Hourly Resolved Climate Response of *Picea abies* beyond its Natural Distribution Range

LARA KLIPPEL[1*], CLAUDIA HARTL-MEIER[1], JENNY LINDÉN[2], MARKUS KOCHBECK[1], KURT EMDE[1] AND JAN ESPER[1]

[1] *Johannes Gutenberg University Mainz, Saarstraße 21, 55122 Mainz, Germany*

[2] *Swedish Environmental Research Institute, Air Pollution and Abatement Strategies, Gothenburg, Valhallavägen 81, 114 27 Stockholm, Sweden*

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Abstract

Norway spruce (*Picea abies* (L.) Karst.) is an economically significant species of timber industry in Germany. However, previous studies reported a drought sensitivity of spruce questioning the suitability of this species when exposed to future climate change. We analyze the species' climate sensitivity by comparing high-resolution stem radius changes of four spruce trees with prevailing weather conditions from April 2012 to December 2014. The study is based on dendrometer data recorded in the Taunus (Germany) in a forest plantation beyond the species natural distribution range. The sub-hourly dendrometer data are decomposed to emphasize diurnal growth patterns and compared with related weather patterns. Our results show that both climate and photoperiod control the timing of spruce growth. Daily radial changes are best explained by relative humidity and temperature variations, but a distinct precipitation signal is not detected. The missing precipitation response is likely related to well-developed Stagnosols at the sampling site in the Taunus preventing transpiration stress to occur. These findings suggest that a balanced water supply attenuates the trees' climate sensitivity even beyond the species natural distribution range and highlights the significance of site selection in plant performance assessments.

Keywords: climatic stress, dendroecology, dendrometer, diurnal cycle, Norway spruce, radial growth

Introduction

Recent climate change in Central Europe, characterized by increasing temperatures (Christensen et al. 2007) but insignificant changes in precipitation (Hundecha et al. 2005), has wide-ranging effects on the distribution, phenology and abundance of plant species (Kovats et al. 2014). Ambient air warming alters the atmospheric evaporative demand and enforces plants to cope with increased water and temperature stresses (Chaves et al. 2002). Trees have long lifespans and limited capacity to adapt to short-term climate anomalies, and are thus vulnerable to heat stress and evaporation changes (Lindner et al. 2010). This concern particularly applies to non-indigenous species, which are cultivated outside their natural distribution range. In Europe, Norway spruce (*Picea abies* [L.] Karst.) has been planted region-wide since the sixteenth century due to the economic advantages of its timber (Spieker 2000). *P. abies* is native in the European Alps, the Balkan Mountains, the Carpathians and Scandinavia, and perfectly adapted to the cold and wet conditions in elevated regions (Figure 1a, Ellenberg 2009, Kölling et al. 2009, Roloff et al. 2010). The species is, however, vulnerable to increased moisture deficits and warmer temperatures, enhancing the risk of economic failure (Kölling et al. 2007).

Recent studies showed that climate change has no substantial influence on *P. abies* within its natural habitat in the European Alps (Hartl-Meier et al. 2014a, Hartl-Meier et al. 2014b, Hartl-Meier et al. 2015). In contrast, other work revealed increased drought sensitivity beyond the natural distribution range. In Southern Germany, spruce showed increased summer drought susceptibility along a climatic gradient from cool/wet to warm/dry conditions (Zang et al. 2014). Esper et al. (2012) showed that growth of *P. abies* in the Taunus (Western Germany) is significantly controlled by May-July precipitation, and Boden et al. (2014) revealed spruce resilience decreased because of more frequent drought events in the recent past in Southern Germany. However, all these studies assess growth variability at monthly resolution, and only limited information exists about the tree's reaction to short-term environmental changes, particularly in sites beyond the species' natural habitat (Figure 1b).

