

Research paper

Environmental control of daily stem growth patterns in five temperate broad-leaved tree species

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Tree ring analysis investigates growth processes at time horizons of several weeks to millennia, but lacks the detail of shortterm fluctuation in cambial activity. This study used electronic high-precision dendrometry for analyzing the environmental factors controlling stem diameter variation and radial growth in daily resolution in five co-existing temperate broad-leaved tree species (genera Fraxinus, Acer, Carpinus, Tilia and Fagus) with different growth and survival strategies. Daily stem radius change (SRC_d) was primarily influenced by the atmospheric demand for water vapor (expressed either as vapor pressure deficit (D) or relative air humidity (RH)) while rainfall, soil matrix potential, temperature and radiation were only secondary factors. SRC_d increased linearly with increasing RH and decreasing D in all species. The positive effect of a low atmospheric water vapor demand on SRC_d was largest in June during the period of maximal radial growth rate and persisted when observation windows of 7 or 21 days instead of 1 day were used. We found a high synchronicity in the day-to-day growth rate fluctuation among the species with increment peaks corresponding to air humidity maxima, even though the mean daily radial growth rate differed fivefold among the species. The five species also differed in the positive slope of the growth/RH relationship with the steepest increase found in Fraxinus and the lowest in Fagus. We explain the strong positive effect of high RH and low D on radial stem increment by lowered transpiration which reduces negative pressure in the conducting system and increases turgor in the stem cambium cells, thereby favoring cell division and expansion. The results suggest that mechanistic models of tree growth need to consider the atmospheric water status in addition to the known controlling environmental factors: temperature, soil moisture and precipitation. The results further have implications for sensitivity analyses of tree growth to climatic changes.

Keywords: air humidity, *Fagus sylvatica*, *Fraxinus excelsior*, point dendrometers, radial stem growth, seasonality of growth, soil moisture, stem water status, water vapor pressure deficit.

Introduction

Radial stem growth in woody plants is controlled on the physiological level by the turgor pressure in the cambial cells, the amount of carbohydrates supplied to the stem cambium and its differentiating derivatives, and the duration of cambial activity (Deslauriers and Morin 2005, Rossi et al. 2006, Lambers et al. 2008). Short-term and seasonal variation in diameter growth is largely caused by fluctuations in the water status of the cambial meristems and hormonal control (Kozlowski and Pallardy 1997). For decades, tree ring analysis has been the principal tool for analyzing inter-annual and intra-annual variation in stem diameter growth of trees, and for relating it to climatic, biotic, age-related and management factors (Cook and Kairiūkštis 1990, Hughes et al. 2011). While the two underlying processes of radial growth, cambial cell division and cell expansion, proceed at timescales of hours to a few days, dendrochronological analysis investigates growth processes at a time horizon of several weeks to millennia depending on the

growth-ring structure, seasonality of cambial activity and tree longevity, leaving in many species a gap in the causal chain between growth at the cellular level and observed diameter increment as manifested in the width of annual growth rings. This has the consequence that climatic variables identified as growth-controlling factors in dendrochronological analysis are not necessarily those factors that determine instantaneous rates of cambial activity. In fact, in temperate regions, interannual differences in the timing of summer rainfall or in summer temperature can markedly alter the seasonal dynamics of cambial activity while annual ring width may remain unchanged (Archambault and Bergeron 1992, Hofgaard et al. 1999). The temporal variation in stem radial growth has been studied in depth in tracheid-based wood, especially conifers, using densitometry and wood anatomical studies (Schweingruber 1996), and by radioactive marking in various types of growth-ringforming evergreen trees (Liphschitz and Lev-Yadun 1986), but in much less detail in broad-leaved trees.

In most temperate forests examined by dendrochronological analysis, climate sensitivity analysis has identified summer rainfall in the recent or in the preceding year as a prominent factor, if not the most important, which explains variation in radial growth rate (Hofgaard et al. 1999, Tardif et al. 2001*a*, Čufar et al. 2008). Soil moisture, temperature and forest management activities (e.g., thinning) have also been found to be influential in many stands (Aussenac and Granier 1988, Archambault and Bergeron 1992, D'Arrigo et al. 1992, Schweingruber et al. 1993, Bréda et al. 1995, Tardif et al. 2001*a*). However, due to their coarse-grained temporal resolution, it remains questionable as to whether tree ring data are qualified to draw conclusions on climatic drivers of instantaneous cambial growth activity.

To study wood formation and radial growth processes at a resolution of days to weeks, several methods have been applied. The production of new cell layers in the xylem can be recorded at weekly time intervals by extracting micro-cores or by pinning (e.g., Mäkinen et al. 2008). Mechanical and electronic high-resolution dendrometers allow for the continuous recording of diurnal stem diameter fluctuations, i.e., at temporal and spatial scales relevant for cambial cell division and expansion (e.g., Kozlowski and Winget 1964, Braekke et al. 1978, Beedlow et al. 1986, Simonneau et al. 1993, Downes et al. 1999, Drew and Downes 2009). Thus, these techniques allow us to study environmental factors directly or indirectly influencing instantaneous rates of cambial growth, instead of integrating over several seasonal growth phases as is done in the analysis of annual tree rings.

