RESEARCH PAPER

Drought responses and their effects on radial stem growth of two co-occurring conifer species in the Mediterranean mountain range

Aylin Güney[1] · Roman Zweifel[2] · Semra Türkan[3] · Reiner Zimmermann[1] · Magnus Wachendorf[1] · Coşkun Okan Güney[4]

Abstract

• *Key message* Patterns of stem radial variations showed that *Cedrus libani* A. Rich. was less limited by summer drought than co-occurring *Juniperus excelsa* M. Bieb. *Cedrus libani* recovered faster from tree water deficit and showed significantly higher radial growth rates and annual stem increments than *J. excelsa*. However, the ability of *J. excelsa* to grow more hours per year may indicate a potential benefit in more extreme conditions.

• *Context* Knowledge about species-specific drought responses is needed to manage productive forests in drought prone areas. Under water shortage, trees commonly show stem shrinkage, which is assumed to inhibit growth.

• *Aims* We investigated whether the two co-existing conifers *Juniperus excelsa* M. Bieb. and *Cedrus libani* A. Rich. (growing at the Taurus Mountains, SW-Turkey) show differences in water relations and stem growth in order to evaluate their respective drought tolerance.

• *Methods* Stem radius changes were hourly monitored over 2 years using high-resolution point dendrometers. Radial stem growth, tree water deficit-induced stem shrinkage, and maximum daily shrinkage were extracted from stem radius change measurements, investigated for their patterns, and related to environmental conditions.

• *Results* *Cedrus libani* recovered from tree water deficit under higher temperature and vapor pressure deficit than *J. excelsa*. The number of hours during which stem growth occurred was higher for *J. excelsa*; however, growth rates and annual increments were significantly lower than in *C. libani*. Both species showed highest maximum daily shrinkage during the driest months indicating the ability to maintain gas exchange all year round.

✉ Aylin Güney
aylinguney13@gmail.com

Roman Zweifel
roman.zweifel@wsl.ch

Semra Türkan
sturkan@hacettepe.edu.tr

Reiner Zimmermann
dr.reiner.zimmermann@uni-hohenheim.de

Magnus Wachendorf
magnus.wachendorf@web.de

Coşkun Okan Güney
coskunokanguney@ogm.gov.tr

[1] Institute of Botany, University of Hohenheim, Stuttgart, Germany

[2] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[3] Department of Statistics, Hacettepe University, Ankara, Turkey

[4] Southwest Anatolia Forest Research Institute, Antalya, Turkey

INRAε ◎ Springer

• **Conclusion** *Juniperus excelsa* showed a more conservative growth strategy while *C. libani* was less limited by summer drought and showed more annual stem increment under the conditions investigated.

Keywords Greek juniper · Lebanon cedar · MARS · Maximum daily shrinkage · Point dendrometer · Tree water deficit

1 Introduction

Future climate scenarios predict that the Mediterranean region will be among the more heavily affected parts of the world in terms of increased frequency and intensity of drought events (Ozturk et al. 2015). In the early past, the Mediterranean region has already experienced an increase in mean annual temperature and severity of summer droughts (Abbasnia and Toros 2019) which affect the vitality and productivity of forests (Tognetti et al. 2019). Studying the growth behavior and tree response to environmental conditions might help to predict how tree species and forests might respond to increased temperatures and water shortage (Anderegg et al. 2015; Rigling et al. 2013).

One way of investigating tree responses to changing environmental conditions is the use of high-precision point dendrometers which allow for monitoring diel stem radius changes (SRC), intra-annual stem growth patterns, and immediate plant water responses (De Swaef et al. 2015; Drew and Downes 2009). Daily SRC are a combination of (1) reversible shrinkage and swelling of elastic tissues (bark and cambium); (2) reversible contraction and expansion of conducting xylem; (3) irreversible stem growth (including wood and bark increments); and (4) thermal expansion and contraction (Daudet et al. 2005; Zweifel et al. 2000).

Since the reversible processes are mainly determined by water transport dynamics within the tree, stem shrinkage and swelling dynamics can be used to quantify drought stress (Aldea et al. 2018; Vieira et al. 2013; Zweifel et al. 2000), canopy water status (Dietrich et al. 2018; Van Emmerik et al. 2017), plant hydraulics (Daudet et al. 2005; Ehrenberger et al. 2012), and even osmoregulation (Barraclough et al. 2019; Lazzarin et al. 2018). There are two variables we focus on: the tree water deficit-induced stem shrinkage called tree water deficit (TWD) (Zweifel et al. 2016) and the maximum daily shrinkage (MDS). TWD quantifies the loss of water from elastic tissues due to an imbalance between water loss (transpiration) and water uptake and reflects the accumulated water deficit also over several days lasting drought periods (Dietrich et al. 2018). It can be used as an indicator for drought stress (Zweifel et al. 2005). In contrast, the maximum daily shrinkage (MDS) quantifies the stem shrinkage over 1 day only (Deslauriers et al. 2007) and is more an indicator for the actual plasticity of a tree to respond to the current environmental conditions in air and soil (Daudet et al. 2005; Giovannelli et al. 2007). A large MDS means a tree is exposed

to a large gradient between water demand and water supply and is able to respond with a large stem shrinkage due to a well-saturated stem tissue (Hinckley et al. 1978; Zweifel et al. 2000). A large MDS therefore indicates a day with open stomata and thus a large transpiration and a high assimilation. A small MDS means either a small gradient between water demand and water supply or a large gradient but under conditions of a low tissue saturation, i.e., already existing stem shrinkage. Thus, a small MDS indicates either a day with low light or a day with closed stomata and thus little transpiration and assimilation.

The reversible shrinkage patterns are contrasted by the irreversible stem increment, in this work called growth (GRO) (Deslauriers et al. 2003; Downes et al. 1999). GRO includes radial size increase only and does not include lignification processes or other processes attributable to growth that increase the wood density (Cuny et al. 2015). According to the zero-growth concept of Zweifel et al. (2016), irreversible stem growth (GRO) is limited to time periods with no stem shrinkage. Both TWD and GRO are derived from this zero-growth approach and together (GRO minus TWD) they equal the original dendrometer data SRC.

