Why trees grow at night

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Summary
- The timing of diel stem growth of mature forest trees is still largely unknown, as empirical data with high temporal resolution have not been available so far. Consequently, the effects of day–night conditions on tree growth remained uncertain.
- Here we present the first comprehensive field study of hourly-resolved radial stem growth of seven temperate tree species, based on 57 million underlying data points over a period of up to 8 yr.
- We show that trees grow mainly at night, with a peak after midnight, when the vapour pressure deficit (VPD) is among the lowest. A high VPD strictly limits radial stem growth and allows little growth during daylight hours, except in the early morning. Surprisingly, trees also grow in moderately dry soil when the VPD is low. Species-specific differences in diel growth dynamics show that species able to grow earlier during the night are associated with the highest number of hours with growth per year and the largest annual growth increment.
- We conclude that species with the ability to overcome daily water deficits faster have greater growth potential. Furthermore, we conclude that growth is more sensitive than carbon uptake to dry air, as growth stops before stomata are known to close.

Introduction
Species-specific responses of tree growth to environmental conditions are crucial for understanding forest dynamics in a world with a rapidly changing climate (Bastos et al., 2020; McDowell et al., 2020). However, knowledge about the physiological and environmental drivers of tree growth is still limited by the temporal resolution of dendrochronological methods. Such data are often coarse and are obtained typically with an annual resolution of the underlying tree ring samples (Schweingruber, 1996; Bast et al., 2018) or, in less frequent cases, small wood samples obtained at (bi-)weekly intervals (Zweifel et al., 2006; Delpierre et al., 2016; Huang et al., 2020; Peters et al., 2021). Daily or even hourly-resolved growth responses of mature forest trees have been rarely recorded (Schurr et al., 2006), most data covers only short periods and were monitored in single stands (Zia & Biondi, 2018; Knüsel et al., 2019; Güney et al., 2020).

However, there is an urgent need for growth information with sub-daily resolution, since the average conditions over a week or a year might affect growth differently than within a specific hour. Growth is not a continuous, linear process but is strongly determined by thresholds of plant water potentials as has been shown for several tree species (Lazzarin et al., 2019; Cabon et al., 2020; Peters et al., 2021). These water potentials vary strongly with the time of day and climate change effects may therefore greatly differ between day and night.

Despite the current lack of hourly-resolved growth data, the theoretical background to explain the mechanisms of cell division and cell expansion in a tree stem is well established (Woodruff & Meinzer, 2011). At the core of the proposed mechanism is the soil–plant–atmosphere continuum including the cohesion-tension theory (Dixon & Joly, 1894), which connects soil water dynamics with tree hydraulics and atmospheric water demand and determines the water potential in the cambium where the new wood and bark cells are formed (Woodruff & Meinzer, 2011). Vapour pressure deficit (VPD) and soil water potential (SWP) become the key drivers of the water potential gradient that determines the water flow through the tree (Steppe et al., 2006; Novick et al., 2016; Carminati & Javaux, 2020). These two variables reflect the water potentials in the air and soil as well as integrate over other environmental variables, for example, temperature and relative humidity.

The essentials about the physiological relationship between tree water relations and growth dates back to the 1960s, when Lockhart (1965) described how a turgor threshold of the
The turgor threshold theory also enabled the development of a method to extract hourly stem radial growth data from continuous, high-precision dendrometer measurements (Fig. 1; Supporting Information Fig. S1). Dendrometer data consist of radial increment due to growth and tree water related shrinkage and expansion of mainly the bark, which need to be separated prior to analysing stem growth. A recent study (Zweifel et al., 2016) presented a separation method (zero-growth approach) based on empirical and theoretical evidence that radial stem growth is suppressed when tree stems are shrinking due to the transpiration-induced lowering of the turgor pressure. In short, growth is equivalent to an incremental increase in stem radius when the measured radius is larger than it was at any point in the past. The authors estimated that > 95% of the growth could be attributed to the correct hour, making for a very robust and credible, but not perfect, separation approach.