A shortcoming of recording dendrometers with respect to growth detection is that, in addition to irreversible growth processes, reversible stem shrinkage (day) and swelling (night) are also contributing to diameter fluctuations (Deslauriers et al. 2007*b*) which requires adapted techniques to extract the growth signal from diurnal diameter fluctuation. The problem of separating reversible and irreversible components of stem diameter variation has been addressed in various studies, and a number of procedures applicable to tree growth records under a variety of climatic conditions have been proposed (Braekke et al. 1978, Herzog et al. 1995, Downes et al. 1999, Tardif et al. 2001b, Wimmer et al. 2002, Deslauriers et al. 2003, Bouriaud et al. 2005, Zweifel et al. 2005). However, this approach has only rarely been used to address the question whether the growth-controlling environmental factors differ between tree species with different phylogeny, morphology and physiology.

This study uses electronic point dendrometers (resolution < 10 μ m, recording interval 30 min) to analyse the influence of rainfall, soil moisture, air humidity, atmospheric vapor pressure deficit, air temperature and global radiation on stem radius changes in five co-occurring temperate broad-leaved tree species. We compared the growth dynamics of five widespread European species of the genera Acer, Fagus, Fraxinus, Carpinus and Tilia in an old-growth mixed forest, species that differ with respect to drought sensitivity (insensitive to moderately sensitive), xylem anatomy (diffuse- vs. ring-porous) and successional status (early/mid- to late-successional). The specific objectives of this study were (i) to test the environmental factors rainfall, soil moisture, air humidity, vapor pressure deficit, air temperature and global radiation in their effect on stem radius changes, and (ii) to compare mean radial growth and seasonal growth dynamics among the five species.

Materials and methods

Study site and tree species

The study was conducted in a species-rich temperate deciduous forest in Hainich National Park (7610 ha) in western Thuringia, Central Germany (51°04'N, 10°30'E). The national park is part of the Hainich plateau range (16,000 ha) which encompasses one of the largest non-fragmented broad-leaved forests in Central Europe. The study site is located in the northeastern part of the national park in the Thiemsburg region. The mean annual precipitation of this site is 590 mm and the mean annual temperature is 7.5 °C (1973-2004, Deutscher Wetterdienst, Offenbach, Germany). Luvisol is the dominant soil type which developed from loess that is underlain by Triassic limestone (Guckland et al. 2009). Soils can dry strongly in summer and show stagnant properties during spring and winter. Mean tree height varies between 27.9 m in the denser part of the forest (614 stems ha-1) to 32.9 m in the less dense forest area (392 stems ha⁻¹) (Gebauer et al. 2008). The average stand age of the canopy trees ranges between 90 and 120 years (Schmidt et al. 2009).

Five abundant broad-leaved tree species from different families were selected for study. From May to September

Species	Number of trees	DBH (cm)	Tree height (m)	Mean bark thickness (mm)	Mean SRC _d (μm day ⁻¹)		
A. pseudoplatanus	5	38.3–76.1	26.8–33.7	8.52 ± 1.71 a	22.6±26.8 a		
F. sylvatica	6	40.8-61.0	28.2–33.1	5.78 ± 1.42 bc	22.4 ± 18.6 a		
F. excelsior	5	24.3-41.2	23.0–28.1	7.56 ± 2.26 ac	56.8 ± 48.2 b		
C. betulus	5	35.2–59.9	24.7–29.2	5.20 ± 1.84 b	13.1 ± 24.1 a		
T. cordata	4	41.3-62.9	24.3-31.7	14.18 ± 3.61 d	8.5 ± 26.8 a		

Table 1. Number of measured tree individuals per species, range of diameter at breast height (DBH) and tree height and mean values (± 1 SD) of bark thickness and daily stem radius change (SRC_d) in June in the five tree species. Significant differences between the species are indicated by different lowercase letters.

2009, stem radius variation was monitored with high precision on four to six individuals of sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), European hornbeam (*Carpinus betulus* L.) and little-leaf linden (*Tilia cordata* Mill.). All 25 selected trees were mature dominant individuals reaching the upper canopy (23.0–33.7 m in height, see Table 1) and located within a maximum distance of 100 m of each other.

Microclimatological and hydrological measurements

Air temperature and relative air humidity were recorded in the upper canopy of the stand with a Rotronic temperature and humidity probe (MP100A Hygromer, Rotronic, Ettlingen, Germany). Measurements were taken every 30 s and stored as half-hourly means with a Campbell CR1000 data-logger (Campbell Scientific Ltd, Cambridge, UK). These data were used to generate instantaneous values of vapor pressure deficit (*D*, hPa).

Volumetric soil water content (Θ , m³ m⁻³) was measured with time-domain reflectometry probes (CS616 Water Content Reflectometer, Campbell Scientific Ltd) installed at three different depths (10, 30 and 50 cm) in close proximity to the studied trees. Data were logged two times a day (00:00 and 12:00 h). The soil water content data at 10 cm depth were used to calculate soil matrix potential (Ψ_s) using the program Rosetta Lite Version 1.0 (Groundwater Software, Groton, MA, USA) (Schaap et al. 1998). The required soil physical parameters (e.g., clay content, bulk density) were provided by Guckland et al. (2009). Hourly values of precipitation and global radiation were obtained from the nearby (2 km) Weberstedt/Hainich meteorological station (Meteomedia GmbH, Bochum, Germany) for the whole year 2009.

Diurnal measurements refer to solar time which is 80 min behind Central European Summer Time (CEST).