Here we investigated the two evergreen conifers *Juniperus excelsa* M. Bieb. (Greek juniper, Cupressaceae) and *Cedrus libani* A. Rich. (Lebanon cedar or Taurus cedar, Pinaceae), both widely distributed along the mountainous areas of the Eastern Mediterranean Basin, especially in the Taurus Mountains (Southern Turkey), where they can form mixed stands at higher altitudes (Nuri and Uysal 2009). *Juniperus excelsa* is slow growing (Özkan et al. 2010) and can be found on poor soils in arid to semi-arid regions (Yücedağ and Gailing 2013), between 500 and 2700 m altitude, with total annual precipitation occasionally as low as 250 mm (Gültekin and Gültekin 2007). *Cedrus libani* is mainly distributed as pure natural stands between 800 and 2200 m altitude with total annual precipitation generally ranging between 600 and 1200 mm but occasionally being as low as 430 mm (Boydak 2003; Durkaya et al. 2013). Both species are known to be frost and drought tolerant (Boydak 2003; Gültekin and Gültekin 2005). Further, several studies showed that they are able to remain photosynthetically/physiologically active at water potentials as low as − 3.0 MPa; therefore, both species can be characterized as anisohydric (Aussenac 2002; Epron 1997; Ladjal et al. 2005; Moran et al. 2017; Voelker et al. 2018).

Despite the knowledge available about the two species (Akkemik 2006; Güney et al. 2017; Touchan et al. 2005),

we still lack of understanding how drought affects their respective growth performance. In this study, we monitored hourly SRC of five *J. excelsa* and four *C. libani* trees over 2 years (2013 and 2014) including dry periods during which both species experienced stem shrinkage lasting for single days up to several weeks. We investigated whether the two co-existing conifers (*J. excelsa* and *C. libani*) show differences in water relations (TWD and MDS) and stem growth (GRO) in order to evaluate their respective drought tolerance. We assume that the ability to grow during dry periods is an indication for drought tolerance quantified as the number of hours with growth and hourly growth rates. We hypothesize (1) that the species with more growth hours during warm and dry conditions has also a larger annual increment. Further, we assume that a short time for recovering from tree water deficit after a several days lasting drought period rather than the maximum tree water deficit value indicates drought tolerance. We hypothesize (2) that the species with a faster recovery from tree water deficit shows an overall better growth performance. Finally, we take maximum daily shrinkage as an indicator for a maintained transpiration and thus assimilation activity and assume that a high maximum daily shrinkage during a dry period indicates a high drought tolerance. We hypothesize (3) that the species able to maintain higher maximum daily shrinkage during dry periods is also able to grow more.

2 Materials and methods

2.1 Study area and tree selection

The study was conducted in the Cedar Research Forest (CRF, 2617 ha) which is located in the southwestern part of the Taurus Mountains in the Elmali district of Antalya (SW-Turkey). The CRF is characterized by an oro-Mediterranean climate with dry summers and cold winters. Mean annual air temperature is 7.4 °C, and mean total annual precipitation is 725 mm, with rainfall mainly occurring during the winter (annual means were calculated for the period 1968–2000 from climate records of a weather station within the CRF at 1665 m asl, Basaran et al. (2008)). The study site was located in the western part of the CRF at 1350 m asl within a mature natural *Cedrus libani–Juniperus excelsa* stand. Mean stand inclination was 25° with NW exposure. Soil characteristics varied between clay and clayey loam with a pH (H_2O) around 7.4 (Basaran et al. 2008). To measure seasonal dynamics of stem radius changes (SRC), five individuals of *J. excelsa* and four individuals of *C. libani*, which were representative for the forest stand at our study site, were randomly selected within a circular plot (radius = 30 m). The selected trees were of suppressed and co-dominant status and had no visible damage. Age at breast height (1.3 m) was estimated by extracting

tree cores with an increment borer (Suunto 300/400 mm, Finland). For characteristics of the studied trees, see Table 1.

2.2 Growth monitoring

Stem radius changes (SRC) were measured with high-precision point dendrometers (linear displacement potentiometers; MMR 10_11 R5K, MEGATRON Elektronik AG & Co., Munich, Germany) on five *J. excelsa* and four *C. libani* individuals. The dendrometers were installed at breast height on the slope-parallel sides of the stem, and shielded from direct sunlight and rainfall by aluminum foil and styrofoam covers. The contact head of the dendrometers was placed at the cortex surface after removing as much of the outermost dead bark as possible without damaging living tissue (Zweifel et al. 2006). The dendrometer signals (resolution: 2 μm, trustable accuracy < 10 μm) were recorded hourly and stored using a data logger (DL2e, Delta-T Devices Ltd., UK) from October 2012 until December 2014.

2.3 Meteorological data

Meteorological data were collected with a WatchDog 2700 Weather Station (Spectrum Technologies Inc., Plainfield, IL, USA) which was installed in an open area close to the study site (1340 m asl, Güney et al. 2020). Air (T_{air}, °C) and soil temperature (T_{soil}, °C), precipitation (Pp, mm), soil water content (SWC, %), relative air humidity (RH, %), and global radiation (GR, W m^{-2}) were measured at 10–30 min time steps and were later converted to hourly and daily values. GR was converted to daily sums and expressed as MJ m^{-2} day^{-1}. Daily means of vapor pressure deficit (VPD, kPa) were calculated from site-specific T_{air}, RH, and air pressure values. Stem temperature (T_{stem}) was measured using thermocouples installed at breast height under the bark and recorded hourly by the same data logger.

