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# Intra-annual stem growth dynamics of Lebanon Cedar along climatic gradients

Aylin Güney<sup>1</sup> · Manfred Küppers<sup>1</sup> · Cyrille Rathgeber<sup>2</sup> · Melahat Şahin<sup>3</sup> · Reiner Zimmermann<sup>1</sup>

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## Abstract

**Key message** Onset of cambial activity in Lebanon Cedar is triggered by stem temperature but may be delayed by high site-LAI. Higher growth rates and tree-ring widths were observed under better water and light availability. Daily stem radius variations were sensitive to humid conditions.

**Abstract** Studies on intra-annual dynamics of stem growth provide useful information on tree growth responses to environmental conditions, but are fragmentary for species from Mediterranean Mountain ranges. Lebanon Cedar is a frost and drought tolerant species, growing between 1000 and 2000 m a.s.l in the Taurus Mountains (Turkey). Foresters see it as a potential candidate for plantation in Central European forests facing global warming. To describe the natural variability of Lebanon Cedar growth dynamics, five study sites were established: four along an altitudinal gradient at a natural site in SW-Turkey and one in a Lebanon Cedar plantation in Central Germany. Two stem growth monitoring methods were used: (1) bi-weekly microcoring during 2013 growing season and (2) point dendrometers during 2013 and 2014. Histological analyses were used to calibrate dendrometer records and to describe cambium phenology. Seasonal dynamics of xylem and

stem radial increments were modelled by Gompertz functions. Onset of cambial activity was observed 1–2 weeks after stem temperatures reached a threshold of 5 °C but could be delayed by high site-LAI. Cedars growing under better light and water availability showed higher growth rates and wider tree rings. Daily stem radius variations (dSRV) extracted from dendrometer records were negatively related to vapor pressure deficit and global radiation; multiple linear regressions explained 30–52% of dSRV variance being dominated by relative humidity, precipitation, and soil water content. Best growth performance was observed at the German site, likely for a continuous water supply throughout the year, underlining the potential of Lebanon Cedar for Central European Forestry.

**Keywords** Lebanon Cedar · Point dendrometer · Microcoring · Cambial activity · Tree-ring formation · Microclimate

## Abbreviations

A	Final annual tree-ring width
bE	Onset of the enlarging phase
bL	Onset of the cell-wall lignification phase
bM	Onset of the mature phase
CA	Cambial activity
cE	Cessation of the enlarging phase
cL	Cessation of the cell-wall lignification phase
CRF	Cedar Research Forest
d	Time required for major period of tree-ring formation
dE	Duration of the enlarging phase
dL	Duration of the lignification phase
DOY	Day of year
dSRV	Daily stem radius variation
dX	Duration of xylogenesis

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EBG	Ecological Botanical Gardens
gR	Global radiation
LAI	Leaf area index
MAT	Mean annual air temperature
Pp	Precipitation
$r$	Mean tree-ring formation rate (during growth period)
rH	Relative air humidity
RSI	Radial stem increase
ST	Stem temperature
SWC	Soil water content
Ta	Air temperature ( $T_{a_{\text{mean}}}$ : daily mean, $T_{a_{\text{max}}}$ : daily maximum, and $T_{a_{\text{min}}}$ : daily minimum)
TAP	Total annual precipitation
$t_p$	Time of inflection point
Ts	Soil temperature
VPD	Vapor pressure deficit

## Introduction

Studies on intra-annual dynamics of stem growth are of high interest, because they allow for an insight on processes underlying tree-ring formation and on factors affecting those processes (Bouriaud et al. 2005; Rathgeber et al. 2011a). Global warming is expected to increase temperatures and the intensity and frequency of summer droughts (Stocker 2014), which will affect dynamics of tree growth and may lead to a decrease in forest productivity (Ciais et al. 2005; Deslauriers et al. 2007). Observing changes in stem radius, cambial activity (CA), and wood formation at high resolution in combination with daily variations of climatic conditions can improve our understanding of how tree growth responds to climate change (Michelot et al. 2012; Rossi et al. 2006b). For this, several methods are available among which dendrometer measurements and repeated microcoring are the most well known. Dendrometers allow for quasi-continuous measurements of variations in stem radius (including bark growth, phloem and xylem formation) over long time periods (Herzog et al. 1995) without creating significant disturbances in cambial and woody tissues nearby. Furthermore, they allow for monitoring of trees reactions to short-term changes in microclimatic conditions. However, when interpreting results one has to take into account water-related swelling and shrinkage of the stem, especially of the bark, which interfere with the stem growth signal (Deslauriers et al. 2007; Downes et al. 1999; Mäkinen et al. 2003; Zweifel and Häsler 2001). Microcoring allows for detailed investigation of tree-ring formation directly at the cellular level by repeatedly

extracting small wood samples. With this method, it is possible to accurately describe phenology of CA and intra-annual dynamics of wood formation (Mäkinen et al. 2008; Rathgeber et al. 2011b; Rossi et al. 2006a), and to describe the kinetics of xylem cell differentiation: radial cell enlargement, secondary wall thickening and lignification, and cell death (Cuny et al. 2014). However, wood samples have to be extracted regularly in defined time intervals, which require repeated wounding of the tree, regular visit of the monitored site, and tedious sample preparation and observation in the laboratory. Combining both methods may lead to more powerful results by minimizing their respective weaknesses. Wood formation monitoring (e.g., microcoring) may help to better understand dendrometer records, which are more widely spread in the scientific community but much less understood. On the other hand, dendrometers may allow exploring tree physiological reactions at higher time resolution (hourly or daily).

For the Mediterranean region, there are several studies investigating intra-annual growth of tree rings either by wood formation monitoring (Camarero et al. 1998; de Luis et al. 2011; del Castillo et al. 2016) or by dendrometers (Vieira et al. 2013). They show that wood formation is site- and species specific and demonstrate the importance of climatic conditions on onset and cessation of growth and of growth performance. So is the cambial onset mainly triggered by temperature in most biomes (Rossi et al. 2007), while, for example, growth cessation may be influenced by water availability in drier regions, such as the Mediterranean or may be limited by photoperiod, e.g., in temperate and boreal regions (Rossi et al. 2006c; Vieira et al. 2014). In co-occurring species, conifers generally show an earlier onset of stem growth than broadleaf species (e.g., Zhai et al. 2012). Studies that combine dendrometer and microcoring are scarce, but they underline the interrelation between wood anatomy and stem radial variation and allow a more precise prediction of tree growth based on climatic conditions (Camarero et al. 2010; Coccozza et al. 2016; Linares et al. 2009; Vieira et al. 2014).

To our knowledge, studies on the intra-annual growth dynamics of the montane Mediterranean Lebanon Cedar (*Cedrus libani* A. Rich) are still very rare. Today, Lebanon Cedar is mainly distributed as pure natural stands along the Taurus Mountain Range of Southern Turkey (800–2200 m a.s.l, Akkemik 2003), which offers biologically and ecologically valuable ecosystems to a large number of endemic species (Kavgacı et al. 2010). Because of its adaptability to temperature extremes and summer drought and its valuable timber, it is one of the major commercial tree species in Turkey (Brooks et al. 2008) used in many forestation and afforestation projects within (Boydak 2007) and outside Turkey (e.g., Italy, Ducci et al. 2007). Its potential for Central European forestry was recently

reviewed, underlining its promising potential for establishing stable and productive forest stands under a changing climate (c.f. Messinger et al. 2015). It is then of interest to learn more about its intra-annual growth dynamics under different site and climatic conditions. We used microcoring and point dendrometers in combination with local weather stations to analyze the dynamics of wood formation of Lebanon Cedar under different climates (sub-continental in Germany and Mediterranean in Turkey) and along a large range of altitudes during the growth periods of 2013 and 2014. To describe natural variability, four measurement sites were established in a Lebanon Cedar forest in SW—Turkey (1000–2000 m a.s.l.) and one within a cedar plantation in Bayreuth, Central Germany (360 m a.s.l.), which represents a potential area for establishing future Lebanon Cedar stands.

The objectives of this study are to describe (1) wood formation phenology; (2) intra-annual radial growth dynamics; (3) comparing results from microcoring and dendrometer records; to (4) better understand which climatic factors drive Lebanon Cedar radial growth. Finally, the growth potential of Lebanon Cedar with respect to climate change will be discussed.

## Materials and methods

### Study sites and tree selection

The study was conducted during 2013 and 2014 on individuals of Lebanon Cedar at five sites of different environmental characteristics and along an elevational gradient (Table 1). Four of these sites (T1–T4) were located at the Cedar Research Forest (CRF), which is within the district of Elmali and situated 130 km southwest of Antalya, Turkey (Fig. 1). The CRF mainly consists of pure natural Lebanon Cedar stands and is characterized by an oro-Mediterranean climate with a drought period during summer (from June to September) and cold winters (Fig. 2). Mean annual value (1968–2000, 1665 m a.s.l.) of air temperature (MAT) is 7.4 °C with absolute air temperature extremes of –31 and +34 °C. Mean total annual precipitation (TAP) is 725 mm with rainfall mainly occurring during winter months (Basaran et al. 2008; Senitza 1989). The fifth study site (O1) was located within a Lebanon Cedar plantation at the Ecological Botanical Gardens (EBG) at Bayreuth, Germany. Seed material of these cedar individuals originated from the same province, where the CRF is located and was germinated and cultivated in Germany in 1978. The 2-year-old seedlings were planted in the EBG in 1980 (Messinger et al. 2015). The EBG is characterized by a transition from oceanic to continental (so-called “sub-continental”) climate with mild-to-cold

winters and warm summers without any drought period during the year (Fig. 2). MAT is 8.2 °C (1971–2000, 360 m a.s.l.), and measured absolute air temperature extremes are –24 and +36 °C. Mean TAP is 724 mm (Foken 2007). To determine Leaf Area Index (LAI) of the sites, hemispherical photographs of the forest canopy were taken from the ground and analyzed using HemiView image analysis software (1999 Delta-T Devices Ltd, Cambridge, UK). To measure seasonal dynamics of stem growth in Lebanon Cedar, nine individuals were randomly selected within a circular plot (radius = 20 m) at each Turkish site (Table 2). None of the selected trees had visible damage. Age at breast height (1.3 m) was estimated by extracting tree cores using an increment borer (Suunto 300/400 mm, Finland). At the EBG, five cedar individuals (Table 2) were selected from a tree row planted parallel along a paved road in 1988 (Messinger et al. 2015).

