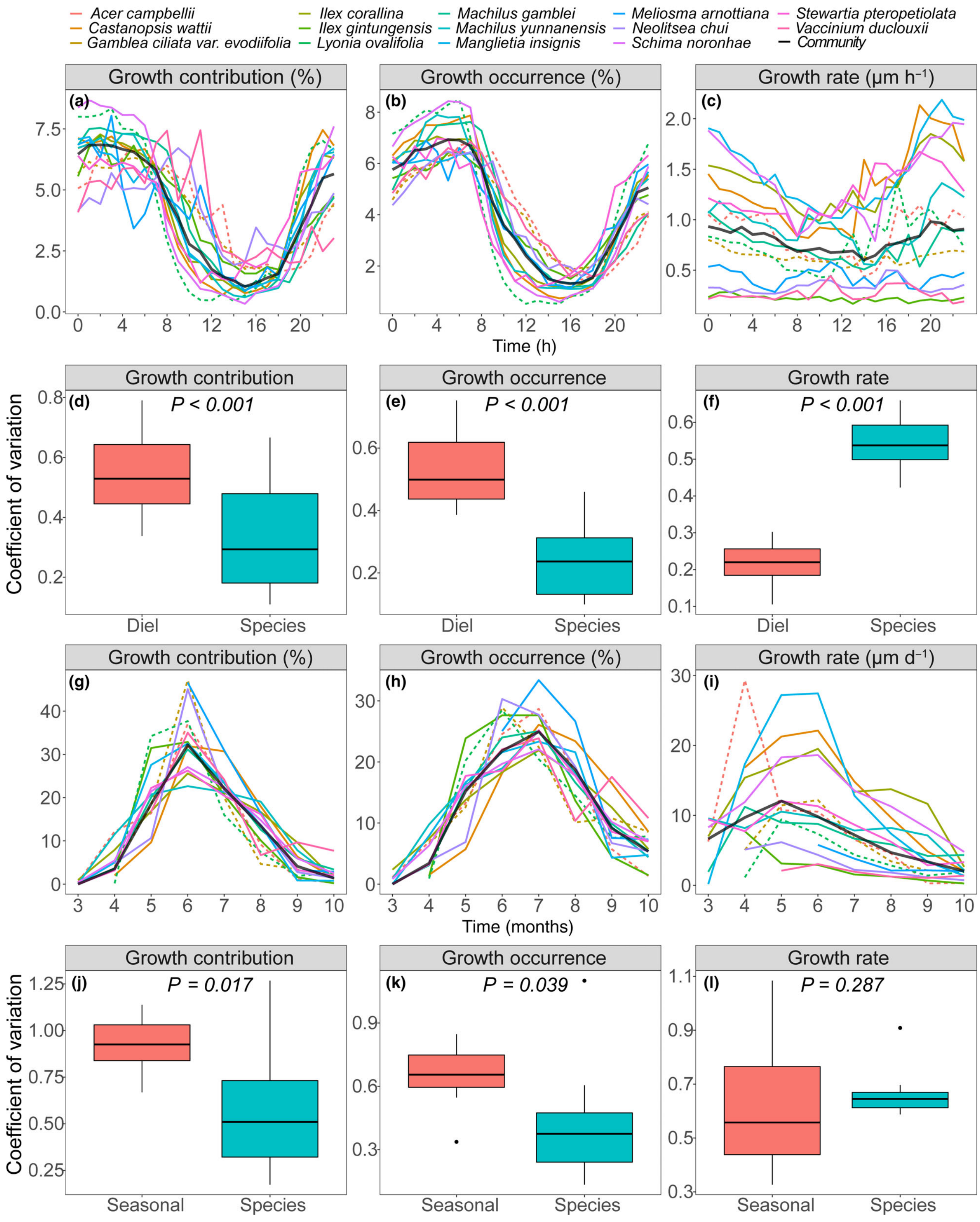


Fig. 2 Diel and seasonal patterns of stem growth across species in a subtropical tree community. (a–c) Lines show median hourly growth contribution, occurrence and rate for all species (coloured) and the community (black). (d–f) Boxplots are the comparisons between coefficient of variation (CV, median, 25 and 75 percentiles with 1.5 × interquartile ranges) of diel variation (red) and species difference (blue) in hourly growth contribution, occurrence and rate. (g–i) Lines show median monthly growth contribution, occurrence and daily growth rate per month for all species (coloured) and the community (black). (j–l) Boxplots are the comparisons between CV of seasonal variation (red) and species difference (blue) in growth contribution, occurrence and rate per month. Dashed lines indicate the three deciduous species.