2.4 Data analysis

Three parameters were extracted from hourly recorded stem radius changes (SRC) (Fig. 1). The rate of (irreversible) growth-induced expansion (GRO$_{rate}$, in μm h^{-1}, Fig. 1b) of the stem and the hourly tree water deficit-induced shrinkage of the stem (TWD, in μm, Fig. 1c) were calculated based on the concept of Zweifel et al. (2016) which assumes zero growth (ZG) during times of stem shrinkage. GRO$_{rate}$ equals zero as soon as stem shrinkage occurs and TWD increases. TWD is calculated as the difference between the last maximum stem radius and the current stem radius (Fig. 1a, c). Consequently, summed up growth-induced expansion of the stem (GRO) is limited to periods when TWD is zero (GRO period) and the stem radius exceeds the last maximum of stem size (in radius) (Fig. 1a). Maximum daily shrinkage (MDS, in μm, Fig. 1d)

Table 1 Main characteristics of the studied trees

| Species/tree ID	Age[1] (years)	DBH (cm)	Height (m)	PCA (m²)	Social status
Juniperus excelsa					
J1	72	21	11.6	20.6	Suppressed
J2	126	38	11.8	22.7	Suppressed
J3	281	67	20.5	53.1	Co-dominant
J4	245	79	16.2	79.9	Co-dominant
J5	>316	111	21.5	73.5	Co-dominant
Cedrus libani					
C1	55	17	13.0	15.3	Suppressed
C2	80	23	14.3	12.8	Suppressed
C3	84	32	19.4	34.2	Co-dominant
C4	60	36	22.2	48.1	Co-dominant

PCA projected crown area; *DBH* diameter at breast height

[1] Age at DBH (for J5 only a tree core of the outer 16 cm including 316 tree rings could be extracted)

was calculated as the difference between the daily maximum and the daily minimum radius of the stem. Absolute TWD and MDS values depend on a number of factors, e.g., a tree stem circumference, and thickness and elasticity of its bark (Zweifel and Häsler 2000), and we therefore used normalized data to compare TWD and MDS patterns between species (Brinkmann et al. 2016). Normalizing was performed by dividing all TWD and MDS values for each individual tree by its respective maximum value (which was defined as 95% of the measured absolute maximum value during the whole measurement period).

2.5 Statistical analysis

Since the data did not fit a normal distribution (Kolmogorov-Smirnov test, $p < 0.05$), the Wilcoxon signed-rank test was used to check for significant differences between years (within the same species). Spearman non-parametric correlation coefficients were calculated between daily values of TWD, MDS, and environmental variables (T_{mean}, T_{min}, T_{max}, T_{soil}, T_{stem}, Pp, SWC, RH, GR, and VPD) using SPSS v20.0 (SPSS Inc., Chicago, IL, USA). Further, TWD and MDS were fit with MARS models and GRO_{rate} was fit with a two-part model (covering both study years). Beforehand, a factor analysis between environmental variables was performed which showed a high correlation between T_{mean}, T_{min}, T_{max}, T_{soil}, and T_{stem}. Therefore, among the temperature variables, only T_{max}, which was the most representative variable, was included in further analyses. Since the relationship between our dependent and independent variables included nonlinearities, multivariate adaptive regression splines (MARS, *caret* package in R, Kuhn 2012), which are less sensitive to multicollinearity, were used to investigate the effects of environmental variables (predictors) on TWD and MDS (response variables). MARS also allows to estimate the relative importance of the variables on TWD and MDS by calculating generalized cross
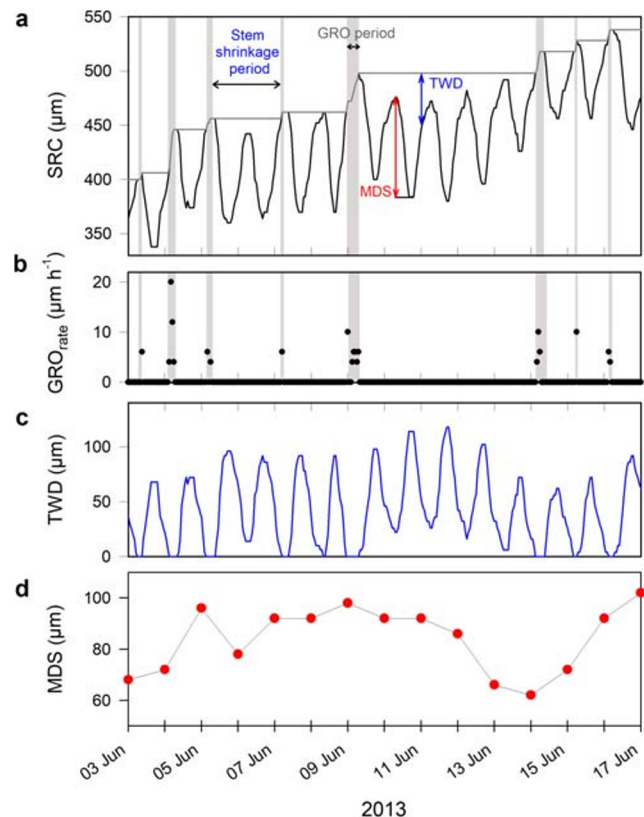
Fig. 1 Extracting GRO_{rate}, TWD, and MDS from hourly recorded stem radius changes (SRC). **a** Hourly measured SRC in a *J. excelsa* tree (J5) during 03 to 17 June 2013 (black line). The dark gray line is based on the ZG concept (Zweifel et al. 2016) which assumes no growth-induced irreversible expansion (GRO) during periods of stem shrinkage (= periods of TWD). Shaded areas indicate periods of GRO (when TWD is zero). **b** Corresponding values of GRO_{rate} (rate of irreversible growth). **c** TWD (tree water deficit-induced stem shrinkage) is the difference between the previous maximum stem radius and the actual stem radius. **d** MDS (maximum daily shrinkage) is the amplitude between daily maximum and minimum stem radius

validation (GCV) and residual sum of squares (RSS) of the model. Further, partial dependence plots are used to better understand the relationship between the environmental variables and TWD and MDS. Optimal MARS models were obtained using 10-fold CV in *caret*. Since our data set of GRO_{rate} consisted of a large number of zero values, we used the *twopm* command in the Stata software 14 (StataCorp, College Station TX, USA). *Twopm* is a command for fitting two-part models on mixed discrete-continuous variables. A binary choice model is fit for the probability of observing either a positive or a zero outcome (cf. Belotti et al. 2015), in our case positive GRO_{rate} versus zero GRO_{rate}. The positive outcome is then fit with an appropriate regression model. We used a two-part model that modeled the positive GRO_{rate} (non-zero values) with a gamma distribution using the generalized linear model (GLM) function and zero GRO_{rate} with a binomial distribution using the logit function.