Measurement of stem radial growth

We used spring-loaded linear displacement potentiometers (model MMR 10_11 R5K, MEGATRON Elektronik AG & Co., Munich, Germany) with an accuracy of <10 μ m to measure diurnal radius variation and stem radial growth. The point dendrometers were mounted on stainless-steel frames which were fixed



Figure 1. Typical diurnal cycle of stem radius variation over three exemplary days in 2009. SRC_d is calculated as the difference between two consecutive stem radius maxima. MXSR, maximum stem radius; MNSR, minimum stem radius; SRS, stem radius shrinkage; SRE, stem radius expansion; SRC_d , stem radius change (increase or decrease) per day.

to the stem with two screws each placed at least 6 cm distant to the measuring point. The screws were anchored at least 5 cm deep into the xylem as recommended by Herzog et al. (1995) and Gall et al. (2002). The tips of the dendrometers were placed directly in contact with the bark which was smoothed before. The dendrometers were mounted at 1.3 m height and were covered with aluminum foil to protect them from direct solar radiation and avoid contact with liquid water. Radial change values were recorded every 30 min by averaging over 60 30-s readings using a CR1000 data-logger (Campbell Scientific Ltd).

Data analysis

Daily stem radius increment (SRI) was calculated after Downes et al. (1999) and Deslauriers et al. (2003). These authors defined three distinct phases of stem radius variation over a 24-h-period (Figure 1). The first phase is characterized by shrinkage of the stem radius from a maximum registered during early morning to a daily minimum occurring after midday. During the second phase, the stem radius expands to a new maximum. According to Deslauriers et al. (2003), the expansion phase also includes the third phase (SRI). This phase is associated with the difference between the maximum stem radii of two subsequent days (Figure 1). Negative values of SRI due to a smaller radius maximum on the following day were included in the analysis and not treated as missing values or set to zero as was done by other authors. Therefore, we prefer to use the neutral term 'daily stem radius change' (SRC_d) instead of 'daily stem radius increment' (SRI).

Alternatively, SRC was calculated as the running mean of daily stem radius change (SRC_d) for time windows of 7 days (SRC_7) and 21 days (SRC_{21}) that were moved along the time

axis (Figure 2f and g) in order to obtain estimates of stem diameter growth with negligible bias by putative stem shrinking and swelling effects, an effect that cannot be excluded for the SRC_d data. That the SRC_7 and SRC_{21} data mainly reflect diameter growth is suggested by the fact that negative SRC values occurred occasionally in the SRC_d time series, but were mostly absent in the SRC_7 series (exception: *T. cordata*) and did not occur at all in the SRC_{21} data set. The SRC running



Figure 2. (a) Seasonal course of mean daily relative air humidity (RH_{mean}) and daily totals of global radiation (l_{tot}), (b) daily mean air temperature (T_{mean}) and daily mean vapor pressure deficit (D_{mean}), (c) soil water content (Θ) at three soil depths (10, 30 and 50 cm) and daily precipitation (P) and (d) soil matrix potential (Ψ_{S}) at 10 cm soil depth in summer 2009 in the Hainich forest. (e) Seasonal development of mean radial stem increment (cumulative SRC_d) for the five tree species in summer 2009 (n = 4-6 individuals each). (f and g) Stem radius change (SRC) of the five investigated species during summer 2009 calculated as the running mean of daily stem radius change (SRC_d) for time windows of (f) 21 days (SRC₂₁) or (g) 7 days (SRC₇) that were moved along the time axis. The running means were calculated for the respective mid-point of each window position (i.e., days 4 and 11 of the windows for SRC₇ and SRC₂₁, respectively).

means were calculated for the respective mid-point of each window position (i.e., days 4 and 11 for SRC_7 and SRC_{21} , respectively).

Statistical analyses were conducted with SAS software, version 9.1 (SAS Institute Inc., Cary, NC, USA). For analyzing the relationship between SRC_d, SRC₇ and SRC₂₁, and various environmental factors, single-factor correlation analyses were calculated with daily precipitation (P), daily totals of global radiation (I_{tot}), daily mean relative humidity (RH_{mean}), daily mean vapor pressure deficit (D_{mean}), soil matrix potential (Ψ_{S}) at 10 cm depth and daily mean air temperature (T_{mean}) as variables. In the case of SRC_7 and SRC_{21} , these variables were also calculated as running means for time windows of 7 or 21 days before their inclusion in the correlation analysis. Subsequently, partial correlation analyses were conducted in order to explore the degree of correlation between SRC_d and environmental variables once the effect of other potentially controlling variables was removed (Table 5). The partial correlation analyses were preceded by a principal components analysis (PCA) which helped to identify the most important environmental variables controlling SRC_d and their inter-relationships (Table 3). In addition, all considered environmental variables were arranged in a correlation matrix (Table 4) and tested for lag effects with cross-correlation analysis.

Results

Microclimatic conditions and soil moisture status

The year 2009 was relatively warm and wet in the study area. Mean annual air temperature in 2009 (8.9 °C) exceeded the long-term mean (7.5 °C). The daily means of air temperature (T_{mean}) during the study period (1 May to 30 September 2009) varied between 7.8 and 23.7 °C (Figure 2b). The vapor pressure deficit (*D*) measured in canopy height (c. 30 m) reached its seasonal maximum in August (highest daily mean: 15 hPa, Figure 2b); the mean daily relative air humidity (RH_{mean}) varied in summer 2009 between 60 and 100% (Figure 2a). The daily totals of global radiation (I_{tot}) reached highest values in June and July with up to 30 MJ m⁻² day⁻¹.