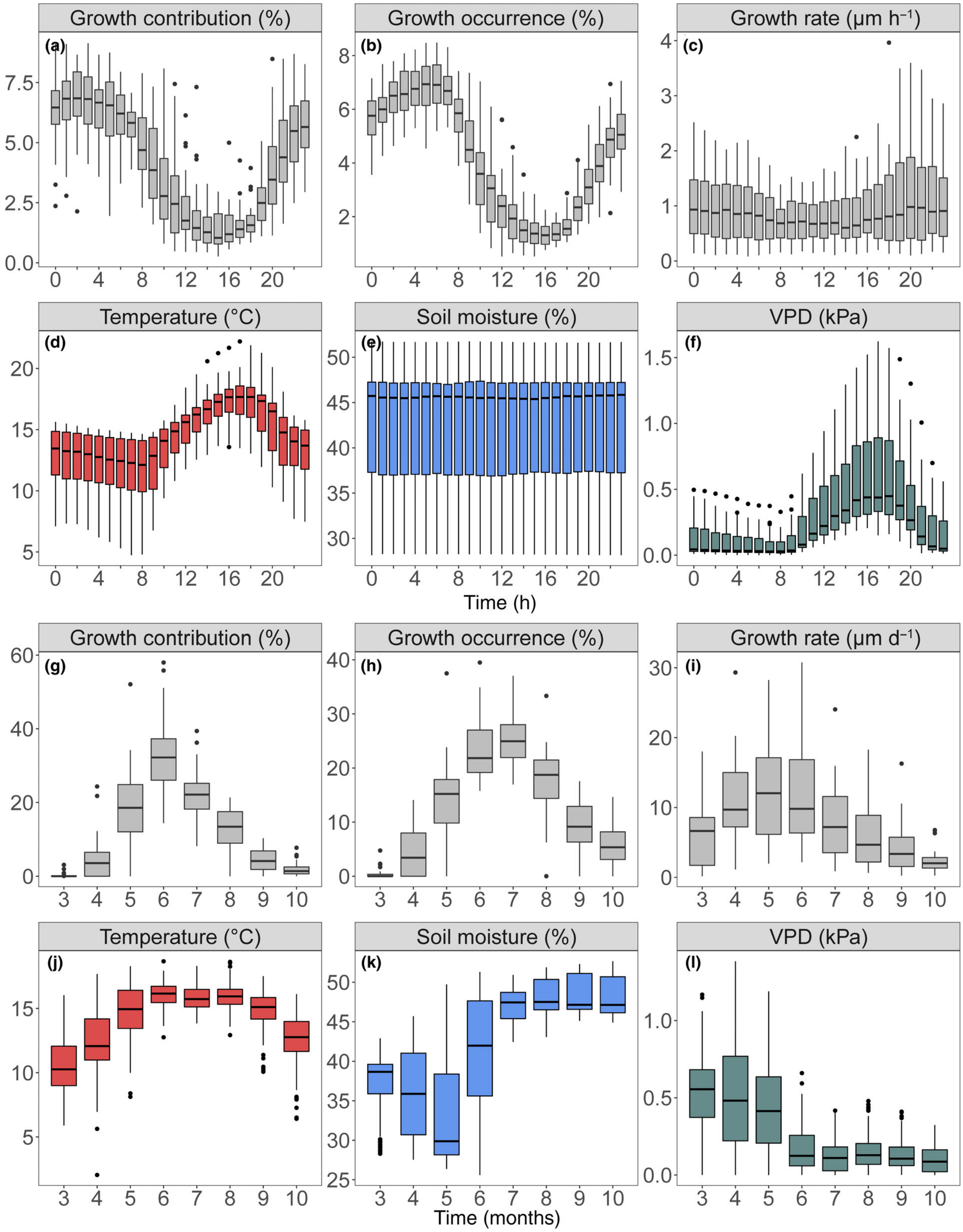


Fig. 3 Diel and seasonal patterns of community-level stem growth and climate in a subtropical tree community. All boxplots show median, 25 and 75 percentiles with 1.5 × interquartile ranges. (a–c) Hourly growth contribution, occurrence and rate at community-level. (d–f) Hourly air temperature, volumetric soil moisture and vapour pressure deficit (VPD). (g–i) Growth contribution, growth occurrence and daily growth rate per month at community-level. (j–l) Daily air temperature, volumetric soil moisture and VPD.