### Microclimate measurements

Meteorological stations (WatchDog 2700 Weather Station, Spectrum Technologies Inc., Plainfield, IL, USA) were installed at T1 and T3 in open areas (Fig. 1) to measure air ( $T_a$ , °C) and soil temperature ( $T_s$ , °C), precipitation ( $P_p$ , mm), soil water content (SWC, %), relative air humidity (rH, %), and global radiation ( $gR$ ,  $W/m^2$ ). At sites T2 and T4,  $T_a$  and rH were measured using HOBO® Pro series loggers (Onset Computer Corporation, MA, USA) mounted on a tree within the plot approximately 2 m above ground.  $T_s$  were measured with thermocouples, and SWC was measured with a Theta Equitensiometer ML-2 (EQ ML2 9-23, Delta-T devices, England) at T2 and a Stevens® Hydra Probe (Stevens Water Monitoring Systems, Inc., Portland, USA) at T4 and recorded using data loggers (DL2e Data logger, Delta-T devices Ltd., Cambridge). Climate data for O1 were derived from the meteorological station at the EBG (360 m a.s.l., BayCEER).  $T_s$  and SWC were measured at a depth of approximately 0.15 m. Stem temperature (ST) was measured using thermocouples and recorded by data loggers (DL2e). These thermocouples were installed at breast height within the outer stem (N facing) under the bark of three cedar individuals to get a representative mean ST per site. Climate variables were measured at 10–30 min time steps and were later aggregated to daily values (daily mean:  $T_{a,mean}$ , maximum:  $T_{a,max}$ , minimum:  $T_{a,min}$ , and sum:  $P_p$ ).  $gR$  was converted from hourly means into daily sums and expressed as  $MJ\ m^{-2}\ day^{-1}$ . In addition, daily means of vapor pressure deficit (VPD, hPa) were calculated from site-specific  $T_{a,mean}$ , rH, and air pressure values for all sites.

A temperature threshold was determined after which CA was likely to start within a defined time span (e.g., 1 week). Therefore, daily means of temperature variables were

**Table 1** Location and characteristics of the study sites

Site	O1	T4	T3	T2	T1
Location	EBG Bayreuth <sup>a</sup>	CRF Elmali <sup>b</sup>	CRF Elmali <sup>b</sup>	CRF Elmali <sup>b</sup>	CRF Elmali <sup>b</sup>
Latitude	49.925915°N	36.57800°N	36.57771°N	36.58520°N	36.58422°N
Longitude	11.582851°E	29.96881°E	29.98542°E	30.02035°E	30.03077°E
Altitude (m a.s.l.)	360	1055	1355	1665	1960
Total plot area (ha)	Single tree row	0.126	0.126	0.126	0.126
Forest type	Plantation	Natural forest	Natural forest	Natural forest	Natural forest (tree line)
Exposure	NS-orientation	NW	NW	NW	NW
Stand inclination	Level terrain	20°	26°	40°	16°
Soil	Clay and sandy loam	Clayey loam to clay	Clay to clayey loam	Clay loam to clay	Clay loam
pH (H <sub>2</sub> O)	4.4–5.3	7.20–8.15	7.23–7.56	7.63–8.03	7.61–7.79
Stand density (trees ha <sup>-1</sup> ) <sup>c</sup>	–	334	533	501	478
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	–	30.0	74.4	46.1	50.4
LAI <sup>d</sup> (m <sup>2</sup> m <sup>-2</sup> )	–	2.3 ± 0.65	3.2 ± 0.89	2.9 ± 0.46	1.04 ± 0.45

Soil properties and pH (H<sub>2</sub>O) values according to Basaran et al. (2008)

<sup>a</sup> Bayreuth, Germany (D)

<sup>b</sup> Elmali, Turkey (TR)

<sup>c</sup> Only trees with a DBH > 10 cm

<sup>d</sup> LAI values were calculated via the HemiView image analysis program (Delta-T Devices, Cambridge, UK) for the Turkish sites

compared in 0.1° steps between all sites within a time frame of 2 months before onset of CA. For dSRV-climate analysis, missing Pp and gR data at T2 and T4 were extrapolated using WorldClim and HemiView (Delta-T Devices Ltd.) data, respectively. An overview about all measured climate variables is given in Table 3.

### Growth monitoring using point dendrometers

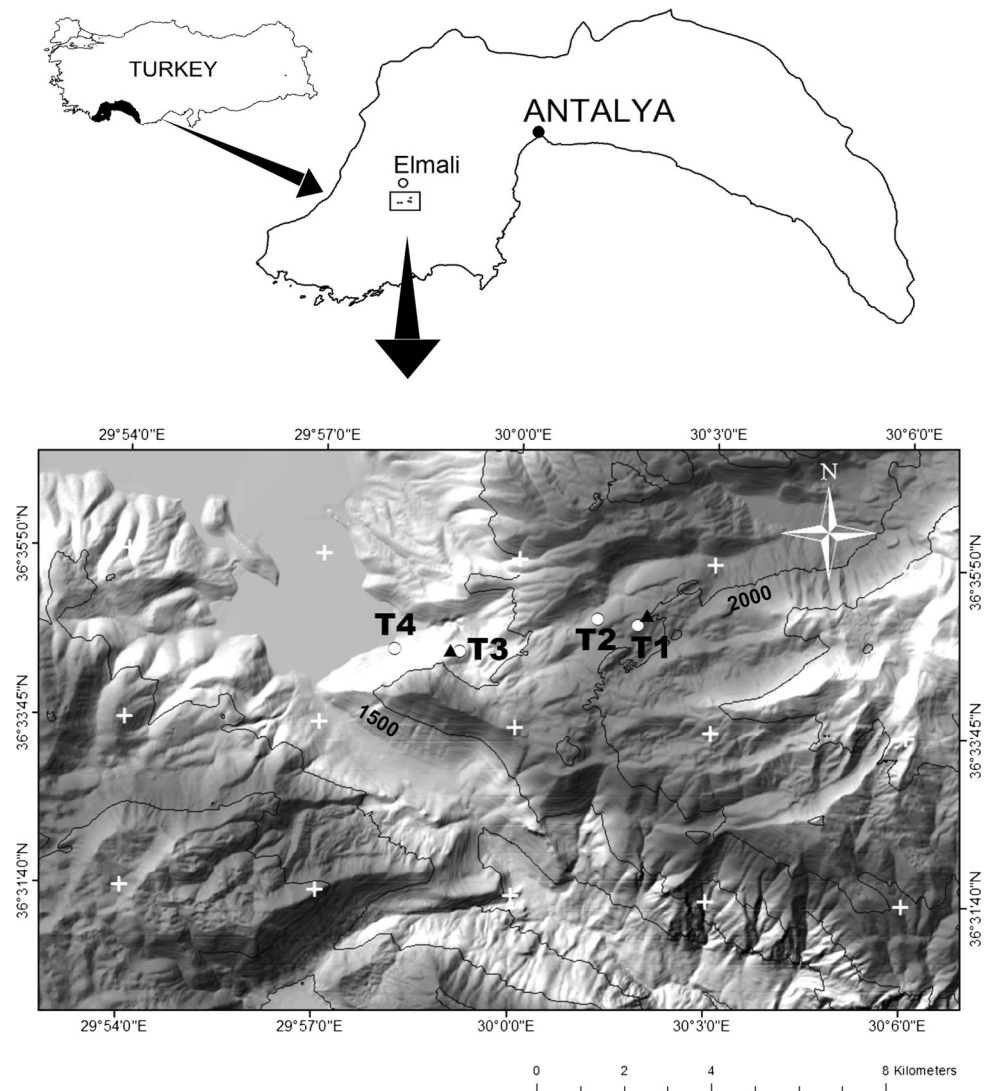
In 2013 and 2014, stem growth was monitored hourly on the nine Lebanon Cedar individuals selected at T1–T4 and the five individuals selected at O1 (Table 2) using point dendrometers (linear displacement potentiometers, accuracy <10 µm; MMR 10\_11 R5 K, MEGATRON Elektronik AG & Co., Munich, Germany). Those were mounted at breast height on stainless steel frames and fixed to the slope-parallel sides of the stem. Steel frames were attached to the stem by two screws which were placed at least 5 cm apart from the measuring point and at least 5 cm deep into the xylem (Herzog et al. 1995). The contact head of the dendrometer was placed at the cortex surface after removing the bark without damaging living tissue (Zweifel et al. 2006). Dendrometers were wrapped up in aluminum foil and covered with styrofoam to protect them from direct solar radiation and precipitation. Radial stem changes were recorded using data loggers (DL2e). To extract stem growth signals from dendrometer records, we used the ‘daily mean approach’ (Deslauriers et al. 2007). Hourly dendrometer records were averaged on a daily basis, and

daily stem radius variation (dSRV) was calculated as the difference between the mean value of two consecutive days (Deslauriers et al. 2007; Tardif et al. 2001). Only the main period of radial stem increase (RSI) was considered for dSRV analysis to exclude measurement variability that is higher than radial growth at the beginning and end of growth period (cf. Deslauriers et al. 2007). This period is defined by a sharp, almost linear increase of the dendrometer records. When initiation of this linear increase was observed, dendrometer records were set to zero. The end of the period of the main RSI was defined as the date when 90% of the annual radial increment ( $A_{90\%}$ ) was reached ( $A$  = upper asymptote, see section “Modeling growth dynamics”).