3 Results

## 3.1 Environmental conditions during 2013 and 2014

At the study site, mean annual air temperatures for 2013 and 2014 were 11.1 °C and 11.5 °C, respectively. Air temperatures reached a maximum of + 37 °C (August 2014) and a minimum of − 13.8 °C (January 2013) (Fig. 2). Paired *t* tests ($p <$ 0.05) conducted for monthly averages showed that, except for April, SWC was significantly lower (between 2.3 and 6%) from March to September in 2013 compared with 2014. VPD was significantly higher (between 0.26 and 0.42 kPa) in May, September, and October 2013 than in 2014. T_{air} and T_{soil} were between 1.3 and 3.3 °C higher in May and June 2013 ($p < 0.05$). Based on these findings and the generally higher average annual values for RH (2013: 42.9%; 2014: 53.2%) and SWC (2013: 12.7%; 2014: 17.3%) and the lower ones for VPD (2013: 1.42 kPa; 2014: 1.17 kPa) in 2014 than in 2013, we call the year 2014 more humid than the year 2013.

3.2 Stem growth and shrinkage dynamics

The year 2013 was characterized by prolonged times of stem shrinkage lasting for several days which allowed for only short periods of GRO (Fig. 3). During spring and summer 2013, only four out of nine trees (J1, J5, C2, and C4) showed little GRO while five trees showed no GRO. Accordingly, GRO_{rate} was low for both species during 2013 (Fig. 3b, Table 4 in Annex). During 2014, all *C. libani* individuals showed a significant increase in stem radius which led to an average increment of 1021 μm (284 μm in 2013, Table 4 in Annex) and mean GRO_{rate} of up to 55 μm day^{-1} (Fig. 3b). In contrast, *J. excelsa* showed an average increment of 259 μm (245 μm in 2013, Table 4 in Annex) and only reached a mean