There remain uncertainties with potential hygroscopic effects of the bark of some tree species when the stem surface is moistened by rain (Oberhuber et al., 2020). Further, the zero-growth approach does not consider the still largely unknown bark degradation processes (Gricar et al., 2015; Güney et al., 2020), especially after frost in the winter period (Zweifel & Häsler, 2000; Charrrier et al., 2017). Uncertainties also remain due to technical issues, for example, the electronic and mechanical temperature behaviour of dendrometers, the way the sensor is anchored in the tree, or the way the raw data is cleaned from outliers and shifts (Haeni et al., 2020). As there is so far no alternative method capable of measuring radial stem growth with a similarly high resolution on mature forest trees, the zero-growth approach lacks an ultimate quality control. The application of another recently developed empirical approach to separate growth from dendrometer data (Mencuccini et al., 2017) did not offer an alternative, as the remaining uncertainties are the same and the approach additionally needs sap flow data not available in this infrastructure.

Meanwhile, the zero-growth approach has become widely accepted and applied (Dietrich & Kahmen, 2019; Schafer et al., 2019; Eitel et al., 2020; Güney et al., 2020; Lamacque et al., 2020; Pappas et al., 2020; Sellier & Segura, 2020). Accordingly, growth is defined as the radial stem increase above a previously reached stem radial maximum (Fig. S1). All stem size changes below this dynamically increasing maximum were attributed to the water conditions of the trees and removed from the growth data. Growth is understood as irreversible stem radial increment, including new bark and wood cells and neglecting any cell maturation processes (e.g. lignification) (Cuny et al., 2015; Rathgeber et al., 2016).

Here, we present the first comprehensive study of hourly-resolved stem growth data from a large, technically homogenous network of 170 trees at 50 sites, continuously measuring stem radius and air and soil conditions (Fig. 1). The key hypotheses of this study address the sensitivity of growth to VPD and SWP as well as the dependence of stem growth on the time of day:

1. We expect diel stem growth to increase overnight and decrease during the day because transpiration reduces water potential and turgor pressure in the cambium, thus inhibiting cell division and cell expansion.

2. We expect stem growth to be favoured under humid conditions and thus improved under conditions of low VPD and high SWP. Furthermore, we expect that stem growth always responds similarly to environmental conditions, regardless of the time of day.

3. We expect stem growth to be species-specific as species are known to have different sensitivities to VPD and SWP (e.g. stomatal regulation) and other factors (e.g. circadian rhythm).

**Materials and Methods**

**Sites and setup**

The 50 sites studied are part of TreeNet (www.treenet.info), a network where stem radius changes of trees are measured continuously using high-precision point dendrometers, in parallel with environmental information of air (VPD) and soil (SWP) in Swiss forests since 2011 (Fig. 1). Most forests were managed sustainably since 1876 and are either deciduous, evergreen or mixed.

Four angiosperms (Fagus sylvatica, Fraxinus excelsior, Quercus pubescens, Quercus petraea) and three gymnosperms (Picea abies, Pinus sylvestris, Abies alba) were analysed between 2011 and 2018 (Fig. 1). All of them fulfilled the minimum criteria of appearing at > 3 sites with > 2 yr of data per time series and a minimum of two individuals per site. Further, only vital, mature and dominant trees that grew more than 100 μm yr⁻¹ were included. The total number of trees per species ranged from 7 to 62. All analyses were based on hourly-resolved data. Further characteristics of species and sites are listed in Supporting Information Table S1.

**Environmental conditions**

Air temperature (TEMP) and relative humidity (ReH) was obtained either from weather stations located at the sites (sources: treenet.info and lwf.ch) or from nearby (mean distance: 8.3 km, maximum: 15.4 km) MeteoSwiss stations (meteoswiss.admin.ch). VPD was calculated from TEMP and ReH.

SWP (MPS-2/MPS-6; Decagon Devices, Pullman, WA, USA) was measured at 10–20 cm soil depth at each of the 50 sites (treenet.info) and corrected for soil temperature (Walhert & Schleppi, 2018). These topsoil water potentials (SWP values) were cross-checked with SWP measurements over 2 m profiles at five sites (Fig. S2).