### Wood formation monitoring with microcores

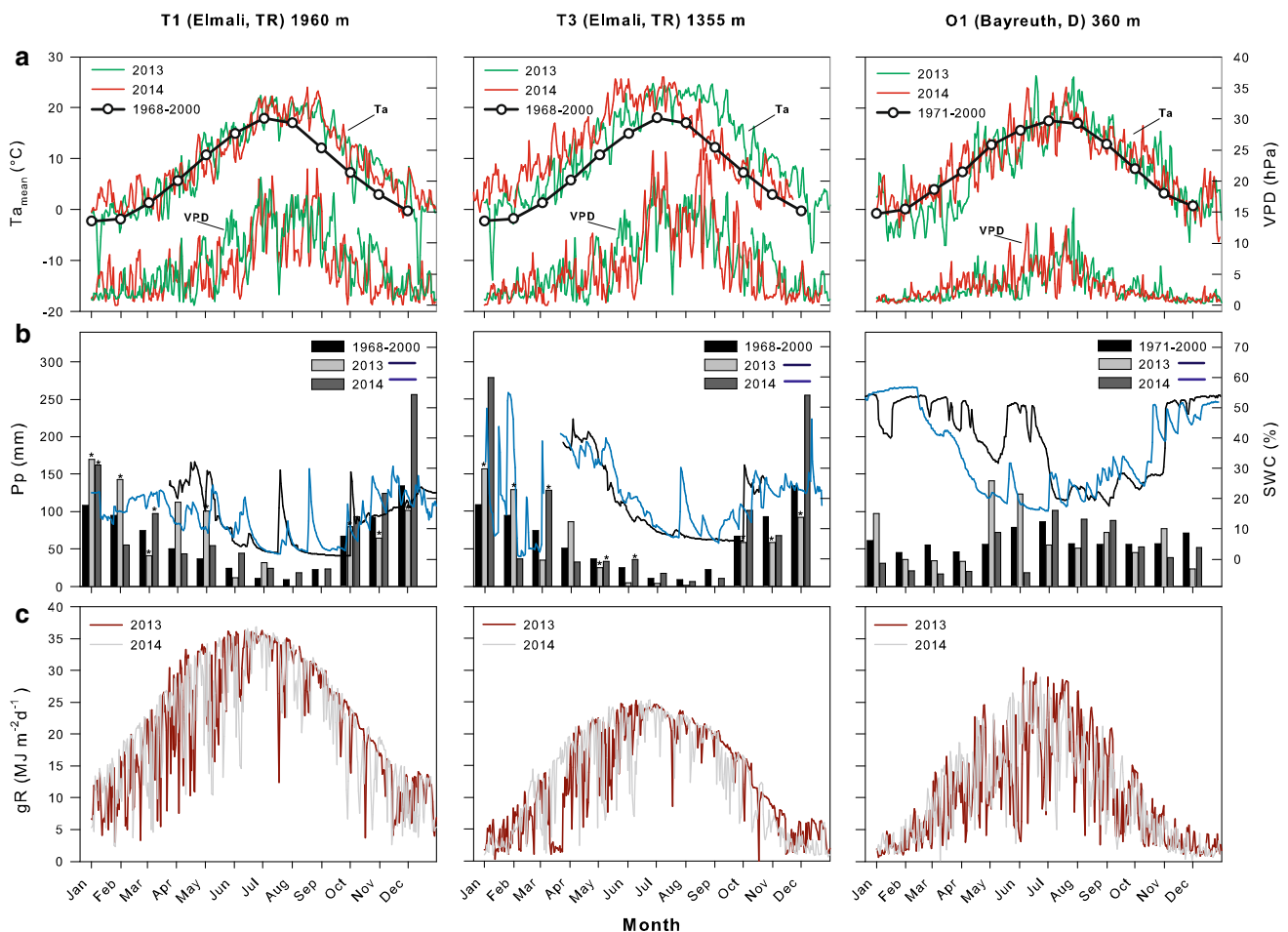
To investigate tree-ring growth at cellular level (microscopically), microcores were extracted bi-weekly during the growing season of 2013 (March to October) from stems of three Lebanon Cedar trees per site (Güney et al. 2015). All individuals chosen for microcoring were also selected for dendrometer measurements (Table 2). Microcores were extracted using a Trephor© (Rossi et al. 2006a) at breast height from the slope-parallel side of the stem and on the stem-side opposite to the dendrometer. Before sampling, the outer bark was carefully removed. To avoid tissue damage and wound reactions, microcores were taken along the stem in a spiral pattern with at least 5 cm distance

**Fig. 1** Location of the four study sites (T1–T4, *white dots*) at the Elmali Cedar Research Forest in Antalya, Turkey. *Black triangles* represent the location of weather stations (at T1 and T3)



between extraction points (Deslauriers et al. 2003a). Samples were stored in a fixative solution and prepared in the laboratory for histological analysis, as described in Güney et al. (2015). Transverse sections of the microcores were examined and photographed under a Zeiss Axioplan microscope. For each sample, the number of cells in the developing tree ring (cells in the cambial zone, enlargement, cell-wall lignification, and mature tracheids) and the current radial width of the tree ring were determined along three radial files per transverse section and then averaged for further data analyses (Deslauriers et al. 2003a; Rossi et al. 2007). For results on cell counts, see Güney et al. (2015). We determined the beginning of CA as a distinct increase in the number of cambial cells (number of cambium cells > number of dormant cambium cells) which are considered to be xylem cells in the postcambial growth stage (Gricar et al. 2006).

Critical dates and durations of wood formation were computed from raw cell count data using the R Package CaviaR, based on logistic regressions (Rathgeber et al. 2011b). The onset of enlarging (bE), cell-wall lignification (bL) and mature phases (bM) and cessation of enlarging (cE) and cell-wall lignification phases (cL) were defined as those dates at which 50% of the radial files were active or non-active. From these critical dates, durations of enlarging (dE) and lignification phases (dL) as well as duration of xylogenesis (dX) could be computed. Because the assumption of normality was not met by all parameters of critical dates and durations, a non-parametric Kruskal–Wallis test was performed to detect if there are significant differences between study sites. If significant differences were present, analyses were followed by Mann–Whitney *U* tests.



**Fig. 2** Climate variables recorded during the growing seasons of 2013 and 2014 at the Turkish sites T1 (left column) and T3 (middle column) and the German site O1 (right column) with **a** daily means of air temperature ( $T_{a_{mean}}$ ; lines with circles represent the long-term average) and vapor pressure deficit (VPD; green lines 2013, red lines 2014), **b** daily means of soil water content (SWC; blue lines 2013,

dark blue lines 2014), monthly sums of precipitation (Pp; black bars long-term average, grey bars 2013, dark grey bars 2014), and **c** daily totals of global radiation (gR; dark red lines 2013, grey lines 2014). For each respective parameter, scales of the y-axis are identical. Bars indicated with a star (in **b**) represent extrapolated Pp data, where site-specific data were incomplete or missing

**Table 2** Characteristics of the studied Lebanon Cedar trees

Site	O1	T4	T3	T2	T1
Number of trees ( <i>n</i> )	4	9	7	7	7
DBH (m)	0.35 ± 0.04	0.34 ± 0.13	0.31 ± 0.15	0.33 ± 0.09	0.26 ± 0.13 (1.68) <sup>b</sup>
Age (year) <sup>a</sup>	35.0	75.0 ± 33.6	89.4 ± 32.9	88.9 ± 16.6	47 ± 12.9 (300) <sup>b</sup>
Height (m)	13.5 ± 1.6	14.8 ± 3.9	18.0 ± 6.5	20.2 ± 1.2	8.8 ± 2.1

Trees which were not used in the analysis (because of sensor damage or loss of data) are not included

Values present mean ± SD

<sup>a</sup> Age at DBH

<sup>b</sup> At T1, one of the study trees was very old; therefore, age and DBH of this tree are listed separately in parentheses

## Modeling growth dynamics

Stem radial growth during a growing season can be accurately described by the Gompertz model, which can fit adequately tree-ring increment (from dendrometers) and cell number increase (from microcoring)

through time (Deslauriers et al. 2003b; Rossi et al. 2006c):

$$y = A \exp[-\exp(b - kt)] \quad (1)$$

where  $y$  is the cumulative sum of growth,  $A$  is the upper asymptote of the total number of xylem cells (or total

**Table 3** Overview of the measured climate variables and measurement devices at the five Lebanon Cedar study sites

Climate variables (unit)	Abbrev.	T1	T2	T3	T4	O1
Air temperature (°C)	Ta	WD	H	WD	H	WS
Stem temperature (°C)	ST	Th	Th	Th	Th	Th
Soil temperature (°C)	Ts	Th	Th	Th	Th	WS
Precipitation (mm)	Pp	WD	ex WC	WD	ex WC	WS
Relative air humidity (%)	rH	WD	H	WD	H	WS
Soil water content (%)	SWC	WD	TE	WD	HSP	WS
Global radiation (MJ m <sup>-2</sup> day <sup>-1</sup> )	gR	WD	ex HV	WD	ex HV	WS

WD WatchDog weather station, H HOBO logger, Th measured using thermocouples, WS Weather station at the EBG, ex data extrapolated via WorldClim (WC) or HemiView (HV), TE Theta Equitensiometer ML-2, HSP Stevens® Hydra Probe

annual tree-ring growth),  $b$  is the  $x$ -axis placement parameter,  $k$  is the rate of change parameter, and  $t$  is the time as day of year (DOY) (Cheng and Gordon 2000). Growth rate of tree-ring formation can be described by the first derivative of the Gompertz function. The inflection point ( $t_p$ ) corresponds to the maximum value of growth rate and can be calculated as  $t_p = b/k$  (Rossi et al. 2006c). The weighted mean absolute cell formation rate ( $r$ ) and the time required for the major period of tree-ring formation ( $d$ ) can be described as

$$r = \frac{Ak}{2(v+2)} \quad (2)$$

$$d = \frac{2(v+2)}{k} \quad (3)$$

where  $v = 0.0001$ , since the Gompertz function is a special case of the Richards function (Deslauriers et al. 2003b). Variables obtained from Gompertz fittings ( $A$ ,  $t_p$ , and growth rate at  $t_p$ ,  $r$ , and  $d$ ) of dendrometer data were compared among study sites using ANOVA. Tests of normal distribution and homogeneity of variances were performed using Kolmogorov–Smirnov and Levene tests ( $p > 0.05$ ). All variables showed the required normal distributions. Differences between sites were assessed using either Tukey or Games-Howell post hoc tests for those cases that did or did not meet the requirements for homogeneity of variances, respectively. Differences between years were compared using  $t$  tests (confidence interval: 95%).

### Statistical analyses

To assess climatic sensitivity of dSRV, Pearson correlation coefficients were calculated between dSRV and climate variables ( $Ta_{\text{mean}}$ ,  $Ta_{\text{max}}$ , and  $Ta_{\text{min}}$ ; mean Ts, mean ST, Pp sum, mean SWC, mean rH, gR sum, and mean VPD). To assess the overall amount of variability in dSRV explained by climate variables and DOY, we used multiple stepwise regression analysis. To reduce collinearity among variables, collinearity diagnosis was performed. To avoid phases of

measurement variability higher than radial growth, only main periods of growth were considered for calculations (Deslauriers et al. 2007). Analyses were performed on both years together via SPSS v20.0 (SPSS Inc., Chicago, IL, USA) with a significance level of 0.05.

## Results

### Climate in 2013 and 2014

In 2013, MAT exceeded the long-term mean (7.4 °C) at all Turkish sites (T1: 8.8 °C, T2: 9.2 °C, T3: 11.1 °C, and T4: 12.6 °C). At O1, it was identical to the long-term mean (8.2 °C). In 2014, MAT exceeded the long-term means and the values of 2013 at all sites (T1: 9.3 °C, T2: 9.4 °C, T3: 11.5 °C, T4: 13.0 °C, and O1: 8.9 °C) indicating a general rise in temperature between 2 years. Maximum VPD values were observed between June and September, reaching up to 20 hPa at the Turkish sites and 15 hPa at the German site (Fig. 2). SWC was lowest at T1 and highest at O1 in both years, while minimum values were reached around September and July, respectively. At the Turkish sites, measured TAP was in both years above the long-term mean (725 mm). TAP was lower in 2013 than in 2014 and tended to be higher at T1 (2013: 754 mm and 2014: 1112 mm) than at T3 (2013: 698 mm and 2014: 1010 mm). Both years exhibited a distinct drought period during summer with the lowest precipitation values reached in August and September 2013 (T1: 0 mm, T3: 1.4 mm). At the German site, TAP in 2013 amounted to 789.7 mm, which was above the long-term mean of 724 mm, while in 2014, it amounted to 600 mm being clearly lower than the long-term mean. Precipitation was evenly distributed over the years, but exceptionally low during June 2014 (18.1 mm).