Fig. 2 Climate conditions at the study site during 2013 and 2014. **a** Daily precipitation sum (bars) and mean soil water content (SWC, solid line). Gray horizontal bars indicate missing precipitation data. **b** Mean (red line), maximum and minimum (gray lines) daily air temperature (T_{air}), and mean daily soil temperature (T_{soil}, black line). **c** Mean daily vapor pressure deficit (VPD)
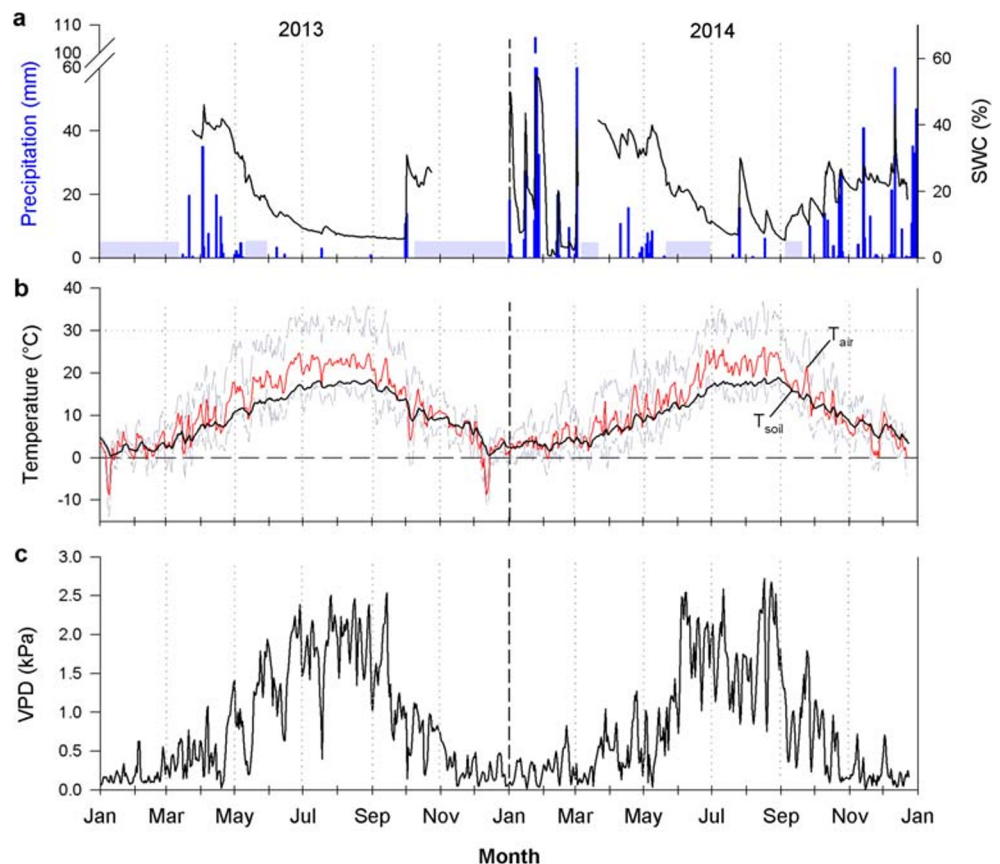
Fig. 3 Annual course of **a** hourly stem radius change (SRC) and daily means of **b** GRO$_{rate}$ (rate of irreversible growth **c** normalized tree water deficit (TWD) and **d** normalized maximum daily shrinkage (MDS) of *Juniperus excelsa* (black symbols and lines) and *Cedrus libani* (blue symbols and lines)). Bold lines in **a** represent mean SRC. Letters indicate individual tree ID
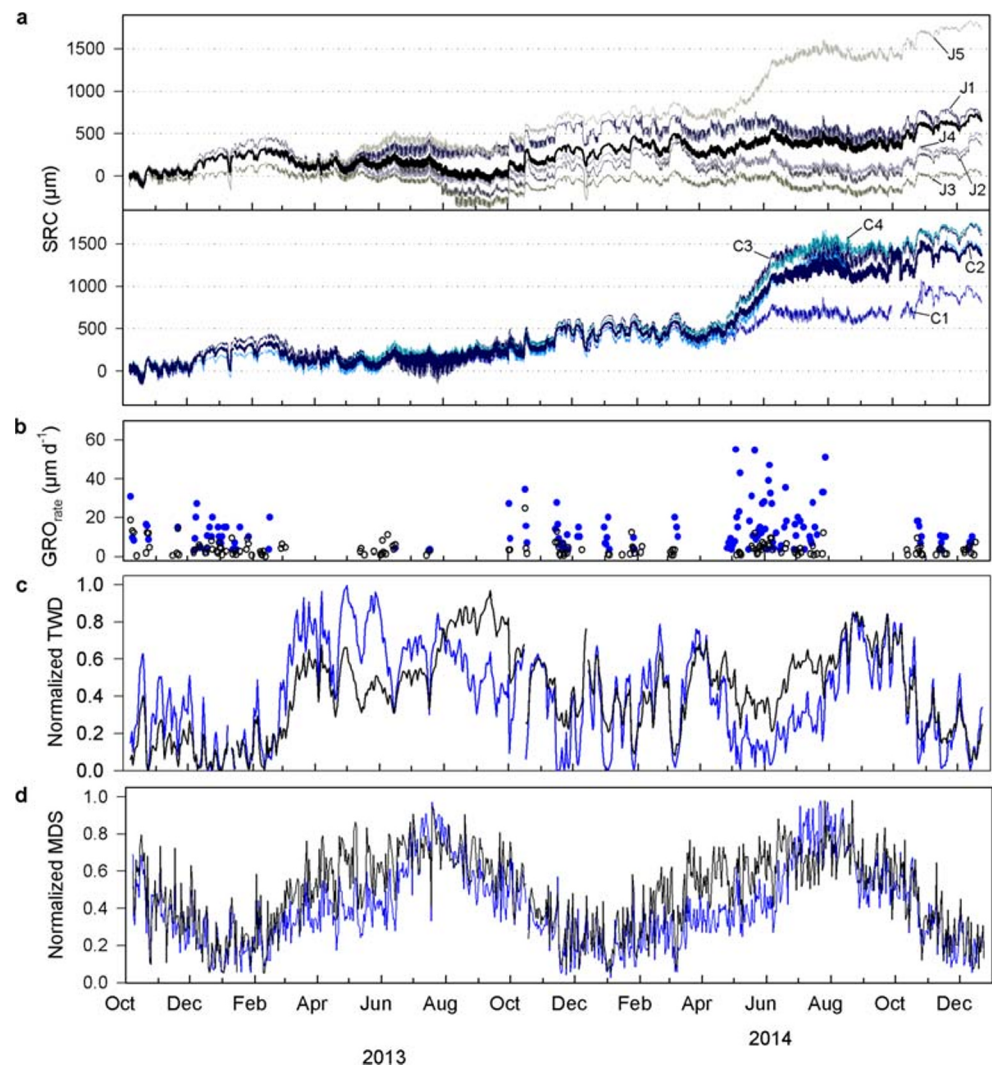
GRO$_{rate}$ of up to 12.2 μm day^{-1} (Fig. 3b). However, two individuals (J2 and J3) showed no GRO and one individual (J5) grew much more than the others in 2014 (Table 4 in Annex). *Juniperus excelsa* grew during 329 h within a year while *C. libani* grew 278.5 h. The linear regression between tree size (DBH) and average tree ring width for the period 2005–2014 (based on extracted tree cores, Table 4 in Annex) was not significant ($p > 0.05$, Fig. 7 in Annex). Interestingly, stem growth (GRO) was detected in almost any month of the year and was not restricted to a specific growth period (Fig. 3b). Compared with total stem growth during 2013 and 2014, the percentage of GRO during the warm season (April to October in 2013 and 2014) was 42% and 69% for *J. excelsa* and *C. libani*, respectively.

Normalized TWD levels were higher in *C. libani* than in *J. excelsa* from April to July 2013 but then, during August to mid-September, TWD started to decrease in *C. libani* and to increase in *J. excelsa* (Fig. 3c). During 2014, normalized TWD was significantly lower in *C. libani* than in *J. excelsa* both during the spring and summer (Fig. 3c, Fig. 4a–b). In

both years, MDS levels were significantly lower during the spring than during the summer in both species and MDS during the spring was significantly lower in *C. libani* than in *J. excelsa*. MDS showed no significant differences between *J. excelsa* and *C. libani* during summer 2013 but was significantly higher in *C. libani* than in *J. excelsa* during summer 2014 (Fig. 3d, Fig. 4c–d). Within the same species, mean annual MDS showed no significant differences between years ($p > 0.05$), while TWD was significantly lower in 2014 ($p < 0.05$) in both species. Mean values of all (absolute) parameters are shown in Table 4 in Annex for each tree, species, and both study years.

3.3 Growth distribution during 24 h and along climatic gradients

Both species grew most at night and in the early morning hours between 2 and 7 AM (Fig. 5). Least growth was observed around midday for *C. libani* and around the evening hours for *J. excelsa*. In *J. excelsa*, almost 90% of the total