**Dendrometer measurements**

Point dendrometers (ZN11-T-IP and ZN11-T-WP, Natkon, Oetwil am See, Switzerland, Fig. 1) were mounted on the stem at breast height. The dendrometers consisted of a carbon-fibre
frame with three stainless steel threaded rods which served as anchors in the wood of the tree stem. A metal sensing pin was gently pressed against the surface of the bark by a spring. The electronic transducer detected changes in the position of the pin and thus stem radius changes measured over the bark. The outermost dead layer of bark under the pin was carefully removed to minimize the effect of hygroscopic swelling. Special care was taken to avoid damaging the living bark underneath.

The dendrometer data were recorded and transmitted with DecentLab logging devices (DecentLab GmbH, Dübendorf, Switzerland) at 10 min intervals or better. The logging resolution was < 1 µm and the temperature sensitivity of the applied dendrometers (including all components and logger) was < 0.3 µm °C⁻¹ and was thus negligible.

**Stem radius fluctuations and growth calculations**

Dendrometer data combine two major processes of the tree stem physiology: irreversible growth and reversible swelling and shrinkage (Fig. S1). Here we use the so called ‘zero growth’
Research (10-min resolution) over the full length of the time series were (R_Core_Team, 2019). The raw dendrometer data of each tree. All analyses and plots were made with R statistical software. Data treatment and statistical methods

The stem growth period was defined as the period of the year when radial increments were detected and was determined separately for each site and species (based on the average of all trees per species and site). The first and last 5% of the stem growth period were excluded to avoid outliers influencing the timing of the growth periods. Hours with growth were flagged as ‘growth hours’, summed up for each individual tree and year (‘growth hours per year’), and further aggregated to species-specific median growth hours per year.

Stem growth period and growth hours

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Data treatment and statistical methods

All analyses and plots were made with R statistical software (R_Core_Team, 2019). The raw dendrometer data of each tree (10-min resolution) over the full length of the time series were quality checked and processed with the R-package TREENETPROC (Haeni et al., 2020). For analyses or calculations that were based on annual values we included annual time series that covered > 90% of the stem growth period only.

Statistical analyses of diel, hourly resolved data were based on aggregated data considering the nested data structure. The aggregation process underwent three steps. First, the daily growth pattern for each tree individual was calculated as the relative contribution of a given hour to the total annual growth (in percentage; the 24 h of a day equal to 100%) in order to normalize the highly varying absolute annual growth between individual trees and to aggregate the data over several years. Second, these relative growth numbers were averaged per site and species. And thirdly, the data were pooled into (1) a growth response of all species and (2) aggregated into a species-specific response pattern. The VPD and SWP data were treated in the same way. All steps included medians with 25% and 75% quantiles. Based on these aggregated data sets, growth probability (%) was quantified as the number of hours with growth relative to the total number of hours in the stem growth phase. Hourly growth rates in absolute number of hours with growth relative to the total number of hours were hardly differing (Table S2). Further, the available SWP for all sites (measured at 10 cm soil depth) largely represented the temporal dynamics of five available soil profiles of 2 m depth. However, the lower boundary for main growth was shifted by about 200–300 kPa upwards between the data used in this study (Fig. 3) and the data from the 2 m soil profile (Fig. S2). The median SWP were hardly differing (Table S2).

VDP and SWP together explained on average 81% of the diel growth variation of all species in a multiple regression model (Table S3). A model that included all available environmental variables (relative humidity, air temperature, net radiation, SWP and the respective pairwise interactions) explained only slightly more, namely 88% (Table S4).

The explanatory power of SWP for diel growth varied considerably among species (Table S3) between 0% (Quercus petraea)
and 27% (*Abies alba*), and was significantly higher for the conifers (20%) than for the deciduous species (5%). Growth decreased for a given VPD with decreasing SWP in some species (*Picea abies*, *Abies alba*, *Quercus petraea*), while interestingly it increased in other species up to a certain SWP (−30 to −150 kPa) and only decreased thereafter (Fig. S3). Or in other words, not all species had the greatest growth under the wettest soil conditions (measured in 10–20 cm).