### Wood formation phenology

Cambium and wood formation phenologies were observed by repeated microcoring during the growing season of



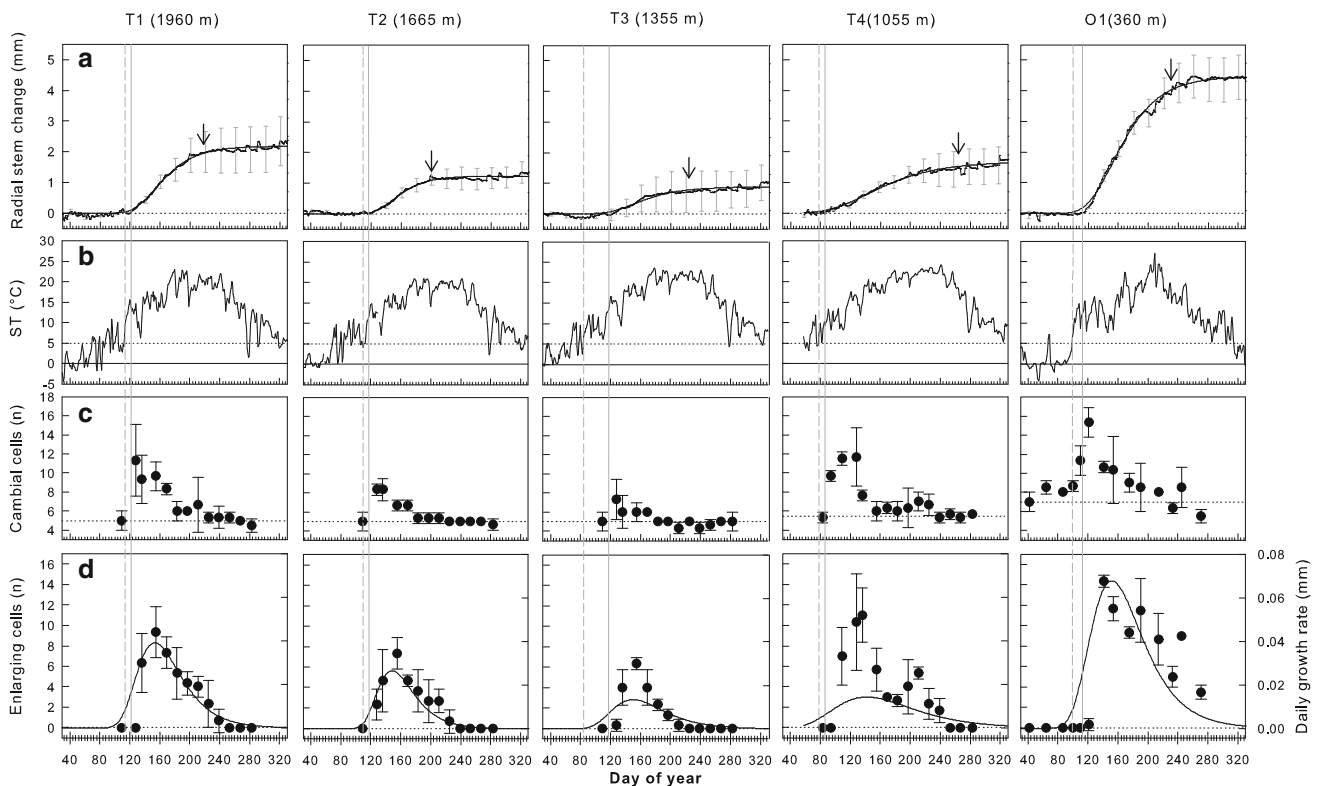
2013. The onset of CA, as characterized by a distinct increase of the number of cambial cells above the cell number of the dormant cambium, could be observed at all study sites (Fig. 3c; Table 4). When daily mean ST continuously remained above a threshold of 5 °C, cambia became active approximately 1–2 weeks later, so, likely, this temperature acts as a signal to the respective cambium. Only at T3, the cambium needed 4 weeks to become active (Fig. 3b–c). Critical dates (DOY) and durations (Table 4) of wood formation phenology showed significant differences ( $p < 0.05$ ) between the five study sites (Table 5), except for bM which started approximately around 11 June (Kruskal–Wallis test,  $\chi^2 = 8.63$ ,  $p = 0.071$ ). Cell enlargement (bE) started first at T4 around 13 April (DOY 102) and last around 4 weeks later at T1 (DOY 130) showing a trend of later wood formation onsets with increasing altitude (Fig. 4a). Beginning of cell-wall lignification (bL) followed bE after 16 days at the earliest (Fig. 4b). Cell enlargement ended first at T3 and last at O1 lasting approximately between 3 and 7 months, respectively (Fig. 4d, f). Cessation of lignification (cL) followed

cE approximately 4–6 weeks later. Only at O1 dates for cE and cL were identical (Fig. 4e). All in all, cessation of wood formation showed no clear altitudinal trend. While dL lasted around 2–4 weeks longer than dE at the Turkish sites, it appeared to last shorter at O1 (Fig. 4f–g). Overall, xylogenesis of Lebanon Cedar growing at different altitudes lasted between 5 and 7 months, with the shortest durations at T3 (about 129 days) and the longest at T4 and O1 (173 and 192 days, respectively) (Fig. 4h), showing an altitudinal trend.

## Radial growth dynamics and inter-annual variability

### Radial growth dynamics

At all sites, dendrometer records were characterized by a ‘plateau’ (Wang et al. 2015) during winter dormancy and early spring and a progressive almost linear RSI during the growing season with typical diurnal stem radius fluctuations of swelling and shrinking (Fig. 3). The beginning of



**Fig. 3** **a** Mean radial stem change of Lebanon Cedar at the Turkish sites (T1 to T3:  $n = 7$ ; T4:  $n = 9$ ) and the German site (O1:  $n = 4$ ) in 2013 and net radial increment modelled by applying the Gompertz function (black smooth line). Arrows point to  $A_{90\%}$  (date when 90% of the annual radial increment is reached). **b** Mean daily stem temperature (ST). Solid black lines indicate 0 °C, and dotted black lines indicate 5 °C. **c** Number of cambial cells and **d** enlarging cells which were determined by microcore sampling ( $n = 3$  trees per site).

Daily growth rate was calculated on the basis of the modelled radial increment. The dashed vertical grey lines indicate the date after which mean daily ST stays above 5 °C. The solid vertical grey lines indicate the date after which the cambium is noticeably active ( $n$  cambial cells  $> n$  dormant cambial cells) and dendrometer records show a continuous increase. At that time, dendrometer records were set to zero. For each respective parameter, scales of the y-axis and x-axis are identical

**Table 4** Critical dates (DOY) and durations of Lebanon Cedar wood formation in 2013 ( $n = 3$  trees/site)

Site	Mean daily $ST > 5^\circ$ (DOY)	Onset of CA (DOY)	bE (DOY)	bL (DOY)	bM (DOY)	cE (DOY)	cL (DOY)	dE (days)	dL (days)	dX (days)
T1	113	120	130 ± 0.0	146 ± 0.0	162 ± 0.0	232 ± 0.0	272.6 ± 4.0	102 ± 0.0	126.6 ± 4.0	142.6 ± 4.0
T2	111	116	117 ± 0.0	146 ± 0.0	162 ± 0.0	232 ± 0.0	275 ± 0.0	115 ± 0.0	129 ± 0.0	158 ± 0.0
T3	84	113	117 ± 0.0	146 ± 0.0	156 ± 17.3	208.6 ± 8.0	250.6 ± 8.0	91.6 ± 8.0	104.6 ± 8.0	133.6 ± 8.0
T4	78	84	104.3 ± 4.04	114.3 ± 4.61	146 ± 0.0	246 ± 0.0	275 ± 0.0	141.6 ± 4.0	160.6 ± 4.6	170.6 ± 4.0
O1	99	111	120 ± 9.2	131 ± 0.0	164 ± 0.0	302.6 ± 7.5	302.6 ± 7.5	182.3 ± 16.7	171.6 ± 7.5	182.3 ± 16.7

Values present mean ± SD. For statistical tests, see Table 5 and Fig. 4  
DOY day of year, *ST* mean daily stem temperature, *CA* cambial activity

net RSI differed only 1–2 days between all trees at one site but varied clearly between sites. In both years, net RSI was recorded approximately 1–2 weeks after daily mean *ST* stayed above a threshold of 5 °C (4 weeks for T3). At this date, dendrometer records were set to zero for growth modeling and dSRV-climate analysis (Fig. 3, shown for 2013). In 2014, after winter dormancy, the critical *ST* threshold of 5 °C was reached about 5 days earlier at the Turkish sites and 8 days earlier at the German site as compared to 2013. Radial growth modelled by Gompertz fittings described the course of RSI from dendrometer records very well ( $R^2 = 0.93$ – $0.99$ ; Table 6; Fig. 3a). To test for between-site differences of parameters obtained from Gompertz fittings, ANOVA was performed (Table 6). Mean *A* varied between 0.98 and 4.47 mm and did significantly differ between sites (ANOVA,  $F = 21.73$ ,  $p < 0.001$  for 2013 and  $F = 12.53$ ,  $p < 0.001$  for 2014) with the highest *A* observed at O1 and the lowest at T2 and T3. Trees at sites with lower LAI tended to have higher *A* (Fig. 5a). Maximum growth rate at  $t_p$  was significantly higher at O1 (ANOVA,  $F = 26.53$ ,  $p < 0.001$  for 2013 and  $F = 6.51$ ,  $p < 0.01$  for 2014). Mean *r* varied between 8.23 and 32.7 μm and was also significantly higher at O1 compared to the Turkish sites in 2013 (ANOVA,  $F = 23.46$ ,  $p < 0.001$ ). Within the Turkish sites, T1 showed highest *r* in both years (ANOVA,  $F = 8.05$ ,  $p < 0.01$  for 2014). Timings of  $t_p$  occurred mainly around the beginning of June (ANOVA,  $F = 1.58$ ,  $p > 0.05$  for 2013 and  $F = 25.06$ ,  $p < 0.001$  for 2014).

*Inter-annual variability*

To test for significant differences between years, *t* tests were performed on parameters obtained from Gompertz curve fittings (Table 6). In 2014, *A* was significantly higher at T1 ( $t = -4.6$ ,  $p < 0.01$ ) and T4 ( $t = -2.3$ ,  $p < 0.05$ ), and significantly lower at O1 ( $t = 4.6$ ,  $p < 0.05$ ) compared to 2013. Changes in *A* at T2 and T3 were not significant ( $p > 0.05$ , Fig. 5b). Maximum growth rate at  $t_p$  showed significant differences at T4 (higher value in 2014,  $t = -7.9$ ,  $p < 0.001$ ) and O1 (higher value in 2013,  $t = 6.7$ ,  $p < 0.01$ ). Mean *r* increased significantly in 2014 at T1 ( $t = -4.8$ ,  $p < 0.01$ ) and T4 ( $t = -6.7$ ,  $p < 0.001$ ) and decreased significantly at O1 ( $t = 6.6$ ,  $p < 0.01$ ). At T3, none of the parameters differed significantly between years.