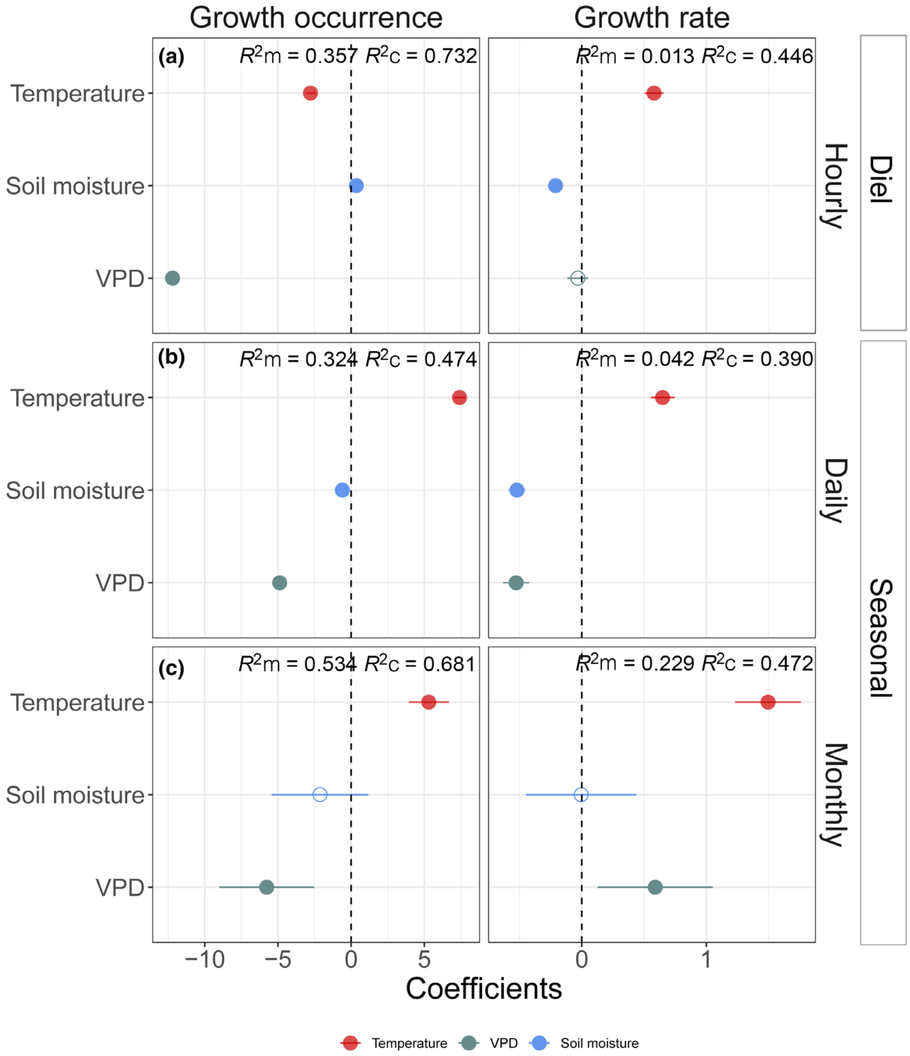


Fig. 4 Climate responses of hourly (a), daily (b) and monthly (c) stem growth in a subtropical tree community. Standardized coefficients (mean and 95% confidence interval) obtained from a generalized linear mixed-effects model (GLMM) for growth occurrence (growth or no growth) and a linear mixed-effects model (LMM) for growth rate. Closed circles are significant at $P < 0.05$ level. R^2m and R^2c indicate marginal and conditional R^2. Please note that monthly vapour pressure deficit (VPD) and soil moisture in GLMM model had high collinearity (variance inflation factor = 5).