Continuous monitoring of daily stem radial changes using dendrometers have been used to assess the tree climate sensitivity and water status on short time scales (Deslauriers et al. 2007). Dendrometer data contain information on daily stem shrinking and swelling, and superimposed growth formation (Downes et al. 1999, Deslauriers et al. 2003, Bouriaud et al. 2005). The daily cycle of water depletion and replenishment is controlled by several factors including rainfall and soil water content, atmospheric vapor pressure deficit, and ambient air temperature (Zweifel et. al 2001, Deslauriers et al. 2007, Vieira et al. 2013, King et al. 2013), whereas the radial stem increments are typically associated with precipitation (Oberhuber et al. 2010), temperature (Mäkinen et al. 2003) and photoperiod changes (Rossi et al. 2006).

We here employ several dendrometers monitoring stem radial changes at high temporal resolution to evaluate the impact of meteorological parameters on cambial activity (Tardif et al. 2001, Deslauriers et al. 2007). Based on hourly resolved dendrometer data collected from four *P. abies* trees in the Taunus (Germany), this study aims at *(i)* detailing characteristic annual and circadian stem variations patterns, and *(ii)* detecting the significance of precipitation events on spruce stem radius increments.

Materials and Methods

Site description and measurements

The study was conducted in a mixed-forest plantation in the Taunus in Germany where *P. abies* is non-native (Table 1, Figure 1a-b). Radius dendrometers (Ecomatic, type radius DR, Dachau/Germany) with a resolution of 2.6 μm were anchored at breast height at the stems of four, ecologically dominant *P. abies* trees (PA1-PA4, Figure 1c-d). The data logger was mounted on an unmeasured tree (Ecomatic, model DL - 15, Dachau/Germany). The sensors measure the displacement of a sensing rod pressed against the stem. We removed the dead bark to minimize biases due to swelling and shrinking processes (Zweifel and Häsler 2001), and obtained data at half-hourly resolution from April 19, 2012 to December 31, 2014. Temperature, precipitation and relative humidity data from a neighboring climate station run by the Department of Geography (Johannes Gutenberg-University Mainz) were used for comparison. Additional cloud cover data were retrieved from a climate station in Geisenheim, 15 km off the study site (Table 1). The annual precipitation sums of 2012 to 2014 are similar to the 30-year average from 1961-1990 (547 mm) indicating that no unusual conditions were monitored, expect perhaps for the April to October vegetation period in 2014, which was slightly more humid compared to the long-term mean of 342 mm (Figure 2). All data were corrected and adjusted to German standard time (UTC+2) and set to hourly resolution.

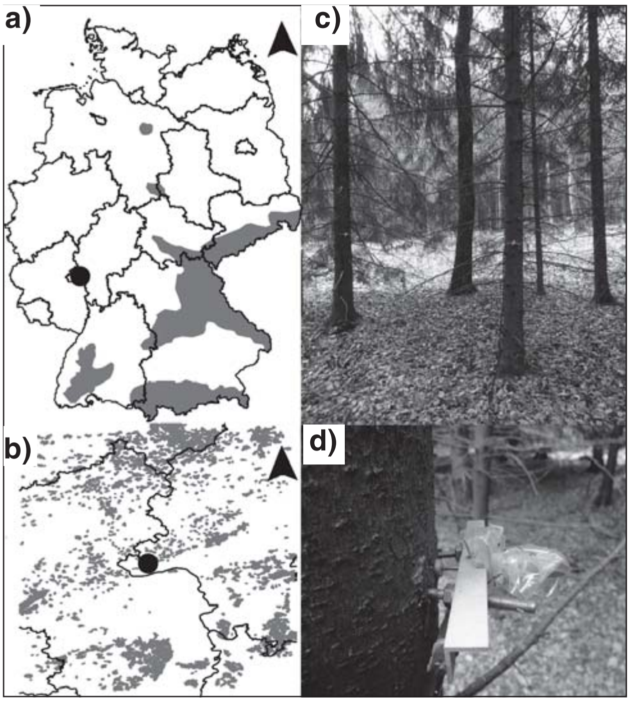

Figure 1. Site location and aspect. a) Map of Germany including the natural distribution range of *Picea abies* in grey; b) Map of the study region including coniferous forests in grey. The black dot indicates the sampling site; c) Monitored *Picea abies* trees, and d) radius dendrometer. Data source: Free GIS data DIVA, EUFORGEN, EEA