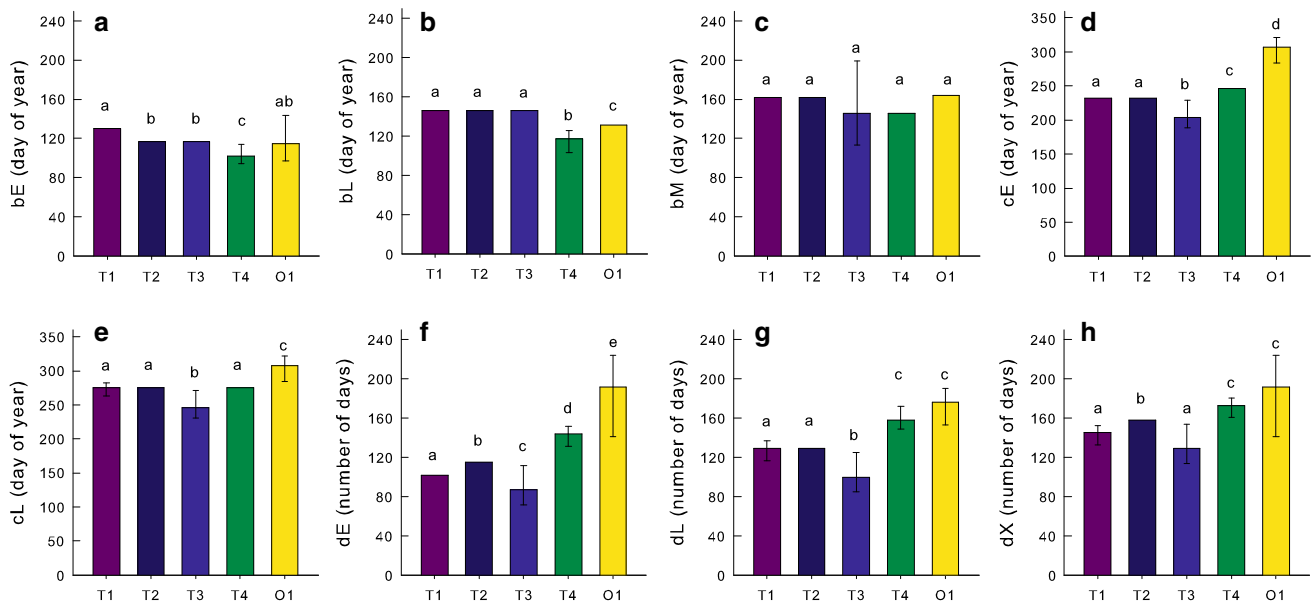
**Relation between wood formation phenology and stem growth dynamics**

For all studied Lebanon Cedar trees, onset of CA, as characterized by a significant increase in the number of cambial cells (Fig. 3c), appeared at the same time when

**Table 5** Statistics for the Kruskal–Wallis test between critical dates (DOY) and durations at the five Lebanon Cedar study sites

	bE	bL	bM	cE	cL	dE	dL	dX
$\chi^2$	9.95	13.90	8.63	13.84	13.03	13.77	13.17	12.81
<i>p</i>	<b>0.041</b>	<b>0.008</b>	0.071	<b>0.008</b>	<b>0.011</b>	<b>0.008</b>	<b>0.010</b>	<b>0.012</b>

Significant values at  $p < 0.05$  are bold



**Fig. 4** Comparison of critical dates (DOY) and durations of wood formation computed from raw cell count data of Lebanon Cedar between the study sites (T1 to T4; Turkish sites and O1: German site) in 2013. bE, bL, and bM stand for onset of enlarging, cell-wall lignification, and mature phases, cE and cL for cessation of enlarging and cell-wall lignification phases, and dE, dL, and dX stand for

durations of the enlarging and lignification phases as well as the duration of xylogenesis. Bars correspond to the 95% confidence limits of the median ( $n = 3$  trees per site). Different letters indicate significant differences among groups ( $p < 0.05$ ) within a graph based on Mann–Whitney  $U$  tests

dendrometer records indicated a net linear increase in stem radii (Fig. 3a, c). At all sites, CA and dE were within the time span of net RSI (Fig. 3). Daily growth rates, calculated as first derivatives on the basis of the modelled radial increment (Gompertz curve fit), followed very well the course of number of enlarging cells obtained from microcores (Fig. 3d). Maximum growth rate occurred around the same time as the maximum number of enlarging cells and before summer solstice (DOY 172).

Gompertz curves fitted very well the measured RSI from both, dendrometer records (Fig. 3a) and microcore samples (not shown). The proportion of variance explained varied between 0.81 and 0.99 ( $R^2$ , Table 6). In 2013, Gompertz fittings on the ring widths from both, microcore samples and dendrometer records, highly significantly correlated with each other ( $p < 0.05$ , Fig. 6). Values for  $A$  were always higher for dendrometer records, except for T4 (Fig. 6a). The larger growth estimates by dendrometers included also phloem cells, while microcores include xylem cells, only. Growth rate  $r$  was very similar for T2,

T3, and O1, higher for dendrometer records at T1 and markedly lower for dendrometer records at T4 (Fig. 6b). Timing of  $t_p$  occurred generally later in microcores (Fig. 6c). Apart from two exceptions (one tree at O1 and T1),  $d$  was always higher for dendrometer records (Fig. 6d).

#### Daily stem radius variation (dSRV) in relation to meteorological factors

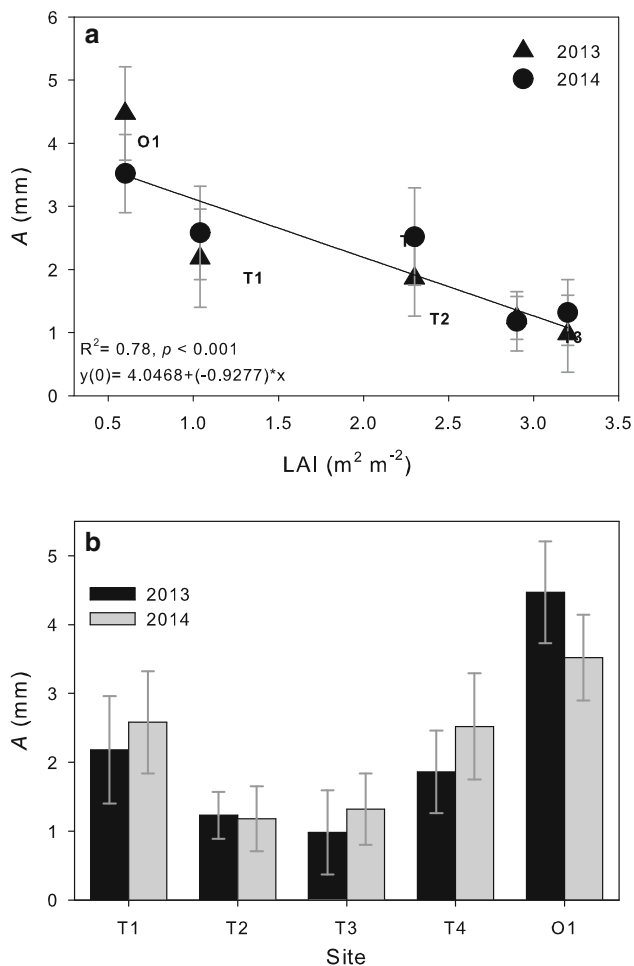
Among the Turkish sites, dSRV were quite synchronous (Fig. 7a–d). During the main period of net RSI (see Fig. 3), dSRV varied from  $-0.057$  to  $+0.128$  mm at the Turkish sites and from  $-0.052$  to  $+0.257$  mm at the German site (Fig. 7e). Only few negative dSRV values occurred during this period. At all sites, dSRV responded quite similarly to meteorological factors. Pearson correlation coefficients were calculated for dSRV and ten climate variables (Fig. 8). At all five sites, dSRV showed closest correlations ( $p < 0.01$ ) to rH and Pp (both positive correlations).

**Table 6** Parameters of Gompertz curve fits on tree-ring growth measured by microcoreing (MC) and dendrometers (D)

Site	Year	Method	<i>n</i>	<i>A</i>	<i>b</i>	<i>k</i> (10 <sup>-2</sup> )	<i>R</i> <sup>2</sup>	<i>t</i> <sub>p</sub> (DOY)	Maximum growth rate at <i>t</i> <sub>p</sub> (μm d <sup>-1</sup> )	<i>r</i> (μm d <sup>-1</sup> )	<i>d</i> (days)
T1	2013	MC	3	1.53 ± 0.42	6.39 ± 1.50	3.89 ± 0.82	0.98	164.2 ± 6.2	16.43 ± 1.42	14.30 ± 1.22	106.0 ± 22.2
		D	7	<b>2.18 ± 0.78<sup>A</sup></b>	5.50 ± 0.30	3.59 ± 0.29	0.98	153.3 ± 5.3 <sup>A</sup>	40.32 ± 11.9 <sup>A</sup>	<b>19.26 ± 5.68<sup>A</sup></b>	111.9 ± 9.0 <sup>AB</sup>
T2	2014	D	7	<b>2.58 ± 0.74<sup>a</sup></b>	5.72 ± 0.53	3.81 ± 0.43	0.99	150.9 ± 6.7 <sup>bc</sup>	45.0 ± 9.62 <sup>a</sup>	<b>24.1 ± 5.17<sup>a</sup></b>	106.3 ± 12.3 <sup>ab</sup>
		MC	3	1.08 ± 0.46	8.27 ± 1.38	5.31 ± 0.96	0.95	156.2 ± 11.7	15.70 ± 4.40	13.67 ± 3.85	76.8 ± 12.9
T3	2013	D	7	1.23 ± 0.34 <sup>AB</sup>	6.50 ± 0.95	4.38 ± 0.71	0.97	148.9 ± 4.7 <sup>A</sup>	27.6 ± 6.98 <sup>AB</sup>	13.20 ± 3.32 <sup>AB</sup>	<b>93.8 ± 17.9<sup>A</sup></b>
		D	7	1.18 ± 0.47 <sup>b</sup>	7.97 ± 1.78	5.44 ± 1.25	0.97	147.0 ± 4.4 <sup>a</sup>	31.35 ± 6.79 <sup>ab</sup>	14.99 ± 3.24 <sup>bc</sup>	<b>77.10 ± 18.1<sup>b</sup></b>
T4	2014	MC	3	0.62 ± 0.23	8.87 ± 3.69	5.73 ± 2.28	0.81	154.4 ± 7.3	10.02 ± 5.61	8.73 ± 4.86	80.7 ± 41.2
		D	7	0.98 ± 0.61 <sup>B</sup>	5.09 ± 1.37	3.06 ± 1.01	0.93	177.4 ± 54.0 <sup>A</sup>	17.34 ± 13.59 <sup>B</sup>	8.23 ± 6.56 <sup>B</sup>	149.4 ± 67.7 <sup>ACD</sup>
O1	2013	D	7	1.32 ± 0.52 <sup>b</sup>	5.42 ± 0.83	3.75 ± 0.67	0.97	145.1 ± 4.3 <sup>a</sup>	24.64 ± 8.12 <sup>b</sup>	12.01 ± 3.96 <sup>c</sup>	109.1 ± 16.6 <sup>a</sup>
		MC	3	2.96 ± 1.07	4.59 ± 1.22	3.09 ± 1.23	0.95	153.2 ± 20.6	27.67 ± 9.66	21.38 ± 5.10	141.5 ± 45.9
O1	2014	D	9	<b>1.90 ± 0.67<sup>AB</sup></b>	2.77 ± 0.40	1.89 ± 0.29	0.97	<b>147.6 ± 14.9<sup>A</sup></b>	<b>15.23 ± 4.97<sup>B</sup></b>	<b>8.89 ± 2.87<sup>B</sup></b>	<b>216.2 ± 35.2<sup>C</sup></b>
		D	9	<b>2.52 ± 0.77<sup>a</sup></b>	4.26 ± 0.68	3.32 ± 0.57	0.98	<b>128.8 ± 5.3<sup>b</sup></b>	<b>41.30 ± 10.64<sup>a</sup></b>	<b>20.40 ± 5.25<sup>ab</sup></b>	<b>123.7 ± 21.7<sup>a</sup></b>
O1	2013	MC	3	3.30 ± 0.78	6.17 ± 1.35	3.66 ± 0.93	0.98	169.8 ± 6.3	50.60 ± 5.48	29.05 ± 3.12	114.0 ± 28.2
		D	4	<b>4.47 ± 0.74<sup>C</sup></b>	4.49 ± 0.33	2.95 ± 0.28	0.99	152.2 ± 4.4 <sup>A</sup>	<b>68.40 ± 8.52<sup>C</sup></b>	<b>32.7 ± 4.09<sup>C</sup></b>	136.4 ± 13.2 <sup>BD</sup>
O1	2014	D	4	<b>3.52 ± 0.62<sup>a</sup></b>	4.04 ± 0.87	2.56 ± 0.55	0.98	158.5 ± 8.7 <sup>c</sup>	<b>46.45 ± 11.25<sup>a</sup></b>	<b>22.36 ± 5.3<sup>ab</sup></b>	161.9 ± 36.1 <sup>c</sup>