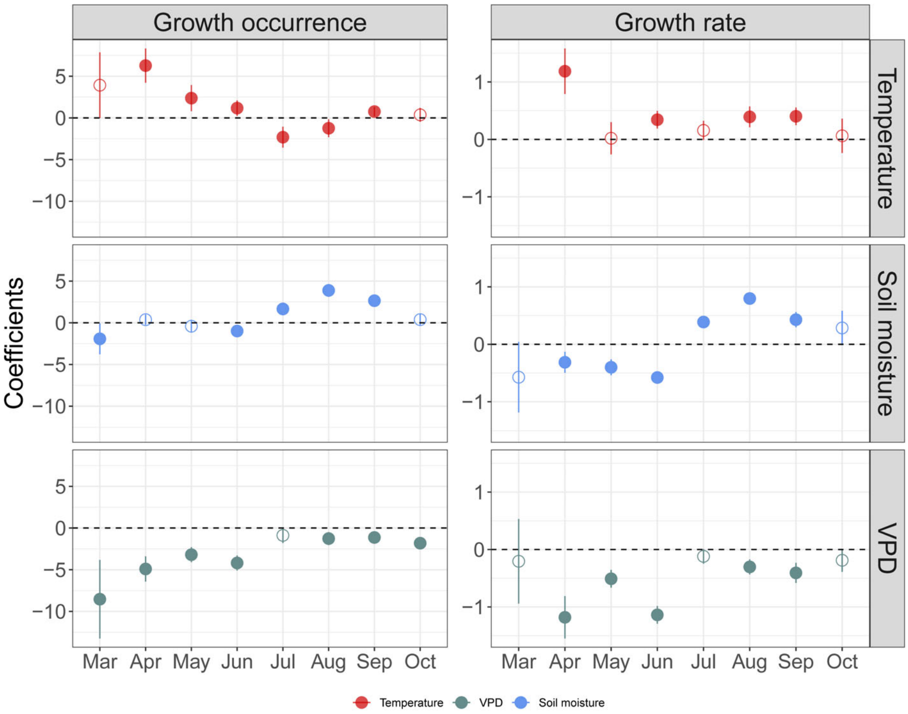
occurrence determined relative contributions to annual stem growth for the tree community (Fig. S2c). The monthly growth contribution to annual stem growth (%) started in April, peaked in June and ceased in October (Fig. 3g). There was a temporal offset in the seasonal patterns of growth occurrence – which peaked in July (Fig. 3h) – and daily growth rate – which peaked in May (Fig. 3i). All three metrics of stem growth (growth contribution, growth occurrence and growth rate) closely followed the seasonal temperature trend as highest temperatures occurred from May/June to August/September (Fig. 3j). The seasonal change in VPD did not follow the trend in temperature: It gradually decreased in spring but dropped to a low level from June onwards (Fig. 3l). Soil moisture decreased during spring months (from March to May), increased in June and was kept at relatively high level from July to November (Fig. 3k).

The mixed-effects model of daily growth occurrence revealed strong associations with seasonal climate (marginal $R^2 = 0.32$, Fig. 4b). In general, trees tended to grow more frequently during days with high temperature and low VPD, independently of soil moisture conditions. In spring (mainly April and May), daily growth occurrence was driven by a higher temperature and lower VPD, but those effects became weaker during the warmer and wetter conditions later in the growing season (Fig. 5). Daily growth rate increased with higher temperature, combined with low soil moisture and low VPD (marginal $R^2 = 0.04$, Fig. 4b). Furthermore, daily growth rate strongly varied while daily growth occurrence coincided among this subtropical tree community (Figs 4b, S5).

When conducting similar analyses for monthly (instead of daily) growth occurrence, we found a positive relationship with temperature and a negative one with VPD but no relationship with soil moisture, confirming the results at daily scale (marginal $R^2 = 0.53$, Fig. 4c). Monthly growth rate was mainly determined by temperature (marginal $R^2 = 0.23$). Among-tree variation contributed little to variation in growth occurrence, but importantly influenced variation in growth rate (Fig. S5).