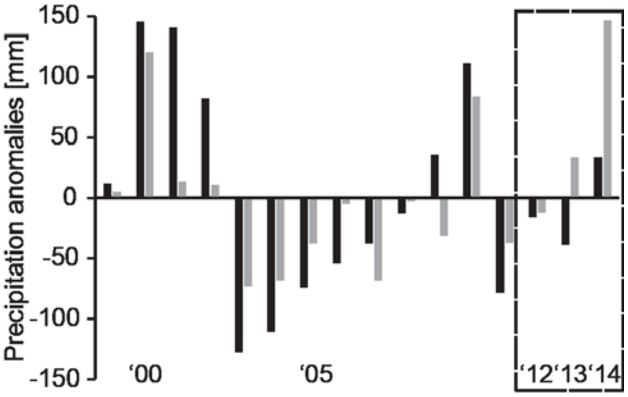

Figure 2. Precipitation anomalies recorded at the Geisenheim climate station from 1999 to 2014 with respect to the 1961-1990 mean. Black bars refer to the whole year and grey bars to the vegetation period from April to October. The dashed box highlights the period covered by the dendrometer analysis

Data analysis

The raw dendrometer measurements were quality checked, and data gaps and odd values (from animal bites etc.) removed. Raw measurements were plotted against time and annually resolved growth patterns analyzed considering abrupt stem radii changes. The diurnal stem cycle was identified considering variables outlined in King et al. (2013). For each metric, the deviation from the daily mean was calculated. The most negative and most positive deviations indicate the daily stem radius minimum and maximum, R_{min} and R_{max}. T_{max} and T_{min} represent the times when R_{min} and R_{max} occurred, and ÄR is the amplitude from R_{min} to R_{max}. To explore monthly characteristics, the hourly deviations from the daily mean were averaged to a monthly mean circadian cycle (King et al. 2013). Hourly deviations from the daily mean were combined to a single time series to evaluate the influence of different climatic parameters along the seasonal course. Using the meteorological data for each month of the vegetation period, four to seven classes of mean daily temperature, relative humidity, precipitation sum, and cloud cover were established. These observations were then used to assign the daily stem cycles to diurnal meteorological patterns representing characteristic daily cycles (King et al. 2013). The classes were defined based on previous results on the coherence of diurnal stem size and climate variations (Downes et al. 1999, Deslauriers et al. 2003). Pearson correlations were calculated between ÄR of every single day and related climate parameters, and significance estimated at $p < 0.05$ (Bortz and Döring 2006).

Table 1. Study area and site characteristics

Site	Hallgarter Zange	50.06 N, 8.01 E
	Elevation	583 m a.s.l.
	Soil Type	Stagnosol, Cambisol
	Bedrock	Sandstone, Siltstone, Quartzite, Argillaceous Slate
	Vegetation	Spruce, oak, beech-birch mixed forest
	Slope	<5%
Climate	Station Geisenheim	49.99 N, 7.95 E
	Elevation	110 m a.s.l.
	Temperature (1961-1990)	9.8 °C
	Precipitation	547 mm

Results

Stem radius increment

Radial stem changes are characterized by a staircase-shaped pattern at annual time scales. A distinct increment from April to August is followed by a period of slowed growth until October (Figure 3). In the remaining months, no substantial changes are detected. Whereas in each year 2012-2014, growth onset and growth cessation occurred roughly at the same date, in the calendar weeks 15 and 16 in April and 33 and 34 in August, the absolute increments differ substantially ranging from 1 to 4 mm among the trees and years. These inter-annual changes are superimposed by highly variable diurnal fluctuations. The latter are characterized by wave-like variations on dry days (Figure 3b), in contrast to the smoothed increment on rainy days (Figure 3c).