The annual precipitation in 2009 was higher (774 mm) than the long-term average (590 mm). Similarly, June, July and September received more rain than the average of these months (Figure 2c).

The volumetric soil water content (Θ) showed a rather smooth time course over the vegetation period, in particular at soil depths of 30 and 50 cm. Rainfall events resulted in marked increases in Θ only when daily precipitation exceeded 20 mm (Figure 2c). Longer periods of soil drought did not occur in summer 2009. The soil matrix potential (Ψ_s) at 10 cm depth remained continuously above -0.06 MPa until July and passed -0.1 MPa only in August and early September (Figure 2d). A soil matrix potential

of -0.1 MPa was identified by Köcher et al. (2009) as a threshold for continuous declines in leaf water potential and sap flux density to occur in the trees of this site.

Stem radius change in relation to environmental factors

The daily change in stem radius (expressed by the SRC_d, SRC₇ or SRC₂₁ values) was analysed in its relation to six microclimatological and soil hydrological parameters (rainfall, solar radiation, air temperature, water vapor pressure deficit, relative air humidity and soil matrix potential in 10 cm depth) with singlefactor correlation analyses (period: 15 May to 15 July 2009). In all five species, SRC_d showed the closest correlation to daily mean relative air humidity (RH_{mean}, positive relation) and mean vapor pressure deficit (D_{mean} , negative) (Table 2). Less tight relations were found to daily radiation totals and daily precipitation. In contrast, the influence of soil matrix potential was significant only in Fagus, while air temperature was not related to SRC in any of the species when analysed on a daily basis (SRC_d). As expected, the importance of the influencing environmental factors changed when the SRC7 and SRC21 values instead of SRC_d were considered (Table 2). The dominant and strong positive influence of air humidity on radius change persisted in three of the five species when the longer integration periods of 7 and 21 days were analysed. In case of Fraxinus, the significance of all influential factors on diameter change decreased with an increase in period length, while Fagus showed an increasing importance of daily mean temperature and also of soil matrix potential when the perspective shifted from 1 to 7 or 21 days.

The partial correlation analysis focused on SRC_d and its relationship to either RH_{mean} or D_{mean} (Table 5) because these two variables showed the closest relation to SRC_d (Table 2), but themselves are partially dependent on other environmental variables such as rainfall, solar radiation and air temperature. This web of relationships is evidenced by the high loadings of nearly all environmental variables (except soil matrix potential) on the first PCA axis (Table 3), and the correlative relationships between several of the variables shown in Table 4. According to the partial correlation analysis, the strength of the SRC_d-RH_{mean} relationship was in all tree species slightly reduced when controlling for precipitation and global radiation, whereas temperature and soil matrix potential had almost no effect (Table 5). The degree of correlation decreased greatly only when D_{mean} was included as a partial variable. Similar patterns were observed for the $SRC_d - D_{mean}$ relationship; this correlation became insignificant in all tree species when we included RH_{mean} as partial variable.

Cross-correlation analysis, conducted for identifying possible time shifts in the effect of precipitation, radiation and temperature on relative air humidity and vapor pressure deficit, did not reveal hidden lag effects among these variables. The obtained correlation coefficients were always highest in the

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Table 2. Pearson correlation coefficients (*R*) for the relationships between daily stem radius change as calculated by three different approaches and six climatological and hydrological factors in the five species (period: 15 May to 15 July 2009). The environmental variables were also calculated as running means in the case of SRC_{7} and SRC_{21} .

Species		Р	/ _{tot}	$T_{\rm mean}$	$D_{\rm mean}$	RH_{mean}	$\Psi_{\rm S}$
A. pseudoplatanus	SRC _d	0.30*	- 0.40**	-0.15	- 0.57***	0.61***	0.07
F. sylvatica	SRC _d	0.27*	- 0.40 **	0.13	- 0.53 ***	0.68***	- 0.30*
F. excelsior	SRCd	0.30*	- 0.38 **	-0.08	- 0.53 ***	0.60***	0.05
C. betulus	SRCd	0.29*	- 0.43 ***	-0.03	- 0.59***	0.70**	-0.15
T. cordata	SRC _d	0.35**	- 0.45 ***	-0.06	- 0.60***	0.71***	-0.10
	-	P_7	l _{tot7}	$T_{\rm mean7}$	D_{mean7}	RH_{mean7}	Ψ_{s7}
A. pseudoplatanus	SRC ₇	0.01	- 0.54***	-0.16	- 0.56***	0.51***	0.27*
F. sylvatica	SRC ₇	0.14	- 0.26	0.60***	- 0.17	0.71***	- 0.63***
F. excelsior	SRC ₇	0.09	- 0.35 **	-0.04	- 0.34 **	0.35**	0.11
C. betulus	SRC ₇	0.27*	- 0.50***	0.33*	- 0.44 ***	0.84***	- 0.51***
T. cordata	SRC ₇	0.50***	- 0.59 ***	0.13	- 0.60***	0.90***	- 0.42 **
		P ₂₁	I _{tot21}	$T_{\rm mean21}$	D _{mean21}	RH_{mean21}	$\Psi_{s_{21}}$
A. pseudoplatanus	SRC ₂₁	0.43**	- 0.63***	0.17	- 0.61***	0.67**	0.10
F. sylvatica	SRC ₂₁	0.29	- 0.36 *	0.90***	- 0.03	0.88**	- 0.75***
F. excelsior	SRC ₂₁	-0.14	0.16	0.29	0.20	0.09	-0.24
C. betulus	SRC ₂₁	0.32*	- 0.47 **	0.83***	- 0.15	0.93***	- 0.72***
T. cordata	SRC ₂₁	0.51***	- 0.64***	0.67***	- 0.39**	0.97***	- 0.57***