### Diel dynamics of stem growth in relation to vapour pressure deficit and soil water potential

The general relationship between the diel growth and the environmental variables VPD and SWP appeared robust across all species (main panels, Fig. 4), resembled the patterns for individual species (small panels, Fig. 4), and was largely independent of the time of the season (Fig. S5). Diel growth responded more

![Fig. 2](image-url)
consistently to VPD, while the growth response to SWP was strongly depending on the time of day. A particular SWP resulted in higher or lower growth depending on the actual time of day, with nocturnal conditions allowing growth over a much larger SWP range compared to daylight hours.

In all species, the median VPD for hours with growth (bold red lines, Fig. 4) was consistently lower than the median VPD of all hours in the entire growth period (bold black line, Fig. 4). Especially during daylight hours, the difference between the two lines increased, while the same deviation for SWP was less dependent on the time of day. However, both the soil and the air were generally drier than required for growth, allowing only a limited number of hours with growth throughout the entire stem growth period. *Quercus pubescens* and *Pinus sylvestris* had the fewest hours with growth (c. 300), while *Fagus sylvatica* and *Abies alba* had more than double (Table 1).

**Timing of peak growth as indicator for annual growth**

Despite the robust 24-h growth pattern across all species and sites, there were clear species-specific differences where the growth of some species peaked earlier at night than of others.
Fagus sylvatica started to increase (13:00 h) and reached the peak (01:00 h) of its median diel growth earlier than all other species, which had growth peaks between 02:00 h and 06:00 h in the early morning and growth minima during midday and early afternoon, between 14:00 h and 16:00 h (Table 1). Of all species, Pinus sylvestris showed the most pronounced growth peak (highest amplitude, Fig. 2d), followed by Picea abies and Quercus pubescens, indicating that growth was more restricted to these specific hours. By contrast, Quercus petraea and especially Fraxinus excelsior had the least pronounced growth maxima and minima, indicating that growth was more evenly distributed over the 24 h than in other species.

Strikingly, the species-specific temporal growth peaks were very closely negatively related with the annual, species-specific number of hours with growth (adj. $R^2 = 0.77$; Fig. 5a; Table 1) and also with the annual radial stem growth (adj. $R^2 = 0.4$; Fig. 5b). Species with their growth peak earlier in the night generally had more hours with growth per year (Fagus sylvatica, Abies alba, Fraxinus excelsior) and also generally grew more than those species with a growth maximum later in the night (Pinus sylvestris, Quercus pubescens).

**Discussion**

Consistent diel growth patterns across species

We found that the trees grew mainly at night, with species-specific growth peaks between 01:00 h and 06:00 h (Figs 4, 5; Table 1), when the trees are presumed to be best replenished with water and thus likely to provide the best conditions to exceed the turgor threshold for cell division and cell expansion (Schurr et al., 2006; Cabon et al., 2020). This timing of growth was consistent with the observation that it takes several hours after nightfall for stems to replenish and to compensate for the tree water deficit caused by the imbalance between transpiration and water uptake during daylight hours. It is this water deficit, which must be compensated for before growth processes are proposed to become likely (Zweifel et al., 2016). Stem growth also occurred during daylight hours (Fig. 2), but with a consistently lower relative contribution to annual growth. Overall, these results are consistent with our hypotheses, which emphasize the importance of tree water relations and their determination by atmospheric and soil dryness, in line with the turgor pressure threshold concept for growth (Lockhart, 1965; Peters et al., 2021).