Daily stem radius changes

The monthly ΔR data reveal a characteristic seasonal pattern (Figure 4). During winter (Nov-Feb), ΔR is smaller than 10 µm and growth peaks seem to occur randomly. From May to August ΔR increases, followed by a decrease in September and October. Only the large ΔR values in April interrupt this otherwise gradual seasonal course. Apart from June and a few minor exceptions, a temporal synchronicity of R_{min} and R_{max} is visible. R_{max} is recorded in the morning between 07:00 and 09:00 and R_{min} in the afternoon between 16:00 and 18:00. The daily cycle gradually changes throughout the growing season so that in June R_{min} is recorded towards the beginning of the day and R_{max} shifts towards the end.

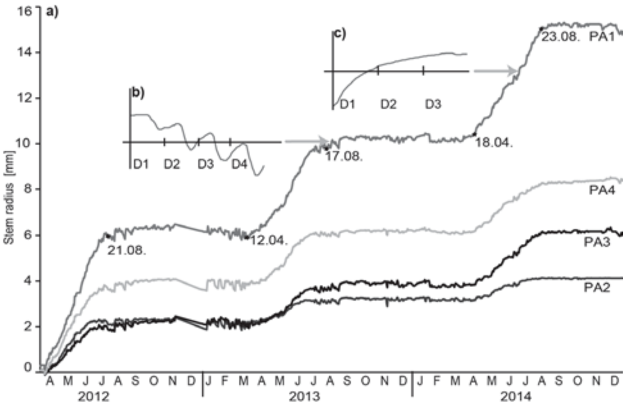

Figure 3: Hourly stem radius changes: **(a)** from April 2012 until December 2014 for each tree PA1 to PA4; **(b)** from August 27, 2013 to August 30, 2013 for PA1 over a period without rainfall, and **(c)** from July 08, 2014 to July 10, 2014 for PA1 over a rainy period. Stars refer to calendar week (CW) of abrupt stem radius changes

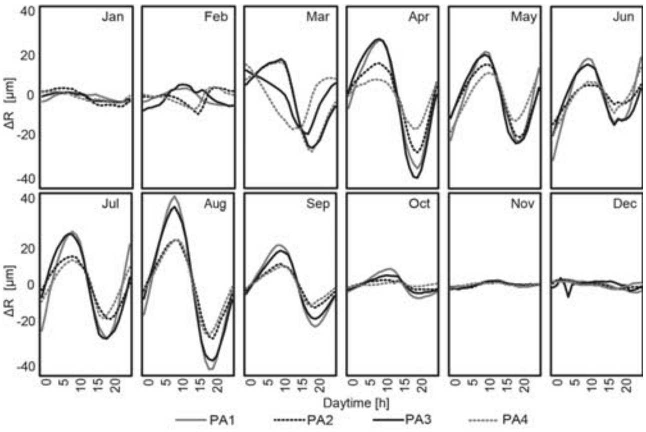

Figure 4. Monthly mean circadian cycle for each tree. Data include averaged hourly values from April 20, 2012 to December 31, 2014. ΔR represents the deviation from the mean stem radius

Considering the classification of diurnal stem and meteorological cycles emphasizes the influence of climatic parameters on ΔR (Figure 5). Pronounced ΔR increases are found in response to temperature with the highest sensitivity recorded in July when the temperatures exceed 25 °C. Here ΔR is most variable and the pattern differs substantially from cooler days. Almost no difference in diurnal growth patterns occurs in June, i.e. the profiles are similar during cold and warm days. When the temperature drops below 0 °C, however, a reversal of the diurnal growth pattern, with R_{min} in the early morning and R_{max} in the afternoon, is recorded. Additionally, ΔR is relatively large with radial changes exceeding 80 µm.

ΔR is also inversely related to precipitation, cloud cover, and relative humidity (Figure 5b-d). As precipitation (>5 mm) correlates with humidity and cloud cover, the diurnal growth cycles associated with these climate elements are similar. During wet days (>10 mm), the wave-like diurnal increments change into a monotonic increase, thereby triggering a temporal shift of R_{min} and R_{max}. A reduced cloud cover coheres with increased ΔR, and an inversion of the diurnal cycle is observed during clear sky days in October.