Values present mean ± SD. Capital letters indicate significant between-site differences (ANOVA) for parameters obtained from dendrometer records in 2013 (lower case letters = significant differences in 2014). Significant differences between years (*t* test, *p* < 0.05) are bold

*n* number of trees, *A* upper asymptote for final annual ring width (in mm), *b* x-axis placement, *k* rate of change parameter, *t*<sub>p</sub> time of inflection point, *r* mean tree-ring formation rate, *d* time required for major period of tree-ring formation



**Fig. 5** **a** Relationship between mean total annual tree-ring widths ( $A$ ) and LAI and **b**  $A$  of Lebanon Cedar obtained from dendrometer measurements and Gompertz fittings for the measurement sites (T1 to T3:  $n = 7$ , T4:  $n = 9$ , O1:  $n = 4$ ) at the end of the growing season in either 2013 (black bars) or 2014 (grey bars). Error bars indicate  $\pm$  SD

Significant negative correlations of dSRV ( $p < 0.01$ ) were found for gR and VPD. Less tight relations were found for  $Ta_{max}$  (negative correlation). Only at O1, dSRV showed a significant positive correlation to  $Ta_{min}$  and SWC. T1, T3, and T4 showed a significant negative correlation and linear relationship to ST. No correlations were found for dSRV and Ts at all sites. At all sites, simple linear regressions showed significant correlations between dSRV and  $Ta_{max}$ , Pp, rH, VPD, and gR (Fig. 9) and none between dSRV and SWC. Multiple linear regression models explained between 30 and 51% of the variation in dSRV during the main period of net RSI (Table 7). Because of different lengths in the growing seasons and for missing data, the number of days analyzed in the regression models varied between sites. Standardized coefficients ( $\beta$ ) show that rH had the greatest influence on dSRV at most sites (except T2 and T3) and for “all sites”. The model for T2 did not include

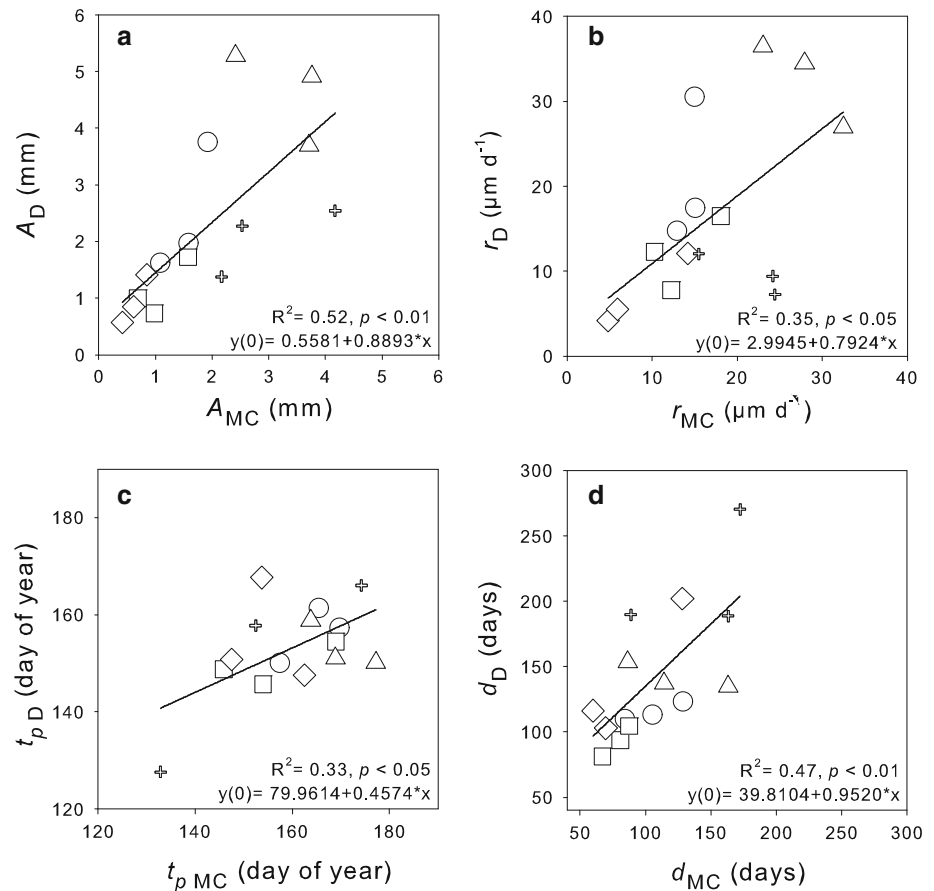
rH but instead of that Ts had the highest impact on dSRV. Pp was present in all models with different degrees of influence. Only at O1, SWC was not included in the model.

## Discussion

### Microcore sampling and dendrometer records in studies on wood formation

In many studies, microcore sampling was successfully used to address interrelationships of growth in various tree species and ecosystems: e.g., with climate (Camarero et al. 2010; Oberhuber and Gruber 2010; Rossi et al. 2008b), with wood formation along altitudinal (Moser et al. 2010) and latitudinal gradients (Huang et al. 2011), in different parts of a tree (Thibeault-Martel et al. 2008) or as related to tree age or social status (Rathgeber et al. 2011a; Rossi et al. 2008a). All these studies contributed to a better understanding of factors controlling wood formation. However, some issues that remain open when using microcore sampling are that it is quite costly and time consuming, which limits sampling intervals. Furthermore, growth heterogeneity in wood formation may result in different wood formation dynamics around the stem. Therefore, attempts of standardizing cell numbers were made (Deslauriers et al. 2008). In our study, we sampled three trees per site at bi-weekly intervals, which in our analysis caused some critical dates to be seemingly the same (e.g., cE and cL at O1, see Table 4). Still, an altitudinal gradient was visible, with earlier onsets (critical dates) and longer durations at lower sites. In comparison, when using dendrometers to record stem radius changes, the quantification of cambial growth and determination of critical timings of wood formation still remain problematic (Chan et al. 2016; Mäkinen et al. 2008). Therefore, most of the studies using dendrometers investigate stem water status and short-term growth responses to changing environmental conditions by extracting dSRV (Drew and Downes 2009; Wimmer et al. 2002; Zweifel and Häslér 2001). Recent promising studies increasingly focus on how to separate cambial growth and wood formation from other signals that lie within the measured dSRV (Chan et al. 2016; Deslauriers et al. 2003b; Zweifel et al. 2016). A combination of both methods (dendrometers and microcoring) is generally used to set dendrometer records to zero when CA or first enlarging cells are detected based on microcore samples (Oberhuber et al. 2014). Dendrometer records in Lebanon Cedar showed the beginning of a quasi-linear increase in radius at the time when onset of CA was detected by a clear increase of cambial cell number. Studies of Linares et al. (2009) on the Mediterranean conifer *Abies pinsapo*, showed that, because of the swelling of the stem, growth

**Fig. 6** Relationships between parameters obtained from Gompertz fittings either for microcore samples (MC) or for dendrometer records (D), as measured on Lebanon Cedar. One symbol represents one tree ( $n$  trees per site = 3, circles T1, squares T2, diamonds T3, crosshairs T4, and triangles O1). **a**  $A$  total annual tree-ring width, **b**  $r$  mean growth rate (during the main period of tree-ring formation), **c**  $t_p$  time of inflection point, **d**  $d$  main period of tree-ring formation



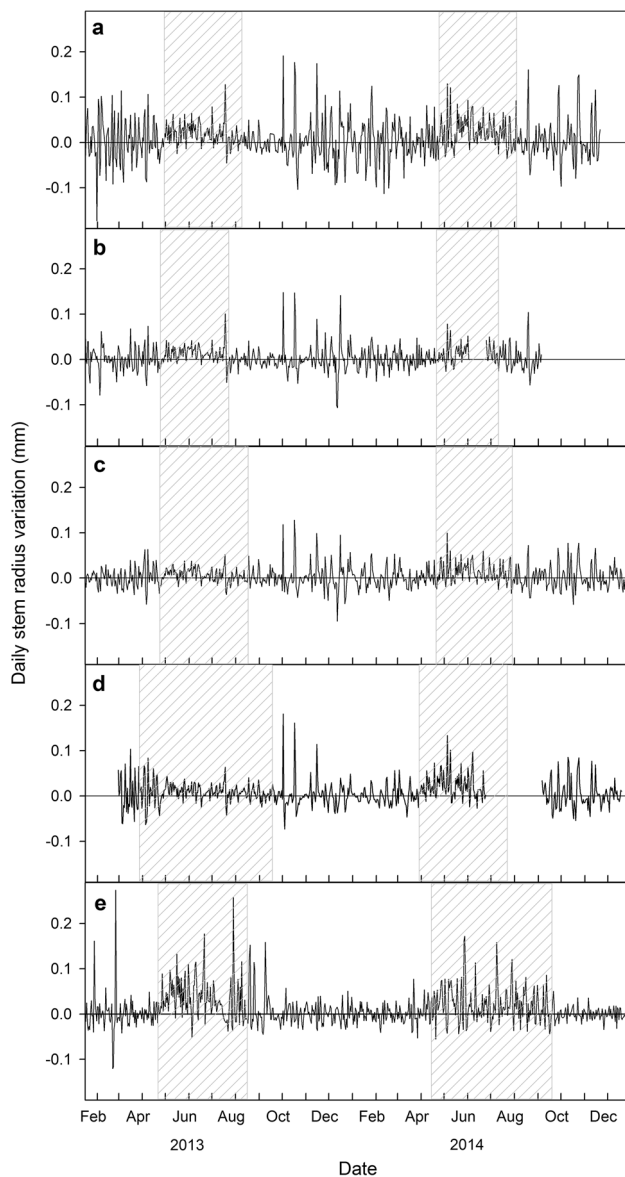
onset seemed to start almost 3 weeks earlier according to dendrometer records than actually measured by microcores. In our study, we could clearly observe the beginning of CA by dendrometers with a difference of only 1–2 days. The phase shift between both methods may be minimized by an almost complete removal of bark and cortex, where the point dendrometers are placed. We, furthermore, have indications (measurement of xylem tension via pressure bomb, data not shown) that at our sites, stems of Lebanon Cedar were already fully rehydrated before onset of CA due to good water supply during early spring (Deslauriers et al. 2003b).