Fig. 4 Box plots for normalized (**a–b**) TWD (tree water deficit), and (**c–d**) MDS (maximum daily shrinkage) of *Juniperus excelsa* (grey) and *Cedrus libani* (blue) during spring (April 1st - June 15th) and summer (June 16th - August 31st) in 2013 and 2014. Values sharing the same letter were not significantly different ($p < 0.05$). In each box plot, data is plotted as the median (midline) and percentiles (box, 25th and 75th percentiles), the whiskers and individual points (outliers) represent all values within and above 1.5 times the interquartile range, respectively. Additionally, means were plotted as red lines
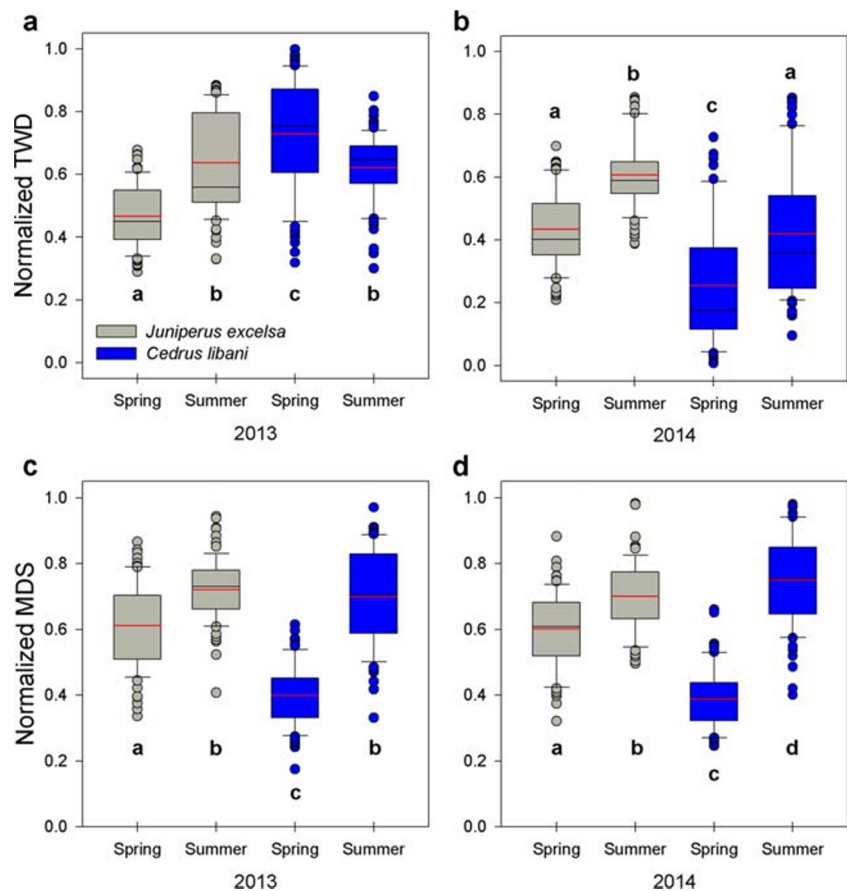
growth (derived from hourly GRO$_{rate}$ data for the whole measurement period) occurred in a VPD range between 0 and 0.24 kPa while the same range accounted for only around 75% of total growth in *C. libani* (Fig. 6), meaning that *C. libani* grew at higher VPD than *J. excelsa*. For both species, 1.9 kPa was the highest VPD at which GRO was measured. The temperature range for GRO was the same for both species (0 to + 20 °C). Although for both species hourly growth rates peaked at 11 °C, *J. excelsa* had a higher proportion of GRO$_{rate}$ at lower temperatures compared with *C. libani*. Minimum RH and minimum SWC during GRO were 34.18% and 3.2% for both species, respectively (Güney et al. 2020).

3.4 Impact of environmental factors on stem radius changes

Generally, air temperature (T_{max}) had the most significant impact on stem shrinkage as high temperatures were related closest to high values of TWD and MDS (Tables 2 and 3). However, while TWD of *J. excelsa* was closest correlated with T_{max}, TWD of *C. libani* was significantly negatively correlated with RH (Table 2) which is also in accordance with the results obtained by MARS models (Table 3). The importance of VPD on TWD was higher in *C. libani* than in *J. excelsa* (Table 3). Further, results from correlation analyses

showed a more significant relationship between SWC and TWD in *J. excelsa* than in *C. libani* (Table 2). TWD was inconsistently affected by SWC in both species. The SWC threshold after which the relationship between SWC and TWD stayed significantly negative was 37.6% in *J. excelsa* and 40.4% in *C. libani* as shown by MARS models (Güney et al. 2020).

GRO$_{rate}$ showed a significantly positive relationship to RH in both species. Further, RH was the coefficient that had the highest explanatory power for GRO (non-zero GRO$_{rate}$) (highest z value, Table 5 in Annex). The probability of observing higher values of GRO$_{rate}$ also increased with increasing RH. Additional to RH, Pp was also positive and significantly related to GRO in *J. excelsa* (Table 5 in Annex). In *C. libani*, additional estimates that increase the probability to observe GRO were T_{max}, VPD, and SWC (significance in decreasing order, Table 5 in Annex).

4 Discussion

4.1 Species-specific stem growth patterns

Juniperus excelsa grew during 15% more hours than *C. libani*, but hourly growth rates and the resulting annual increments were about 60% lower in *J. excelsa* compared with *C. libani*.

Fig. 5 Frequency distribution of GRO (irreversible growth) within 24 hours for the two species investigated (grey bars: *Juniperus excelsa*; blue bars: *Cedrus libani*). During the whole measurement period, the number of hours during which GRO occurred was 658 for *J. excelsa* and 557 for *C. libani*. Periods with highest and lowest GRO are indicated by filled and empty horizontal bars, respectively
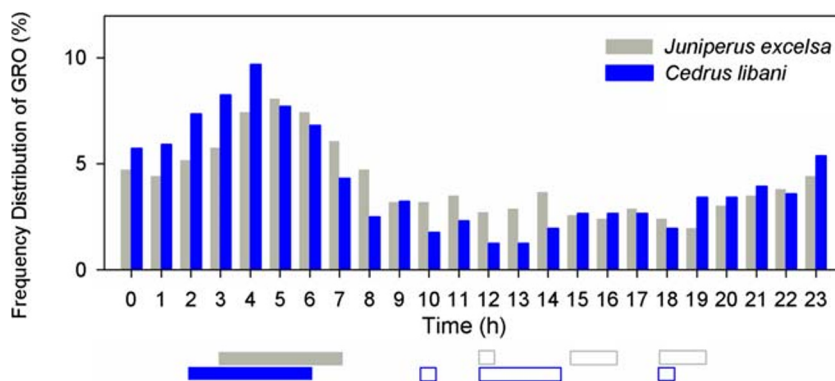
This is in line with the findings of tree ring studies from Turkey which also show lower annual growth increments of *J. excelsa* than *C. libani* (Avsar and Tonguc 2003; Carus 2004; Saatcioglu 1969). Further, in our study, *C. libani* was able to grow more during the warm period (April to October) and during times of higher temperatures and VPD compared with *J. excelsa* (Fig. 6). Our results therefore suggest that, at similar sites, *C. libani* is generally able to grow more than *J. excelsa* under the warm and dry conditions investigated.