Changes in temperature and relative humidity alter the magnitude of ΔR, whereas changes in precipitation cause a temporal shift of R_{max} and R_{min}. The influence of cloud cover is overall difficult to assess due to the seasonally varying superimposition by other climate variables. Pearson correlations between ΔR and the seasonal (April-September) climate variable confirm the findings. Significant negative correlations are found for relative humidity (r= -0.34 to -0.72, $p < 0.05$) and significant positive correlations are recorded for temperature (r= 0.32 to 0.50, $p < 0.05$), except for the months of June and July. For precipitation, only a weak but still significant correlation was found ($r < 0.2, p < 0.05$).

Stem radius response to periods without rain

The longest rainless period lasted 18 days (Figure 6a). Despite this persistent drought ΔR and stem radius continuously increase over 15 days. Only in the last 2 days, ΔR starts stagnating and stem radius decreases. However, this pattern is not consistent over different periods without rain. A rain-free period lasting 3 days (Figure 3b) is characterized by a stem radius decrease and ΔR increase. The analysis of all days without rain after a single precipitation event revealed a clear pattern, the longer the period after a precipitation event, the greater the daily ΔR amplitude. For the first two days after a precipitation event, ΔR reaches 41 µm, while for the ninth and tenth subsequent days ΔR equals 72 µm. (Figure 6b).

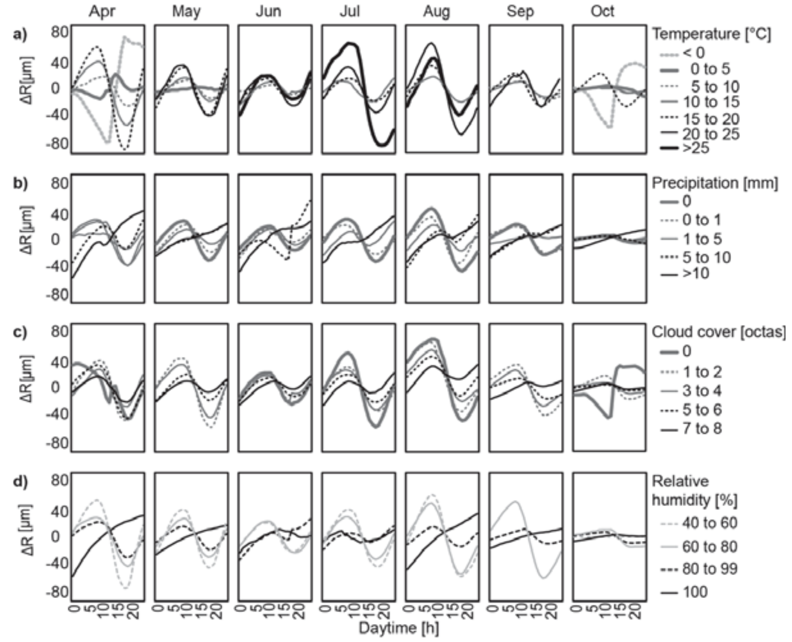

Figure 5. Classification of daily stem radius changes according to prevailing: **(a)** temperatures, **(b)** precipitation, **(c)** cloud cover, and **(d)** relative humidity of the respective day. For temperature and precipitation classification, we used data from the station at the Hallgarter Zange. Cloud cover data were derived from the DWD station in Geisenheim