Different effects of vapour pressure deficit and soil water potential on growth

Radial stem growth was associated with high mean SWP (−6 to −65 kPa) and low mean VPD (0.11–0.24 kPa, Table S2), emphasizing the commonly known negative influence of dry air and soil on growth processes (Zweifel et al., 2006; Pappas et al., 2020). However, these daily mean values did not account for diel dynamics and they did not reflect how differently SWP and VPD were generally related to stem growth at an hourly resolution (Figs 3, 4). VPD consistently limited the main growth (>75% of annual growth) to a range <0.4 kPa (Fig. 3), largely independent of species (Fig. S3) and time of day (Fig. 4), while SWP showed a much wider and more species-specific range of main growth (>−900 kPa). Especially at night (Fig. 4), stem growth consistently occurred even at lowered SWP, suggesting that growth is possible under moderate soil dryness if VPD is low enough at the same time. The more linear relationship between VPD and stem growth (over 24 h) than that between SWP and growth (Fig. 4).
also underlines recent findings that VPD increasingly limits tree growth due to an increasingly warmer climate (Novick et al., 2016; Grossiord et al., 2020; Peters et al., 2021).

Increased VPD also restricted stem growth under wet soil conditions, because high atmospheric water demand on a sunny day increased transpiration faster than root water uptake, leading to tree water deficit (Hinckley & Bruckerhoff, 1975; Zweifel et al., 2005) and presumably reduced turgor pressure below the growth threshold in the cell-dividing tissue, i.e. the stem cambium (Steppe et al., 2006; Cabon et al., 2020). Because the observed VPD threshold for main growth was so low and VPD generally increases so rapidly with daylight, growth inhibition occurred on any sunny day (Fig. 4). Growth in the afternoon was only observed when VPD remained low, that is, on rainy or cloudy days. This was sometimes even the case when little rain fell during a period with dry soils (Fig. S6). However, the additional meteoric water was not sufficient to moisten the soil to the depth where the soil sensors were installed (10–20 cm), but may have increased water uptake by the topmost roots near the soil surface. In addition, small rain events moisten the surface of a tree, reduce transpiration and can rehydrate the plant via water uptake through the leaves (Goldsmith et al., 2017) and thus have the potential to increase negative water potentials and could also raise turgor pressure above the growth threshold from above.

The importance of humid air for the physiological performance of a tree has also been demonstrated for the redwood tree giants (Simonin et al., 2009). Our results suggest the importance of small rain events not only for these giants, but most likely also for the growth of temperate tree species, particularly in an increasingly drier environment (McDowell et al., 2020), as also recently suggested by Dietrich & Kahmen (2019). Low VPD is most likely not directly responsible for growth, but it seems to be a strong indicator for leaf surface wetness, which induces the necessary relaxation of low water potentials. However, SWPs that were too low (Fig. 3) did not allow for growth either. We assume that under such conditions the tree’s growth physiology cannot be sufficiently stimulated by atmospheric moisture alone. Overall, our results suggest that under moderately dry soil conditions, information on air humidity is essential to accurately estimate stem growth.

Species-specific diel timing of growth

Despite the generality of the daily growth trends, the seven species studied consistently differed in the timing of the growth peaks (Table 1; Fig. 5), and it was striking that the earlier a nocturnal growth peak of a species was reached, the higher the number of hours with growth per year and the annual radial growth of the stem were (Fig. 5).

Interestingly, we did not find a consistent grouping of species in Fig. 5 with respect to wood types (gymnosperms, angiosperms), wood anatomy (ring-porous, diffuse-porous, tracheids) or foliage type (evergreen needles, deciduous leaves). However, the ranking of species along the linear regression line between time of day of maximum growth and the annual number of hours with growth was at least partly explainable by the respective SWP and VPD ranges for growth (Table S2). The drier the average site conditions where a species occurred, the fewer hours with growth were measured, which is consistent with the generally known limitation of growth by drought (McDowell & Sevanto, 2010; Korner, 2015; Pappas et al., 2020). This was especially true for the two most extreme species in our study, Abies alba (growing mostly under humid conditions) and Quercus
pubescens (growing under driest conditions). Though, this was not consistently true for all species between these two extremes (Tables 1, S2), which might also be due to averaging the wide range of conditions that some of the species covered (e.g. Pinus sylvestris, Fig. 1).