 SRC_d , difference between the radius maxima of two consecutive days; SRC_7 , apparent daily increment as calculated by a 7-day-running mean of SRC; SRC_{21} , apparent daily increment as calculated by a 21-day-running mean of SRC; P, precipitation; I_{tot} , radiation; T_{mean} , air temperature; D_{mean} , vapor pressure deficit; RH_{mean} , relative air humidity; Ψ_S , soil matrix potential.

Significant correlations are in bold.

Significance levels: $*P \le 0.05$; $**P \le 0.01$; $***P \le 0.001$.

Table 3. Differentiation of the six environmental factors and daily stem radius change (SRC_d) in the data set of the five species according to a PCA. Given are the loadings of the selected variables along the four most important axes. The eigenvalues of the axes are indicated by the numbers in brackets. Numbers in bold indicate a close relationship of that variable to the respective axis.

Variables	Axis 1 (0.506)	Axis 2 (0.175)	Axis 3 (0.118)	Axis 4 (0.105)
SRC _d	0.572	0.236	0.646	-0.350
Ρ	0.602	-0.008	0.191	0.756
l _{tot}	- 0.812	- 0.307	0.305	0.066
T _{mean}	- 0.632	0.510	0.401	0.147
$D_{\rm mean}$	- 0.962	0.058	0.113	0.109
RH_{mean}	0.915	0.170	0.074	0.002
Ψs	0.178	- 0.886	0.317	-0.031

Table 4. Table of Pearson correlation coefficients for the interrelationship between six climatological and hydrological variables used in the analysis of diameter growth–environment relationships (data refer to the period 15 May to 15 July 2009).

	Р	I _{tot}	$T_{\rm mean}$	$D_{\rm mean}$	RH_{mean}	$\Psi_{\rm S}$
Р	1.00	-0.44	-0.32	-0.51	0.53	-0.12
l _{tot}		1.00	0.50	0.84	-0.73	0.07
$T_{\rm mean}$			1.00	0.59	-0.20	-0.20
$D_{\rm mean}$				1.00	-0.89	-0.03
RH_{mean}					1.00	-0.08
Ψs						1.00

P, precipitation; I_{tot} , radiation; T_{mean} , air temperature; D_{mean} , vapor pressure deficit; RH_{mean}, relative air humidity; Ψ_{S} , soil matrix potential.

runs without consideration of time shifts in the relationships between the environmental variables (results not shown). In our data set, past variation in precipitation, radiation and air temperature thus had no significant influence on the actual values of air humidity and vapor pressure deficit.

A deeper analysis of the effect of atmospheric water status on SRC_d focused on air humidity instead of vapor pressure deficit because RH_{mean} had a larger explanatory power. All five species revealed highly significant ($P \le 0.001$) linear positive relationships between RH_{mean} and SRC_{d} in June when maximum growth occurred. However, the species differed with respect to the mean slope of the SRC_d-RH_{mean} relationship (Figure 3). The steepest slope (2.91) was found for Fraxinus with highest increment rates, the lowest (1.18) for Fagus. Despite these differences, all five species showed a highly synchronous day-to-day variation in SRC_d with increment peaks always coinciding with air humidity peaks in the range of 80 to 100% RH and minimum increments, or even radius decreases (daily rates), occurring on days with reduced air humidity (typically <75%, Figure 4: data from June as example). While Acer, Carpinus, Tilia and Fraxinus exhibited negative SRC_d values (i.e., a radius decrease on a daily basis) when the daily RH_{mean} value fell below 75%, negative stem radius changes from day to day were the exception in Fagus (Figures 3 and 4).

The air humidity effect on daily stem radius change showed a distinct seasonality in the growing season in all five species (Figure 5). The RH_{mean} influence was relatively small in May

Table 5. Pearson correlation coefficients (*R*) for the relationship between daily stem radius change (SRC_d) and either RH_{mean} or D_{mean} while controlling for the effect of a third variable (partial correlation). The second column shows the correlation coefficients for single-factor correlations (SRC_d) vs. RH_{mean} or D_{mean}), the following columns display the correlation coefficients for the same relation when the effect of the respective partial variable had been removed.