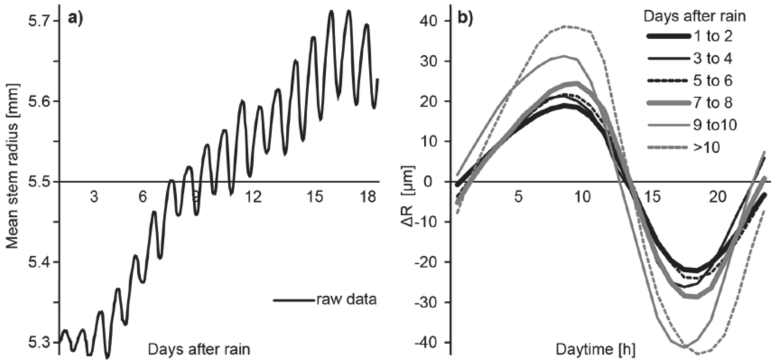

Figure 6. Precipitation sensitivity of *Picea abies*. **(a)** Overall radius changes in the longest consecutive period without rain from July 5 to July 22, 2013. **(b)** Mean circadian cycles classified according to time to the last rain event

Discussion

Seasonal and daily stem radius changes

Our high resolution dendrometer records allow an evaluation of growth reactions (Irvine and Grace 1997) and daily stem radius fluctuations in response to water movement (Deslauriers et al. 2007, Turcotte et al. 2009). After an absence of stem changes during winter, related to the tree dormancy (Perry 1971), a strong increase of stem radii in April marks the onset of growth and re-hydration, responses that are both captured as a displacement of the bark (Tardif et al. 2001, Gruber et al. 2009). During the period of strong stem increment (Figure 3a), the cambium starts producing the plant's xylem and phloem (Schweingruber 1983). Thin-walled early wood cells with a larger lumen are formed and, due to the water uptake and biomass production, radii expand rapidly (Plomion et al. 2001). The slowed growth-rate in August (Figure 3a) marks the transition to latewood production (Rossi et al. 2006). At this time, stem radii increase only marginally because, inside the enlarged cells, thick walls with high lignin content are formed for stabilization purpose (Cherubini et al. 2004, Gruber et al. 2010). Growth onset occurs when air temperature, measured at the study site, exceeds 5 °C underscoring the significance of temperature control on cambial activity (Vaganov et al. 1999, Rossi et al. 2007). The timing of growth onset when monthly mean temperatures reaches the 5 °C threshold is in line with findings by Rossi et al. (2007), introducing an average minimum temperature for xylogenesis of 4-5 °C. Additionally, the photoperiod causes growth synchronization (Smith 2000). Temperature allows metabolic activities to be maintained during cell development while photoperiod acts as a signal regulating the growth rate in accordance with the seasonal course (Rossi et al. 2006).

As shown previously (Kozlowski and Winget 1964, Devine et al. 2011), daily shrinkage and swelling procedures vary seasonally. The mechanisms controlling these processes persist throughout the growing season, but are absent during winter dormancy. The warm season fluctuations comprise daytime stem shrinkage and nocturnal stem swelling (Irvine and Grace 1997, Offenthaler et al. 2001) in the elastic phloem (Zweifel et al. 2000) resulting from a radial transfer of water between phloem and xylem (Pfautsch et al. 2015). For photosynthesis and gas exchange, plants open the stomata and simultaneously lose water vapour through transpiration (Hetherington et al. 2003). Transpiration water loss at the leaf level is subsequently aspirated through the stem, causing stem shrinkage (Zweifel 1999). During night, when stomata are closed, transpiration ceases and water reserves replenish leading to the swelling of the stem (Steppe et al. 2006). R_{max} occurs when the internal stem water reserves are refilled, and R_{min} occurs at maximum depletion (Zweifel and Häsler 2001).

Climatic response

It is well known that temperature controls atmospheric water vapor saturation indicating that these two variables cannot be treated independently. Transpiration increases with increasing temperature, causing greater stem water depletion and increased ΔR (Will et al. 2013). Stem ΔR variations thus represent a hygroscopic response to air humidity changes (Lövdahl and Odin 1992). Regarding the seasonal course, the highest ΔR was found in August, although peak values were reported for July in an Alpine or Mediterranean environment (Vieira et al. 2013, King et al. 2013). Tardif et al. (2001) showed that a small amplitude between day and night temperatures narrows stem radius changes, which typically occurs in July in the Taunus region.