Discussion

We studied intra-annual stem growth and its climatic drivers for 14 common tree species in a montane, subtropical forest with a monsoon climate. Species largely differed in absolute stem growth rates, but diel and seasonal growth patterns were



		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Growth occurrence	Marginal R^2	0.016	0.033	0.029	0.07	0.102	0.111	0.103	0.039
	Conditional R^2	0.94	0.708	0.745	0.569	0.482	0.711	0.566	0.416
Growth rate	Marginal R^2	0.088	0.061	0.042	0.083	0.025	0.077	0.07	0.02
	Conditional R^2	0.424	0.576	0.564	0.567	0.559	0.679	0.62	0.246

Fig. 5 Climate response of daily stem growth from March to October in a subtropical tree community. Standardized coefficients (mean and 95% confidence interval) obtained from a generalized linear mixed-effects model (GLMM) for growth occurrence (growth or no growth) and a linear mixed-effects model (LMM) for growth rate. Closed circles are significant at $P < 0.05$ level. Temperature in March in LMM model was excluded due to high collinearity with vapour pressure deficit (VPD).

strikingly similar. Trees mainly grew before dawn when VPD was low. Over a year, trees mainly grew during May–August when climate conditions were warm and moist. Growth–climate analyses at various temporal scales confirm that atmospheric conditions (VPD and temperature) strongly determine when stem growth occurs during the day and the year. However, the rate of stem growth is mainly determined by temperature, and much less by moisture conditions. Below we discuss these results in the light of our expectations and compare them to those of other dendrometer studies.

Diel and seasonal stem growth patterns across species

We predicted that diel and seasonal growth patterns would be similar across species and associated with climatic conditions, but that stem growth rate varies between species. We found consistent diel and seasonal patterns in growth contribution and growth occurrence among study species (Fig. 2). Importantly, such temporal patterns overruled possible species differences and thus imply strong convergence in the timing of growth at diel and seasonal scale in the studied tree species community (Figs 2, S5). Such consistent diel and seasonal growth patterns were also found for other broadleaf tree species (van der Maaten *et al*., 2018; Zweifel *et al*., 2021; Kaewmano *et al*., 2022). We found only marginal differences in growth patterns between 11 evergreen and 3 deciduous species (Fig. 2; Table 1), which suggests that biophysical limitations drive growth timing across tree species (Martin *et al*., 2017).

Compared with other studies in tropical lowlands or temperate regions (Mendivelso *et al*., 2016; Wagner *et al*., 2016; Etzold *et al*., 2021), the climatic conditions in our study site induce relatively little variation in soil water, but strong seasonality in temperature (Fig. 3). Thus, soil moisture seems not to limit growth at our site (Fig. 3), contrasting with temperate forest sites where it does (e.g. Zweifel *et al*., 2021). Instead, we find that seasonal timing of stem growth is most closely linked to temperature seasonality (Figs 4, S5) and, to a lesser extent, also atmospheric moisture conditions during relatively dry spring months (Figs 3j–l, 5). Seasonal temperature variation overrules functional differences among species and led to strong convergence in the diel and seasonal timing of stem growth in our study forest.

In contrast to the interspecific consistency in the timing of growth, we found that the rate of growth varied largely among study species and showed weak or no diel or seasonal pattern (Figs 2, S5). Although stem growth rate may vary between species and trees (Volland-Voigt *et al*., 2010; van der Maaten *et al*., 2018), our study design with few trees sampled per species does not allow disentangling effects of species and trees (Figs 2, S5). This could be accomplished in future studies with a larger sample size per species. Furthermore, daily growth rates need to be interpreted with care, as they were aggregated from hourly values of stem diameter changes that are result from both structural growth as well as diel stem shrinking and swelling caused by negative pressure in xylem and refilling of vessels (Steppe *et al*., 2006, 2015; Zweifel *et al*., 2016; Meng *et al*., 2021). Detailed tree growth modelling can help to unravel the contributions of these processes to stem dynamics and provide a clear understanding of stem growth (Peters *et al.*, 2023).

What climatic factors drive diel stem growth?

We expected stem growth in this tree community to occur mainly at night. We observed that night and early morning hours indeed contributed most to annual stem growth (72%, Fig. 3), and that this pattern was driven by the diel pattern of stem growth occurrence (Figs 3, S2). Our results for subtropical trees are in line with the findings for broadleaf and conifer trees in temperate forests (Ziaco & Biondi, 2018; Meng *et al.*, 2021; Zweifel *et al.*, 2021) where stem growth peaked before dawn due to high growth occurrence when trees were replenished with water, and declined rapidly in the morning hours (Zweifel *et al.*, 2021). In conclusion, diel patterns in growth occurrence lead to large stem growth before dawn and thus drive the diel patterns in growth contribution across 14 subtropical broadleaf species.