Species	${\rm SRC}_{\rm d}$ vs. ${\rm RH}_{\rm mean}$	Partial variable					
		P	I _{tot}	T _{mean}	$D_{\rm mean}$	$\Psi_{\rm S}$	
A. pseudoplatanus	0.61***	0.55***	0.51***	0.60***	0.27*	0.62***	
F. sylvatica	0.68***	0.66***	0.62***	0.73***	0.54***	0.69***	
F. excelsior	0.60***	0.54***	0.51***	0.60***	0.31*	0.60***	
C. betulus	0.70***	0.67***	0.63***	0.71***	0.47***	0.70***	
T. cordata	0.71***	0.66***	0.62***	0.71***	0.47***	0.70***	
	SRC _d vs. <i>D</i> _{mean}	Р	l _{tot}	$T_{\rm mean}$	RH_{mean}	Ψ_{s}	
A. pseudoplatanus	-0.57***	-0.50***	-0.47***	-0.60***	-0.08	-0.57***	
F. sylvatica	-0.53***	-0.47***	-0.37**	-0.75***	0.23	-0.56***	
F. excelsior	-0.53***	- 0.47 ***	-0.43***	-0.61***	-0.01	-0.53***	
C. betulus	-0.59***	-0.54***	- 0.47 ***	0.71***	0.09	-0.60***	
T. cordata	-0.60***	-0.53***	- 0.47 ***	-0.70***	0.07	-0.61***	

P, precipitation; I_{tot} , radiation; T_{mean} , air temperature; D_{mean} , vapor pressure deficit; RH_{mean}, relative air humidity; Ψ_{s} , soil matrix potential. Significant correlations are in bold.

Significance levels: $*P \le 0.05$; $**P \le 0.01$; $***P \le 0.001$.



Figure 3. Mean daily stem radius change (SRC_d) as a function of daily means of relative air humidity (RH_{mean}) for the five studied species. Each of the 30 data points marks a day in June 2009 and represents the mean of 4–6 tree individuals. Note different scales of the *y*-axes.

(correlation coefficients of 0.2–0.5) and increased rapidly at the end of May to reach a peak of air humidity sensitivity in June (R = 0.6-0.8). In July, August and September, the RH_{mean} influence decreased continuously in all species.

With a correlation analysis, we investigated the relationship between a species' mean SRC_d in June and its bark thickness (see Table 1). The two parameters were not correlated across the five-species sample (all tree individuals: R = -0.20, P = 0.35; species means: R = -0.29, P = 0.64).

Radial stem increment: temporal fluctuation and seasonal dynamics

The dendrometer readings at 30-min intervals registered not only the diurnal stem radius fluctuations due to wood and bark shrinking and swelling with high accuracy (Figure 1), but also produced reliable data on irreversible stem increment when observation periods of 1-3 weeks (SRC7 and SRC21 data) were considered (Figure 2f and g). Accordingly, the five species differed largely in their cumulative stem radius increment in the growing season 2009 with by far highest increment totals in Fraxinus (~5.8 mm), medium values in Fagus (~2.8 mm) and lowest values in Carpinus (~1.7 mm), Acer (~1.5 mm) and Tilia (~1.2 mm, means of 4-6 individuals). Radial growth rates (SRC7) exceeded maxima of 70 μ m day⁻¹ in *Fraxinus* and reached peak rates of 20–40 μ m day⁻¹ in the other four species (Figure 2g). We calculated diameter increment means during the study period (1 May to 30 September) in the range of 8.5–22.6 µm day⁻¹ for the Fagus, Acer, Tilia and Carpinus trees (species differences not significant), while Fraxinus exhibited a significantly higher mean value (56.8 μ m day⁻¹).

The five co-occurring species differed also with respect to seasonal growth dynamics (SRC₂₁ values) (Figure 2f). *Fraxinus* reached high growth rates already in early May, while the other species increased their radial growth rate in May only gradually. While *Acer* slowed down its diameter growth already at the end of June and terminated it at the end of July, the other four species continued growth until early September (Figure 2e and f).



Figure 4. Fluctuation of mean daily relative air humidity (RH_{mean}) and mean daily stem radius change (SRC_d) of the five species for a 30-day period in mid-summer (June 2009). Mean of 4–6 trees per species.



Figure 5. Seasonal change in the correlation coefficient (R) of the relationship between mean daily stem radius change (SRC_d) and mean daily relative humidity (RH_{mean}) for the five studied species. Given are values of R calculated for the respective mid-point of a correlation analysis with a moving time window of 31 days. Mean of 4–6 trees per species.

When analyzing stem radius changes with a moving calculation window of 7 days (SRC₇), a high synchronicity in the growth rate fluctuation among the five species was visible. The peaks and lows of radial growth were mostly matching in the period from early June until the end of the growing season in September (Figure 2g), while the absolute size of the stem radius change differed up to fivefold among the species.

Discussion

Extracting growth rate from daily stem radius variation

The following processes are contributing to circadian cycles in stem diameter: expansion of dead conducting xylem elements due to the relaxation of internal tensions (Irvine and Grace 1997, Cochard et al. 2001, Offenthaler et al. 2001, Sevanto et al. 2002), reversible water status-related dehydration and rehydration of living tissues (bark and phloem), thermal expansion and contraction, and irreversible radial growth (Kozlowski and Winget 1964, Simonneau et al. 1993, Zweifel et al. 2000, Daudet et al. 2005). Dehydration/rehydration effects in bark and phloem and radial growth typically explain more than 90% of the stem radius fluctuations (Dobbs and Scott 1971, Molz and Klepper 1973, Zweifel and Häsler 2000, Zweifel et al. 2005), but the ratio between the two processes may change with climatic conditions and both may be difficult to separate from each other. The fraction of reversible stem shrinkage and re-expansion in total diameter change is higher when trees are growing slowly as in cold climates or at the beginning and end of the growing season (Zweifel and Häsler 2001).