High ΔR values during April are also affected by a reduced number of data points. The data from January to mid-April comprise only two years, so that their variance is increased compared to the remaining months integrating three years of data. Frost shrinkage and thaw expansion cause a reversal of T_{max} and T_{min} at temperatures below 0 °C. During night, xylem water freezes and is no longer available. The osmotic concentration in the tissue increases relative to the liquid remaining in the bark, so that water moves from the bark into the xylem. During the day, the temperatures increase and thawing reverses the processes (Zweifel and Häsler 2000). Zweifel et al. (2000) concluded that the amplitude during a severe frost phase is 5-10 times larger than during the active phase in summer. King et al. (2013) reported the opposite, however, reaching R_{max} = 131 µm in April and R_{min} = 80 µm in October.

The temporal shift of R_{min} and R_{max} in June in the Taunus spruce data seems to be related to changing precipitation amounts controlling ΔR (Chan et al. 2016). On days without precipitation the pattern might represent typical shrinkage and swelling processes due to transpiration changes, but during days with higher amounts of precipitation the pattern reflects the amount of absorbed rainwater used for refilling internal water storages (Turcotte et al. 2011). The impact of cloud clover is superimposed by variables controlling seasonality, e.g. the temperature inversion on sunny days in October. If the opposite had been the case, all monthly ΔR values within a class would show roughly the same amplitude. King et al. (2013) applied the same methodological approach in the European Alps and discovered similar findings for precipitation, but a better coherence between ΔR and temperature. These differences likely result from the colder conditions in the elevated Alpine sites (Neuwirth et al. 2004). Additionally, King et al. (2013) observed overall greater diurnal amplitudes and less variance among sampling sites. The reduced variance is likely also related to the larger number of trees and consideration of different species, however. Overall, a distinct attribution of stem radius changes remains challenging due to cross-correlation among tested climatic factors (Oberhuber et al. 2010).

Drought exposure of Picea abies

An extended rainless period results in a more negative atmospheric water potential and amplified transpiration. We found increased ΔR values indicating stomata were open permanently during daytime during such periods (Arve et al. 2011). Due to soil water saturation, the diurnal uptake of water keeps up with transpiration (Vieira et al. 2013). The breakdown of gas exchange prevents water loss, drought-induced hydraulic failure and xylem cavitation (Hartl-Meier et al. 2015, Arve et al. 2011, Raven 2002). As a result, stem radii decrease as water replenishment ceases due to potentially empty soil water reservoirs (Lassoi et al. 1979). In our study, the last two days of the longest dry period (18 days) indicate the starting point of such a drought stress (Chaves et al. 2002). However, soil conditions are rather moist at this site (Stagnosol) likely compensating potentially earlier drought effects and ensuring water supply over at least two weeks (Turcotte et al. 2011, Zech et al. 2014). This finding is conflicting with previous work revealing decreasing ÄR values with increasing drought persistence (King et al. 2013). The conclusions drawn here are, however, preliminary as the three years studied here do not included a rainless period exceeding 18 days (Figure 2). As only in the last two days of the longest rainless period revealed a stem radius stagnation, the trees' response to water scarcity has to be tested in further analyses.

Conclusions

Using high-resolution dendrometer data, distinct control of temperature on the onset and cessation of wood formation is shown for *P. abies* beyond its distribution range in Germany. Daily stem radius changes are related to water movement resulting from altering water potentials in the atmosphere. The diurnal stem cycle is primarily influenced by temperature and relative humidity affecting the amplitude of daily radius changes (ΔR). Precipitation effects act superimposing on the diurnal cycle by temporally shifting R_{max} and R_{min}. With respect to precipitation sensitivity, we found indications of drought-induced stress only after 16 days without rain, i.e. *P. abies* at this site does not suffer from a lack of rainfall for two weeks. Great soil water capacity likely diminishes an otherwise perhaps stronger sensitivity in stands on poorer soils. Since no rainless period exceeding 18 days occurred during the 2012-2014 study period, further work including more persistent drought periods might improve our understanding of the trees' response to water shortage in the Taunus region.

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