Furthermore, we expected more stem growth to occur during day hours in the moist month after June when VPD largely drop (Fig. 3). We indeed observed higher growth occurrence from 09:00 to 20:00 h in the moist month of July (*c.* 33%, Fig. S3) compared with the relatively dry month of May (*c.* 23%), which was associated with decreased VPD (Fig. S4). The shifts in diel growth patterns over the season suggest that moist atmospheric conditions mitigated water limitation and allowed growth to take place during the daytime (Aldea *et al.*, 2018; Ziaco & Biondi, 2018; Meng *et al.*, 2021). Nevertheless, this seasonal shift was relatively small and growth occurrence predominantly occurred before dawn.

We expected that the diel pattern in stem growth would be driven by VPD, combined with high soil moisture. We found strong negative effects of VPD, but weak effects of soil moisture and negative effects of temperature on growth occurrence (Fig. 4a). Such VPD effects on subtropical trees are consistent with results from temperate ecosystems where VPD combined with soil moisture determined the variability in diel stem growth (Zweifel *et al.*, 2007, 2021). Specifically, temperate trees mainly grew under conditions with VPD < 0.4 kPa (Zweifel *et al.*, 2021), since such conditions allow cambial tissues to rehydrate at night and increase turgor pressure to reach the threshold required for stem growth (occurrence; Steppe *et al.*, 2006; Zweifel *et al.*, 2007; Peters *et al.*, 2023). The much lower VPD (0.1 kPa) at night and early morning hours for our study trees are thus expected to favour stem growth in our study (Fig. 3). In addition to the strict constraint of atmospheric humidity, soil moisture had a wide range allowing for stem growth: trees grew relatively well under moderate dryness with volumetric soil moisture < 5% (Zweifel *et al.*, 2021; Tumajer *et al.*, 2022). Thus, soil moisture had a relatively weak effect on diel growth occurrence compared with VPD in our study (Fig. 4). Indeed, soils remained relatively moist across day and night (volumetric soil moisture > *c.* 40%, Fig. 3e) and across seasons (> *c.* 30%, Fig. 3k), suggesting that soil moisture does not set constraints on stem growth in our study system. Overall, diel stem growth of our study species is mainly limited by atmospheric water demand, which is supported by studies on other species and climates (Herrmann *et al.*, 2016; Aldea *et al.*, 2018; Zweifel *et al.*, 2021; Camarero, 2022). Yet, more studies in (sub-)tropical forests are required to test whether these findings hold more generally across forest types.

What climatic factors drive seasonal stem growth?

We predicted that trees in a seasonal monsoon climate mainly grow during warm-wet months. We observed that trees consistently followed seasonal growth pattern with *c.* 88% of annual growth achieved during the warmest and moist period (May–August; Figs 2g,h, 3g,h; Table 1). This seasonal growth pattern is consistent with observations for trees in temperate forests (Oberhuber *et al.*, 2014; Güney *et al.*, 2016; van der Maaten *et al.*, 2018; Tumajer *et al.*, 2022), where *c.* 80% of the annual stem growth was achieved in the warmer months May–August (Etzold *et al.*, 2021), and in boreal forests (Rossi *et al.*, 2006, 2007; Gruber *et al.*, 2009). However, seasonal timing in growth across 14 species in our tree community showed lower variability (Fig. 3) compared with this timing for seven species in temperate forests (Etzold *et al.*, 2021). In conclusion, seasonal stem growth patterns in our study community align with that of temperate and boreal forests.

We predicted that seasonal stem growth patterns were associated with temperature (Huang *et al.*, 2020), in combination with moist conditions in atmosphere and soil. We indeed found a strong positive effect of temperature, in combination with a negative effect of VPD and weak effect of soil moisture on growth occurrence at daily and monthly scales (Fig. 4b,c). The observed temperature effect in this study was consistent with several studies across a range of biomes (boreal to tropical) and tree taxa (conifers and broadleaf species). Table 2 provides an overview of these studies and their results. Furthermore, we also found stronger effects of temperature and VPD in spring but much weaker effects afterwards when climate conditions became warm and moist (Figs 3, 5), confirming the role of temperature to trigger stem growth but with a remarkable role for VPD in spring as well. In addition to the temperature effect, our climate–growth analysis showed a negative effect of VPD on stem growth occurrence of study trees, which is in line with observations from boreal, temperate, subtropical and tropical forests (Table 2). The dominant effect of temperature relative to VPD at the seasonal scale (Fig. 4b) is confirmed by the highest growth peaks coinciding with the highest temperatures around summer solstice rather than lowest VPD (Rossi *et al.*, 2006, 2007; Güney *et al.*, 2016; Etzold *et al.*, 2021). Overall, our results show that temperature plays a critical role in seasonal growth dynamics at our study site and elsewhere (Jiang *et al.*, 2014; Oberhuber *et al.*, 2014; Güney *et al.*, 2016; Tian *et al.*, 2017; Etzold *et al.*, 2021; Tumajer *et al.*, 2022).