Physiologically this means that low water potentials in the elastic stem tissues of *C. libani* are faster replenished and thus the negative water potentials and the lowered cell turgor are faster
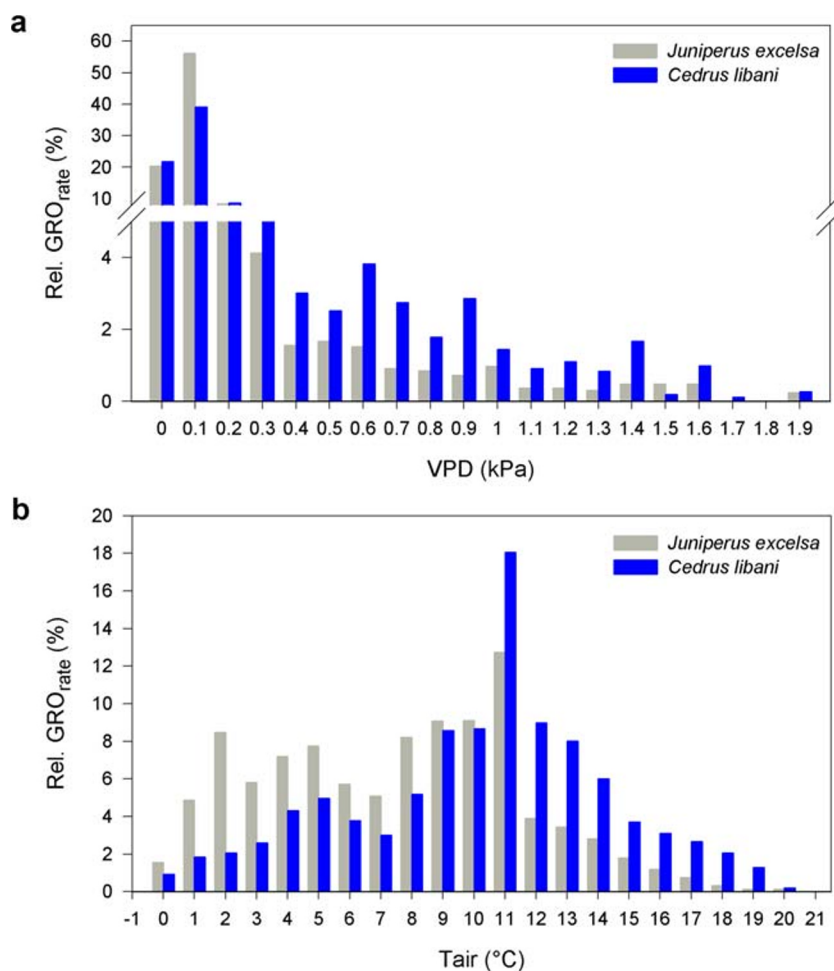
Fig. 6 Frequency distributions of relative growth rates (GRO$_{rate}$) shown as the percentage of total growth of *Juniperus excelsa* (grey bars) and *Cedrus libani* (blue bars) compared to measured (**a**) vapour pressure deficit (VPD) and (**b**) air temperature (Tair) during hours with GRO. Zero GRO$_{rate}$ values are not included. Values are shown for both study years (2013 and 2014). Total range of measured VPD and Tair during the measurement period were 0 to 5.48 kPa and −11.2 to 36.3°C, respectively

Table 2 Correlations between daily means of GRO$_{rate}$, TWD, MDS, and daily climate variables in *Juniperus excelsa* (Je) and *Cedrus libani* (Cl) during 2013 and 2014

	T_{mean}	T_{min}	T_{max}	T_{soil}	T_{stem}	Pp	SWC	RH	GR	VPD
TWD_Je	.71**	.66**	**.74****	.69**	.69**	− .35**	− .49**	− .66**	.55**	.72**
TWD_Cl	.42**	.37**	.45**	.35**	.41**	− .25**	− .17**	− **.54****	.33**	.47**
MDS_Je	.77**	.70**	**.80****	.70**	.76**	− .25**	− .32**	− .59**	.74**	.77**
MDS_Cl	.78**	.74**	**.79****	.76**	.78**	− .22**	− .40**	− .54**	.65**	.74**

$N = 458$ days (due to data gaps). Spearman's rho coefficient was calculated. Level of significance: $*p < 0.05$, $**p < 0.01$. For each dependent variable, the strongest correlation is in bold

GRO$_{rate}$ rate of irreversible growth; *TWD* tree water deficit; *MDS* maximum daily shrinkage; *T* temperature; *Pp* precipitation; *SWC* soil water content; *RH* relative air humidity; *GR* global radiation; *VPD* vapor pressure deficit

returning to the level allowing for cell division and cell expansion (Dietrich et al. 2018; Lockhart 1965; Mencuccini et al. 2017; Zweifel et al. 2006) than in *J. excelsa*. This could also explain why, during the 24-h cycle, conditions that allowed for GRO were reached earlier in the night in *C. libani* (Fig. 5). The ability to recover from low water potentials is not solely driven by passive processes related to the availability of water but can be altered by active osmoregulation (Tyree and Jarvis 1982) which

Table 3 Estimation of the relative importance of environmental variables (predictors) in the MARS models based on generalized cross validation (GCV) and residual sum of squares (RSS). Variables are ranked from high to low according to their importance