The very close linear relationship between the timing of the diel growth peak and the annual number of hours with growth (adj. $R^2 = 0.77$) suggests a general mechanistic reason governing it. We speculate that those species that are able to grow earlier at night (Fig. 2) generally have more hours available under suitable conditions per night and therefore have a better chance of accumulating more hours with growth over the season. However, the results also showed that the species with an earlier growth peak (Fagus sylvatica, Abies alba, Fraxinus excelsior) also reduced their growth earlier (Fig. 2) and therefore did not take full advantage of the generally moistest conditions around dawn. By contrast, species with a late growth peak (Pinus sylvestris, Quercus pubescens) may not have had enough time to grow long enough due to the environmental constraints, resulting in pronounced growth peaks around dawn (Fig. 2), a reduced number of growing hours per night and per growing season, and thus reduced absolute annual stem growth (Fig. 5).

What alters the species-specific nocturnal growth peaks?

The generally drier conditions under which some of the species grew could be part of the answer. However, we speculate on other reasons as well. First, the species-specific morphological differences, for example, bark thickness or water transport capacity of the wood (Steppe et al., 2006) could play a role. Fagus sylvatica, as the species with the earliest growth peak, has by far the thinnest bark tissue of the species studied (Ilek & Kucza, 2014) and therefore may need less water and time to replenish its shrunken tissue. Further, an efficient water transport system such as the ring-porous wood of Fraxinus excelsior could help to accelerate the replenishment of the tree’s water deficit (Brinkmann et al., 2016; Klesse et al., 2020) and thus induce a faster increase in cambium turgor after nightfall. Second, the increase of turgor pressure could additionally be enhanced by osmoregulation, a process actively altering a cambium cell’s turgor even during periods when water potentials in the xylem are low due to increased transpiration, as has recently been shown for several tree species (Zweifel et al., 2014; Barraclough et al., 2019; Lazzarin et al., 2019). And third, the circadian rhythm has been shown to play an important role in explaining species-specific phenological traits, for example, bud burst or the molecular regulation of annual growth (Singh et al., 2017; de Dios & Gessler, 2018; Huang et al., 2020). Fagus sylvatica is known to follow the circadian rhythm (de Dios et al., 2015) more closely than other species. We, therefore, speculate that there might also be an influence of the circadian clockwork on diel growth. Our assumption is based on the unique, temporally irregular pattern of the growth response to VPD of Fagus sylvatica (Fig. 4). Fagus is the only species where the otherwise constant relationship between VPD and growth disappeared during the night. Such a pattern suggests a decoupling of growth from VPD and would for example be expected if a species closed its stomata completely regardless of environmental conditions, for example, initiated by a circadian rhythm. Such a mechanism also has the potential to explain the unusual diel growth pattern of Fagus sylvatica and possibly other species.

Potential limitations of the results

Any result is only as good as its underlying data quality and premises. This work relies on technically correct measurements of radial stem size changes in micrometre resolution, consistent and reproducible handling of the partially erroneous dendrometer raw data (Haeni et al., 2020) and on the zero-growth approach that separates the dendrometer data into irreversible radial growth due to new cells and reversible swelling and shrinking due to water relations in the tree (Zweifel et al., 2016).

The homogeneous technical design of the network (www.treenet.info) with the use of only one type of high-precision point dendrometers, the uniform hardware for recording the data, the automatic data transfer to a central database and the automated routine for uniform cleaning and quality checking of the raw data helped to optimize the reliability of the data. However, the remaining technical uncertainties due to undetected data outliers despite the automated cleaning procedure and manual data checking, or the remaining temperature sensitivity of the measuring instruments despite a setup developed to minimize this effect, can never be completely avoided. In this work, it can be assumed that such effects are levelled out by the aggregation steps of the huge data set, or affect all measurements in the same systematic way and are thus of little relevance to the results presented. Also not to be completely excluded are potential artefacts due to episodic hygroscopic swelling of the bark when the stem surface is wetted by rain (Oberhuber et al., 2020). However, this potential effect was minimized by using point dendrometers (not band dendrometers) and removing the dead outermost bark layer under the measuring pin. The still largely unknown processes of bark decomposition (Gricar et al., 2015) are mainly assumed to occur during winter and therefore also have little relevance for this work.