Thus, a positive change in stem radius from one day to the other does not necessarily reflect cambial growth but may

partly be caused by stem swelling due to alterations in the water status of xylem and bark. This is reflected by the occasional occurrence of negative diameter changes in the SRC_d data. Nevertheless, Rossi et al. (2006) proved for conifers that high-resolution dendrometers and repeated micro-coring in the xylem led to similar results with respect to the recording of cambial growth activity at the time of maximum growth. In any case, we have several reasons to assume that the extracted daily positive stem radius changes in our data set are mainly caused by cambial growth processes when longer integration periods of 7 or 21 days are used while water status-related stem volume changes might have a significant influence on the day-to-day diameter change only in the SRC_d data. First, we investigated the relation between bark thickness and calculated mean radial increment across the 25 tree individuals from five species studied (Table 1). We found no significant correlation which excludes the possibility that the calculated apparent growth rates were in reality mostly expansion processes of bark tissue in moist periods. Second, we found a large increase in the degree of atmospheric coupling of the SRC_d values from May to June which cannot be explained by physical rehydration processes but which is most likely caused by seasonal growth rhythms under endogenous control. Moreover, the prominent RH signal persisted in most species when the observation window was extended from 1 to 7 or 21 days; the risk of misinterpreting diameter increases due to swelling as growth processes should be much smaller in these longer integration periods. Finally, we selected the data from mid-summer (mid-May to mid-July) or June with maximum radial increment for analyzing growth-climate relationships. In this period, diurnal stem radius changes due to swelling and shrinking normally do not exceed daily radial growth rates and the daily SRC7 and SRC21 figures were indeed always positive in the five species in this period (except for a few negative SRC7 values in Tilia). Thus, the conditions for the extraction of growth patterns from stem radius changes are most promising during mid-summer (Deslauriers et al. 2007b).

Seasonality of growth rate and growth control in the five species

In the study year 2009 with a wet and warm summer without pronounced dry periods, all five species showed maximum daily radial growth in June and July which is in accordance with results from other studies on the growth dynamics of temperate broad-leaved trees (e.g., Mund et al. 2010). Čufar et al. (2008) detected highest stem growth rates in beech in June and concluded that the rainfall amount in May prior to this peak growth period is of high importance for the annual growth-ring width of *Fagus*. Our growth data for the five species with a resolution of 1 day point to a particularly tight coupling of growth to the atmospheric water status in June when peak increment occurred but indicate a remarkably small effect of

atmospheric moisture in May (Table 5, Figure 5). We assume that the marked seasonality in radial increment and the climatic control of growth in the five species are reflecting an endogenous control of cambial activity which is exerted through bud and leaf phenology, the seasonal dynamics of photosynthetic capacity and the supply of photosynthates for stem growth (Cufar et al. 2008). A girdling experiment with young Juglans plants showed that radial growth completely ceased 3 days after the inhibition of photoassimilate transport to the cambium (Daudet et al. 2005) which indicates the importance of carbohydrate supply and hormonal growth regulators (Evert et al. 1972) for cambial activity over time spans of several days. The pronounced species differences in the timing of growth cessation in late summer may have been caused by species differences in the seasonal production of growth-promoting hormones; the Acer trees reduced their stem increment already in July while the other four species continued radial growth until September. Nevertheless, stem water status is assumed to be the principal growth-controlling factor on short (hours, days) and medium time spans (weeks, months) in temperate broad-leaved trees (Zweifel et al. 2006).

Weather dependence of growth

Among the six environmental factors examined for their influence on daily stem radius change, we found the strongest effect by mean daily relative air humidity and vapor pressure deficit. In all five species, the largest increase in stem radius was found on days with highest RH and lowest D; the other hydrological variables—soil moisture and rainfall, and temperature and radiation had a much smaller or even insignificant influence on a daily basis. These results confirm the frequently recognized dominant effect of water availability on stem diameter growth in temperate trees (e.g., Orwig and Abrams 1997, Lebourgeois et al. 2005). However, these findings contrast with the results of tree ring studies in temperate broad-leaved trees which, in most cases, evidence a dominant influence of the summer precipitation amount of the recent year, or of the preceding year, on annual ring width (Tardif et al. 2001a, Čufar et al. 2008). Dendrochronological studies typically show largest rainfall effects in drier and warmer regions and a decrease in the importance of this factor toward moister and colder climates (e.g., Bréda et al. 2006, Vittoz et al. 2008). Air humidity and vapor pressure deficit have only rarely been identified as dominant growth-influencing factors in dendrochronological climate sensitivity analyses (e.g., McLaughlin et al. 2003) and the importance of these atmospheric factors is usually secondary to the effects of seasonal and annual rainfall totals and temperature.

The apparent discrepancy between our dendrometer study and dendrochronological investigations with respect to the relative importance of atmospheric moisture status, precipitation and temperature as controls of stem diameter growth is

possibly a consequence of different time scales of investigation. Dendrochronological studies typically analyse growth in time periods of several months to years, thus integrating over consecutive episodes of cambial cell division and expansion growth. This is a time horizon that may cover distinct changes in soil moisture as caused by fluctuating precipitation intensities. In contrast, precision dendrometers with a resolution of minutes or hours may record cambial activity and cell expansion quasi in situ, because a typical mitotic cycle lasts for ~24 h. Rainfall events with subsequent infiltration into the soil may take hours to reach the absorbing roots and pronounced increases in soil moisture with physiological significance may only manifest after larger events and sometimes with a delay, if soil hydraulic conductivity is moderate to low. Thus, we assume that changes in atmospheric moisture status and evaporative demand during a day and between consecutive days are rapid enough to influence tree water status on a daily time scale, while rainfall and resulting soil moisture variation exhibit a more coarse-grained event structure which may, under certain edaphic conditions, be of secondary importance for the actual tree water status and thus for cambial activity.