Overall, dendrometer records and microcores provided useful results concerning the radial growth patterns in Lebanon Cedar, and the Gompertz function was suitable for modeling its growth dynamics because of its monotonous growth pattern (Linares et al. 2009). Comparing Gompertz curve fittings on ring width data from microcoring and dendrometer records shows a highly significant correlation (see Fig. 6). Measured  $A$  were more likely to be higher in dendrometer records and timings of  $t_p$  occurred later in microcores. This seemed apparently to be mainly caused by phloem growth. Growth heterogeneity around the stem could have also lead to differences

between dendrometer and microcore results. Our results show the potential that both methods could be linked if approaches may be found that minimize or neutralize effects, such as, e.g., phloem growth. Therefore, further studies which combine both methods are needed to increase the compliance of results obtained from dendrometer records and microcores. In the long term, it may be possible to continuously monitor actual wood formation in high resolution and to differentiate between the different phases of the developing tree ring with the help of dendrometer records.

### Growth behavior of Lebanon Cedar at different sites and climates

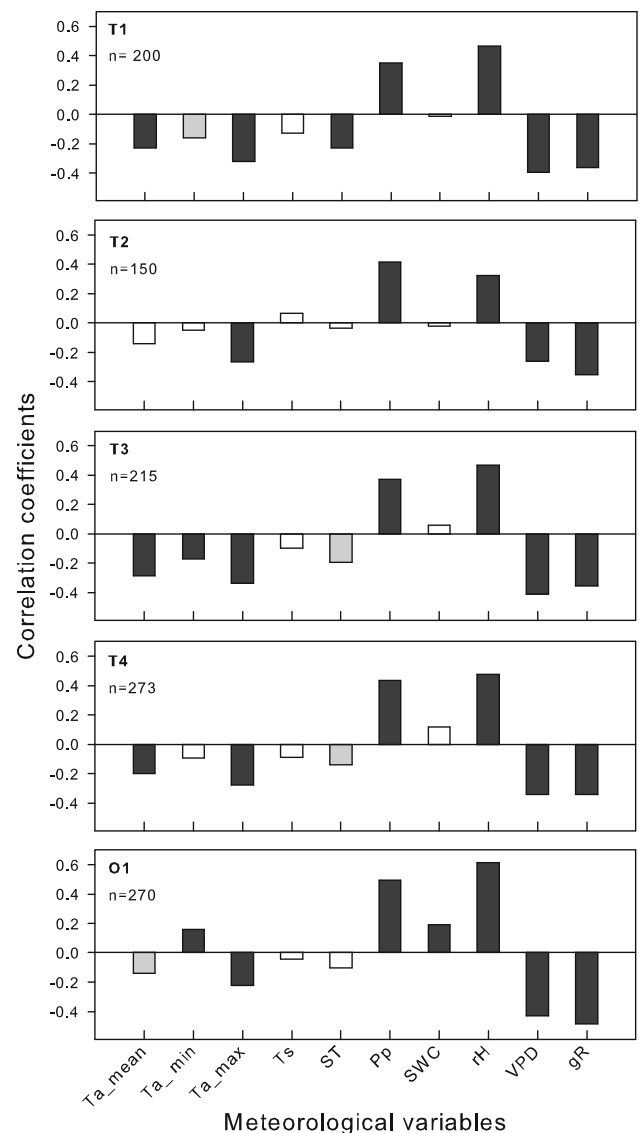
Growth behavior of Lebanon Cedar varied with respect to site-climate and other site characteristics but revealed no marked altitudinal gradient. Its annual course of stem growth was typical for trees of the temperate region starting in spring, ending in autumn, and resting during winter (Mäkinen et al. 2003), resulting in the characteristic “s-shape” (logistic growth curve), as, e.g., reported by Rossi et al. (2006b). We did not observe any severe stress symptoms at any of the study sites that might have



**Fig. 7** Annual courses of mean daily stem radius variations (dSRV) in Lebanon Cedar measured in 2013 and 2014 at the Turkish sites **a** T1 1960 m, **b** T2 1665 m, **c** T3 1350 m, **d** T4 1055 m, and **e** the German site O1 360 m. Grey shadings indicate the main periods of net radial stem increases considered for dSRV analysis

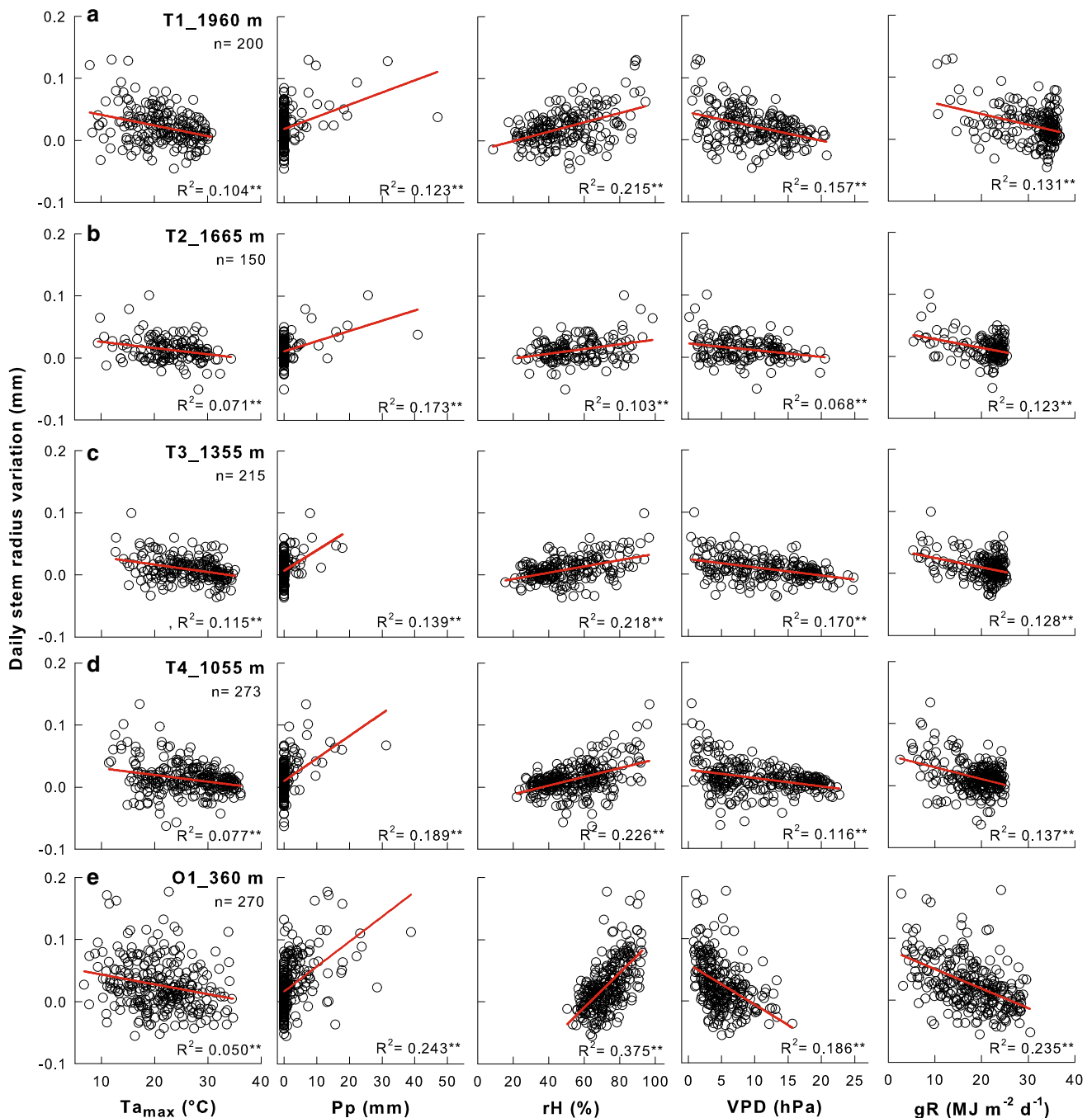
markedly early terminated or interrupted growth. A bimodal growth pattern with cambial rest during summer drought, as reported for some conifers from the Mediterranean, was also absent (Camarero et al. 2010; de Luis et al. 2007; Linares et al. 2009; Liphshitz and Lev-Yadun 1986; Vieira et al. 2014).