Essential for the quality of the results is the reliability of the zero-growth approach. The approach builds on the widely accepted turgor threshold theory for cell growth (Lockhart, 1965; Steppe et al., 2006; Muller et al., 2011; Lazzarin et al., 2019; Cabon et al., 2020; Peters et al., 2021) and is based on the assumption that the turgor threshold for growth cannot be exceeded once a tree stem starts to shrink (Zweifel et al., 2016). The approach has been shown to be largely reliable based on several indirect tests and theoretical considerations on a handful of temperate tree species, but lacks an ultimate test with an independent measurement method. Therefore, a residual uncertainty about the accuracy of the approach remains. Any deviation of the initial stem shrinkage from the stop of cell growth would affect the results presented. However, even if the time at which a tree stem begins to grow, determined by the zero-growth approach, were not absolutely precise, this would hardly affect the growth response curves shown, since stem shrinkage occurs quite rapidly at dawn, which means that crossing the threshold for growth
would only be delayed for a short period of probably less than an hour. Such a systematic shift in initial growth would not affect the daily VPD-GRO or SWP-GRO patterns, but could in the worst case lead to slightly shifted VPD and SWP ranges for growth. However, this reasoning does not cover the objection if someone disputes the correctness of the turgor threshold theory for growth, which is the most critical premise of this article.

Conclusions

Hourly-resolved growth data opened a new dimension in the analysis of stem growth responses to changing environmental conditions. Diel growth dynamics as a function of VPD and SWP showed robust general patterns as well as small but consistent, species-specific deviations from them. The dependence of growth on very low atmospheric water demand (low VPD) and its temporal decoupling from periods of photosynthesis suggests that carbon allocation to radial stem growth is mainly sink-driven on a diel scale. It also suggests that growth depends primarily on tree water conditions and only secondarily on current carbon allocation, at least in the short term.

The higher drought sensitivity of the growth process compared to the carbon assimilation process may explain why even starving trees do not exhaust their carbon reserves under drought stress, since in a dry period, carbon assimilation seems possible for longer than radial stem growth. The fact that the timing of peak growth within the 24-h cycle has such strong explanatory power for the overall growth performance of a species suggests a subtly balanced interplay between the different carbon source and sink dynamics and highlights the close link between a tree’s water relations and its growth. The findings that trees grow mainly at night and that VPD, in addition to SWP, has a strongly limiting influence on growth is key to better understand climate change effects on forest growth dynamics.

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Author contributions

Conceptualization: RZ, FS, SE. Methodology: RZ, FS, NB, WE, AG, MH, RLP, LW, MW, KZ, SE. Investigation: RZ, SB, MH, LW, MW, SE. Visualization: RZ, RLP, SE, KZ. Funding acquisition: RZ, NB, WE, LW, SE. Project administration: RZ, SE. Supervision: RZ, WE, SB, SE. Writing – original draft: RZ, FS, SB, NB, WE, AG, MH, RLP, LW, MW, KZ, SE.

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Data availability

All underlying data is made available in a data repository (https://www.pangaea.de).

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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* Scheme of processes determining stem radius changes (SRCs) measured by point dendrometers mounted on the stem surface, and a data example.

*Fig. S2* Comparison of soil water potential (SWP) data from different soil depths.

*Fig. S3* Species-specific, hourly-resolved, radial stem growth in the measured space of vapour pressure deficit (VPD) and soil water potential (SWP).

*Fig. S4* Comparison of measured growth data with the interpolated ones in the contour plots.

*Fig. S5* Growth response patterns in relation to vapour pressure deficit (VPD) and soil water potential (SWP) grouped for the months April to August.

*Fig. S6* Examples of stem growth under moderately dry soil conditions.

**Table S1** Tree species and its occurrence at the different sites with different expositions and vegetation compositions.

**Table S2** Species-specific averages of vapour pressure deficit (VPD) and soil water potential (SWP) for hours with stem growth.

**Table S3** Explanatory power of vapour pressure deficit (VPD) and soil water potential (SWP) for diel growth with multiple linear regression models.

**Table S4** Explanatory power of environmental variables for hourly-resolved diel growth with multiple linear regression models.

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