From the high significance of the air humidity and vapor pressure deficit effects in our analysis, we hypothesize that both atmospheric moisture parameters are key determinants of short-term fluctuation in cambial water status in the examined trees as long as significant soil desiccation is absent. During the main period of stem growth in 2009, soil matrix potential stayed well above -0.1 MPa in 10 cm soil depth of the Hainich forest and thus did not expose the trees to significant drought stress. We predict that the influence of atmospheric water status on radial stem growth should be particularly large in comparison with soil water status and rainfall when the climate is humid or semi-humid lacking long drought periods. Soil texture should also influence the relative importance of soil vs. atmospheric water status on stem radial growth, for example, through a low hydraulic conductivity in clay-rich soils, which may dampen the effect of rainfall events on tree water status, while we would expect a particularly large effect of soil moisture on radial growth on coarse-grained sandy soils with a small water storage capacity and a higher moisture fluctuation.

Several existing high-precision dendrometer studies examining weather effects on stem growth obtained results which are in accordance with these predictions. For example, in boreal forest trees in Quebec, Canada, the largest influence on daily radial growth was exerted by rainfall while temperature and *D* were only secondary factors (Tardif et al. 2001b, Deslauriers et al. 2003). In a dry subtropical *Eucalyptus* forest in SE Australia, Downes et al. (1999) found soil moisture to be a major determinant of daily radial stem growth, while Drew et al. (2008) identified temperature together with rainfall in a nearby *Eucalyptus globulus* Labill. plantation to be of primary importance. In colder climates, the influence of temperature on radial growth is expected to increase relative to the hydrological factors. At the temperate alpine tree line, temperature has been found to be a primary driver of daily radial growth (Gruber et al. 2009). However, stem growth can also be negatively related to temperature (Deslauriers et al. 2007*a*) because cold-adapted trees may suffer under hot summer days (Zweifel et al. 2006).

Radial stem growth is driven by two processes, cell division and cell expansion in the cambial zone, with the latter being particularly sensitive to turgor reductions (Hsiao and Acevedo 1974). Several factors and processes are decisive during cell expansion: the exceeding of a turgor threshold (Lockhart 1965), cell wall loosening as mediated by expansins, the promotion of expansion by hormones, mainly auxin (Lambers et al. 2008), and the postponed deposition of secondary cellwall components (Larson 1994). According to Domec and Gartner (2002), the formation of early wood in conifers is triggered by high auxin concentrations. Thus, environmental factors with an influence on cell water status and endogenous factors (including carbohydrate availability) are interacting during cell expansion. However, the bulk of empirical evidence indicates that the water status of the cambium is playing a central role in controlling radial stem growth. Observational data and modelling results suggest that radial growth in woody plants is occurring mainly during the night hours when turgor is high (Dünisch and Bauch 1994, Steppe et al. 2006). Since the stem cambium is situated on the flow path from the soil through the plant to the atmosphere, it seems logical that not only soil moisture (and precipitation), but also the atmospheric moisture status at the opposite end of the water flow path are influencing radial growth. It may well be that small amounts of rainfall exert a positive effect on cambial activity not by increasing soil water potential, but through a reduction in transpiration rate due to lowered D or leaf wetting and a sudden release of negative pressure in the conducting system (Hsiao and Acevedo 1974, Steppe et al. 2006, Zweifel et al. 2006).

Conclusion

From our analysis of stem radius change in five temperate broad-leaved tree species at observation windows of 1, 7 or 21 days, we conclude that cambial growth during mid-summer 2009 was primarily influenced by air humidity (and vapor pressure deficit) in this mixed stand, while rainfall, soil moisture status and air temperature were playing only a secondary role. Radial increment linearly increased with relative air humidity in all five species and showed a pronounced seasonality in its RH dependence with highest sensitivity to air humidity in June during peak growth. We explain the RH effect on radial growth mainly by a reduced transpiration rate, and thus a reduction in negative pressure in the conducting system which increases

turgor in the cambial cells and their differentiating derivatives and promotes cell division and cell expansion. Whether the water status of the cambial cells in the stem xylem of trees is mainly influenced by rainfall and soil moisture patterns or by the atmospheric water status, might depend on the time scale considered and is likely to vary with climate and soil physical conditions. We speculate that an assumed close coupling of cambial growth with the variation in air humidity is only detectable when growth is analysed on a daily basis; however, stem swelling and shrinking are often confounding the analysis at this time scale. Supplementary analyses of stem diameter change at longer temporal scales (several days to a few weeks) and direct observation of cambial cell division may be needed to refine the analysis of environmental control of radial growth processes in temperate trees. Our findings suggest that the understanding of hydrological effects on the stem water status and cambial activity of trees needs to consider both soil water status and atmospheric water status as controlling factors.

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Conflict of interest

None declared.

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