A clear threshold in temperature and initiation of CA in spring was reported in several studies on conifers of high altitudes which range from 4 to 5 °C for daily  $T_{a_{min}}$  and 7.2–9.5 °C for mean ST (Anfodillo et al. 2012; Deslauriers et al. 2008; Rossi et al. 2007, 2008b). We observed an ST



**Fig. 8** Pearson correlation coefficients between daily stem radius variation (dSRV) of Lebanon Cedar and meteorological climate variables ( $T_a$  air temperature,  $T_s$  soil temperature,  $ST$  stem temperature,  $Pp$  precipitation,  $SWC$  soil water content,  $rH$  relative air humidity,  $VPD$  vapor pressure deficit,  $gR$  global radiation) at the five study sites during the main growth period in 2013 and 2014.  $T_s$ ,  $ST$ ,  $SWC$ ,  $rH$ , and  $VPD$  represent daily means, and  $Pp$  and  $gR$  represent daily sums. Level of significance:  $p < 0.05$  for grey bars;  $p < 0.001$  for dark grey bars (n.s. = white bars)

threshold of 5 °C after which the cambium needed 1–2 weeks to become active (except at T3). During this time, air temperatures sometimes dropped below zero for a short while, but living tissues seemed to be sufficiently isolated by the bark. The delay in onset of CA at T3 could underline the importance of light availability on growth of Lebanon Cedar. T3 had the highest stand density and LAI, and when taking the exposition and slope of this site into account, favorable light conditions at the beginning of the



**Fig. 9** Relationship between daily stem radius variation (dSRV) of Lebanon Cedar and daily meteorological climate variables during the main growth period in 2013 and 2014 ( $T_{max}$  maximum air temperature,  $Pp$  precipitation sum,  $rH$  mean relative air humidity,

$VPD$  mean vapor pressure deficit, and  $gR$  global radiation sum) at the five study sites (**a–d** Turkish sites; **e** German site). For each respective parameter, scales of the y-axis and x-axis are identical.  $n$  number of days per site. Level of significance: \* $p < 0.05$ ; \*\* $p < 0.01$

growing season may have occurred later than compared to the other sites. Lebanon Cedar as a light-demanding species (Senitzka 1989) might, therefore, had to face a delay of becoming physiologically and photosynthetically active, since assimilated carbon is needed for structural investment into new xylem cells (Rossi et al. 2007). A delayed rise of sap flux density (measured, but not shown) underlines the

suggestion that unfavorable light conditions in early spring could lead to a delay in growth initiation at T3. In fact, light availability influences the overall growth performance: Trees of sites of the highest LAI and stand density (T2 and T3) exhibited the lowest growth rates and formed the thinnest tree rings (dendrochronological analysis performed on 15 trees per site; data not shown). Furthermore,



**Table 7** Results of the multiple linear regression analysis between dSRV (dependent variable) and meteorological variables for Lebanon Cedar during the growth period of 2013 and 2014

Site	<i>n</i>	<i>R</i> <sup>2</sup>	b0	Climate parameter	Regression coefficient	$\beta$	<i>t</i>	<i>p</i>
T1	200	0.35	25.67	rH	0.75	0.46	6.92	<0.001
				SWC	-1.69	-0.39	-5.38	<0.001
				Pp	1.68	0.30	4.76	<0.001
				DOY	-0.16	-0.17	-2.40	<0.001
T2	150	0.37	-15.01	Ts	4.79	0.90	5.44	<0.001
				Ta <sub>max</sub>	-2.49	-0.66	-6.17	<0.001
				Pp	1.31	0.33	4.77	<0.001
				SWC	0.83	0.31	2.19	<0.05
T3	215	0.33	40.70	SWC	-1.08	-0.58	-4.82	<0.001
				rH	0.53	0.49	6.81	<0.001
				DOY	-0.24	-0.41	-3.48	<0.01
				Pp	1.82	0.21	3.28	<0.01
T4	273	0.32	-17.91	rH	0.71	0.48	7.13	<0.001
				Pp	2.20	0.26	4.71	<0.001
				SWC	-0.59	-0.21	-3.36	<0.01
O1	270	0.52	-206.11	rH	3.20	0.70	11.89	<0.001
				Ta <sub>mean</sub>	3.49	0.37	6.19	<0.001
				DOY	-0.32	-0.31	-6.01	<0.001
				Pp	1.73	0.21	4.34	<0.001
All	1108	0.30	-16.31	rH	0.68	0.41	12.84	<0.001
				Pp	2.25	0.32	11.69	<0.001
				SWC	-0.45	-0.17	-5.62	<0.001

Climate parameters are listed according to their weight in the model (from high to low)

The multiple regression analyses followed the general model  $dSRV = b_0 + b_1 \times x_1 + b_2 \times x_2 + \dots + b_i \times x_i$ , where  $b_0$  is the constant and  $b_i$  represents the respective regression coefficient

For all Models and parameters, the level of significance (*p*) is <0.05

*n* number of days analyzed, *R*<sup>2</sup> coefficient of determination,  $\beta$  standardized coefficient which shows the relative importance of the independent variable, and *t* value of *t* statistic

light availability appears to play an important role concerning culmination of growth. At all sites, growth culminated before or around summer solstice, which leaves enough time for the trees in the remaining growth season to complete the differentiation of newly formed tracheids before winter (Rossi et al. 2006c, 2008b).

Compared to 2013, in 2014, annual tree rings were significantly wider at the Turkish sites T1 and T4, which could be explained by the fact that in 2014, TAP was higher and summer drought was less severe. Other studies from Mediterranean ecosystems (Camarero et al. 2010; Linares et al. 2009; Vieira et al. 2014) and dendrochronological studies on Lebanon Cedar (Akkemik 2003) showed that low precipitation was an important factor limiting tree growth during summer and Ren et al. (2015) demonstrated how precipitation triggers onset of xylogenesis in Qilian juniper. The earlier onset of growth (the threshold ST of 5 °C was reached approximately 1 week earlier) allowed for a longer period of xylogenesis and, thus, could have favored the formation of wider tree rings (e.g., Lupi et al. 2010). Furthermore, the favorable

growth conditions at the beginning of the growing season seemed to cause higher growth rates which also corresponded with wider tree rings in Lebanon Cedar. This was already stated in other wood formation studies on conifers (Cuny et al. 2012; Rathgeber et al. 2011a). Tree rings at O1 were significantly narrower in 2014, although the threshold ST of 5 °C was reached earlier in 2014 than in 2013 at O1 causing a longer period of xylogenesis. We, therefore, suggest that the less favorable growth conditions (TAP was lower and rainfall in June 2014 was markedly low at the EBG) lead to lower growth rates thus causing narrower tree rings. At T2 and T3, tree rings were generally very narrow showing no significant differences between the study years (2013 and 2014) as compared to the other sites. Therefore, we suggest that, besides microclimatic conditions, other factors (soil properties, nutrient availability, etc) may also play an important role; obviously, wood-formation patterns in Lebanon Cedar are quite site specific (del Castillo et al. 2016).

Analysis of microclimatic effect on dSRV leads to a better understanding of how Lebanon Cedar responds to

short-term changes in climate (Urrutia-Jalabert et al. 2015). During the main growth period, dSRV was positively related to Pp and rH and negatively related to  $T_{a,max}$ , VPD, and gR. The positive effect of Pp and humidity on SRV was to be expected and had been reported for several conifer and broadleaved species (Deslauriers et al. 2003b; Köcher et al. 2012), as they directly favor cell enlargement by increasing the water status in the stem (Steppe et al. 2015). In comparison, high  $T_{a,max}$ , VPD, and gR exert negative effects on cell turgor and, therefore, tend to inhibit cell enlargement and growth (Pantin et al. 2012). Multiple linear regression analyses allowed for an insight into combined effects of climate parameters on dSRV and revealed that rH, SWC, and Pp dominate dSRV. As to be expected, stem growth in Lebanon Cedar was favored by humid conditions during the main growing season, which is in accordance with results from temperate ecosystems (Köcher et al. 2012; Köstner et al. 1998). Downes et al. (1999) stated that soil water is a major determinant of CA. The absence of SWC in the model of O1 (see Table 7) may be due to the generally much moister climate at the EBG with water supply evenly distributed throughout the year. This is in accordance with findings of Köcher et al. (2012) who predict that the influence of atmospheric water status on daily stem growth patterns in temperate broadleaved species is large in comparison with soil water status when for generally moist conditions, no drought periods come up. The rate of the variation in our models showed that dSRV cannot be explained by climate data alone (Downes et al. 1999), and such unknown effects of parameters other than climate should be investigated in future studies; they may increase the explanatory power of the models.

### Forecasts on the use of Lebanon Cedar and response to future climate change

Results from our Turkish study sites show that this species is well adapted to its current local climate conditions but also shows good growth performance under Central European climate. Lebanon Cedars robustness was demonstrated by reforestation projects performing broadcast seeding in bare karstic lands in the Taurus Mountains (40,457 ha until 2005) (Boydak 2007). Successful afforestation projects in Inner-Anatolian regions (Akgül and Yılmaz 1986) show that Lebanon Cedar is even capable of growing under continental-like climate conditions exhibiting cold winters and low TAP in combination with elongated drought periods during summer [e.g., in areas around Ankara: MAT of 11.6 °C and TAP of 344 mm, Turkish State Meteorology Service (2005)]. Planting success amounted to 70–90% inside and 50–80% outside of its range, respectively (Boydak 2007). We, therefore, expect that in the close future, Lebanon Cedar will not face severe

growth stress at its natural distribution range even under expected climate changes in the Mediterranean becoming drier and hotter (Stocker 2014). The discussion intensifies whether it is a potential forest species to establish plantations and/or to substitute indigenous species, e.g., in Central European regions also facing climate change (Huber and Storz 2014; Messinger et al. 2015). Even though local TAP and MAT at the German study site (EBG, Northern Bavaria) are very similar to the Turkish sites, the fact that annual precipitation is distributed evenly throughout the year seems to be one of the most favorable growth conditions. Growth potential of Lebanon Cedar at the EBG was recently evaluated by Messinger et al. (2015). They showed that the cedar individuals exhibited extraordinary growth with no visible signs of biotic and abiotic damages until now. Furthermore, despite developing wide tree rings, wood properties of felled individuals showed no loss of wood quality (Risse 2013). As a light-demanding species (Senitz 1989), it showed best growth performance in stands of low tree density (Messinger et al. 2015) and low LAI as also observed in our study. Another study in Lebanon Cedar stands near Isparta, SW-Turkey, showed that thinning treatments lead to increases of diameter, basal area, and stem volume (Carus and Catal 2010). Therefore, in plantation projects, it must be ensured that spacing for Lebanon Cedar is sufficient to develop its full growth potential.

### Conclusions

Our study provided insights into intra-annual stem growth of Lebanon Cedar under different site- and climate conditions. High-resolution dendrometer records allowed for assessing climatic sensitivity of dSRV. For precise definitions of critical dates and durations of cambial phenology, microcoring and histological analyses were essential. Further studies on tree-ring formation combining both methods are needed (1) to increase their accuracies and (2) to find traits within dendrometer data which may allow an identification of critical dates and durations consistent to findings from microcoring.

Onset of CA in Lebanon Cedar was observed 1–2 weeks after ST reached a threshold of 5 °C. In this light-demanding species, the delayed start of CA at T3 might be coupled with a relatively high site-LAI. Trees from study sites with lower LAI showed higher growth performances. At short-time scales, primarily moist atmospheric conditions seemed to favor stem growth. Best growth performance was observed for the German site, where water supply was evenly distributed throughout the year.

Lebanon Cedar is tolerant to extremely low winter temperatures and high summer temperatures accompanied

by drought periods (see Turkish sites), but shows extraordinary growth under more humid climate with continuous water supply (see German site). Therefore, it appears to be a promising forest species to adapt well to future climate scenarios in the Central European region and should be considered for further studies focusing on growth performance under different site and climate conditions.

**Author contribution statement** AG and RZ generated the study design. AG, RZ, and MŞ performed the field work. AG, MK, and CR analyzed data. AG wrote the manuscript with contributions from MK and CR. All authors have revised and approved the final manuscript.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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