In addition to the timing of seasonal growth, we found the magnitude of seasonal growth to increase mainly with temperature (Fig. 4). Our findings agree with the notion that higher temperatures favour metabolic processes (Parent & Tardieu, 2012), cambial activity (Cabon *et al.*, 2020) and in turn stem growth rate (Tumajer *et al.*, 2022). This seasonal temperature effect on

Table 2 Seasonal-level climate–growth analysis of dendrometer data (for full list, see Supporting Information Table S1).

	Effect of climate drivers								
	T (%)		*P* (%)		VPD (%)		SM (%)		
Biome	+	–	+	–	+	–	+	–	Studies
Boreal	30	30	30	0	0	30	0	30	10
Temperate	22	31	43	1	4	37	12	1	94
Subtropical	25	38	88	0	0	63	75	0	8
Tropical	11	6	22	0	0	17	6	6	18
In total	21	28	42	1	3	35	14	4	130

Green and orange blocks represented positive (+) and negative (–) effects, respectively. For each type of biomes and each climate driver (temperature (*T*), precipitation (*P*), vapour pressure deficit (VPD) and soil moisture (SM)), we calculated the percentages of positive or negative effects in the number of studies shown at the end of each row.

growth rate for our study trees was consistent with the findings for temperate trees (Aldea *et al.*, 2018; Hinko-Najera *et al.*, 2019; Tumajer *et al.*, 2022) and boreal trees (Gruber *et al.*, 2009). Thus, in forests where productivity is (seasonally) limited by low temperatures, high temperatures not only trigger stem growth at the onset of growing season (Huang *et al.*, 2020) but also stimulate stem growth rate later during the season, as long as moisture availability is sufficient.

Conclusions

We present one of the first community-level studies of intra-annual stem growth in a species-rich forest. We show that seasonal growth patterns are mainly driven by temperature and VPD in this tree community, and that stem growth during the day mainly occurred before dawn associated with low VPD. Low VPD and high soil moisture during very moist summer months (such as July) seem to slightly release daytime constraints on growth, but this effect was minor. Temperature not only favoured stem growth at the seasonal scale but also increased diel growth rate when moisture availability permitted growth. Species identity had a strong influence on the magnitude of stem growth, probably reflecting different functional traits and ecological strategies across tree species. However, species strongly converged in intra-annual stem growth patterns in this tree community, implying that our community-approach allows understanding intra-annual dynamics but cannot be used to estimate absolute stem growth rates at the forest scale. More studies on intra-annual growth patterns and their climatic drivers are needed in (sub-)tropical climates and forest types to increase their representation in global level assessments of the responses of woody productivity to increasing climate variability.

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Competing interests

None declared.

Author contributions

Z-XF designed the experiment and collected the data. BZ did the analyses. Z-XF, FS, BK and PAZ contributed to the methodology and the conceptualization. BZ, FS and PAZ wrote the manuscript, and all authors revised it.

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Data availability

The data are available from the Mendeley Data (https://data.mendeley.com/datasets/wx5y4t67g8/1).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Monthly temperature and precipitation at the study site during 2017–2021.

Fig. S2 Growth contribution in relation to growth occurrence and growth rate in diel and seasonal levels.

Fig. S3 Diel growth probability in May and July of subtropical trees and the climate conditions.

Fig. S4 Climate responses of diel stem growth in May and July in a subtropical tree community.

Fig. S5 Variance in hourly, daily and monthly stem growth explained by fixed and random variables.

Table S1 Seasonal-level climate–growth analysis of dendrometer data (Full list).

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