	Variable	GCV	RSS
TWD_Je	T_{max}	100.00	100.00
	RH	47.75	47.29
	GR	37.83	37.43
	SWC	22.84	22.08
	VPD	1.80	1.35
	Pp	0.00	0.00
TWD_Cl	RH	100.00	100.00
	SWC	48.97	57.05
	VPD	44.53	52.19
	GR	43.18	49.38
	T_{max}	37.84	43.76
	Pp	0.00	0.00
MDS_Je	T_{max}	100.00	100.00
	Pp	42.35	44.16
	VPD	38.22	39.68
	SWC	24.54	26.72
	GR	9.31	10.73
	RH	0.00	0.00
MDS_Cl	T_{max}	100.00	100
	Pp	30.96	29.73
	VPD	30.96	29.73
	SWC	23.06	21.61
	GR	5.16	4.89
	RH	0.00	0.00

has been reported for anisohydric species like *C. libani* (Ladjal et al. 2007) and also *Juniperus* spp. (Voelker et al. 2018; Willson et al. 2008). Under water deficits, plants accumulate osmolytes (e.g., sugars, amino acids) in the cytoplasm which increases the osmotic concentration inside the cell (Bray 1993). Due to the increased osmotic concentration, water can move into the cambium and bark cells so that a positive cell turgor is maintained despite the low xylem water potentials which allows plants to remain physiologically active during drought and might thus be able to grow (Arndt et al. 2008; Barraclough et al. 2019; Lazzarin et al. 2018; Mencuccini et al. 2013; Morgan 1984).

Another possible reason for the generally better growth performance of *C. libani* may be attributed to its deeper taproots that access deeper water reservoirs (Baquedano and Castillo 2007; Boydak 2003; Sevim 1961) than the ones of *J. excelsa* (Gültekin and Gültekin 2005; Tümen and Hafızoğlu 2003). *Juniperus excelsa* not only was a less good grower during dry periods, but also showed large differences in GRO among the individuals (especially during 2014). We speculate that rather the heterogeneous soil conditions, which lead to different water availability for the individuals, than the different tree sizes or the different social status (Fig. 7 in Annex) could explain the different growth reactions (Fisher and Gardner 1995; Sass-Klaassen et al. 2008). Mesozoic limestone, which is predominant at our study site, has been reported to show large variations in soil depth, SWC, and stoniness and a rapidly changing soil water availability within a year and at short spatial scales (Basaran et al. 2008; Özkan et al. 2010). Since all *J. excelsa* individuals (J1–J4) that showed a decreased or inhibited growth in 2014 were grouped on the east side of the study site (Güney et al. 2020), we suspect that soil water availability might have been lower there. Unfortunately, no subplot-specific SWC measurements were available to confirm this speculation.

4.2 Seasonal stem growth patterns

The Mediterranean climate with a distinct heat and drought period inhibits growth in the summer (Fig. 2) usually leading to the well-described bimodal growth pattern with peaks before and

after this period (Aldea et al. 2018; Camarero et al. 2010; Vieira et al. 2014). In this study, the trees of both species grew before and after the dry period (Fig. 3) as expected; however, there were no clear growth peaks (except for *C. libani* in spring 2014) and stem radial increment was detected in almost any month also during winter time. Particularly *J. excelsa* utilized many hours in these winter months. From a physiological point of view, it is not un-likely to detect stem growth in these cooler and moister days, since these periods obviously offer better growth conditions than the summer months. It could be seen as a strategy to survive in an area being increasingly exposed to drought. As long as the tem-perature remains above zero, there is no obvious physiological reason why the evergreen trees should not be able to grow, except for an inner clock eventually avoiding that (Rossi et al. 2006, 2007). The fact is our results are unexpected and so far hardly supported by other investigations with alternative growth measurement methods. Güney et al. (2015) investigated xylogenesis of *C. libani* from the same area during 2013 and stated the growth cessation to take place at the end of September, but sampling was performed until the end of October only and the winter months were not explored.

However, there are also some reservations to be considered with dendrometer measurements in general (Drew and Downes 2009; Ilek et al. 2016) and with the zero-growth concept (Zweifel et al. 2016) in particular. The zero-growth concept assumes no growth during periods of stem shrinkage which appears to be physiologically reasonable (Hinckley and Lassoie 1981; Hsiao et al. 1976; Lockhart 1965). However, there is also evidence that a certain fraction of growth might be assigned to the wrong time periods with this approach. Zweifel et al. (2016) quantified this temporally wrongly assigned fraction of growth to be < 5% of annual increment for different species but not covering the two species of this study. The smaller an increment in a μm resolution is, the higher is the risk for a misinterpretation in general. In this work, the irreversible growth increments during winter months, however, were > 200 μm and thus far larger than being discarded as measurement- or method-induced errors.

Another unknown factor which potentially affects the interpre-tation of the results is the ignored degradation of the bark cells (Gričar et al. 2015) particularly during wintertime with frost (Zweifel and Häsler 2000). Such a process could mask growth in the sense that a potential increment is underestimated when the bark degradation led to a loss of bark volume (radial stem size) before a growth period. Unfortunately, there is very little known about such degradation processes and the related tissue size chang-es in the bark (Gričar et al. 2015). However, we question that these processes play such an important role for the species in this study.

4.3 Stem shrinkage as an indicator for growth performance

Stem shrinkage results from an imbalance between the water loss by transpiration and the water uptake from the soil. The

shrinkage can either be quantified as tree water deficit (TWD) including the absolute shrinkage from the past maximum stem size (Zweifel et al. 2016) or as maximum daily shrinkage (MDS), reflecting the dynamics of a single day only (Garnier and Berger 1986). TWD normalized with its maximum over the 2-year investigation is thus an indicator for drought stress, whereas MDS is a proxy for the ecophysiological activity of a tree, i.e., transpiration and assimilation. We assumed that a faster recovery from TWD indicates a better growth performance un-der drought. *Cedrus libani* showed a faster recovery from high TWD particularly during the hot and dry summer months 2013 when the TWD of *C. libani* started to decrease together with the decreasing VPD in August (Fig. 2, Fig. 3, and Fig. 8 in Annex), whereas the TWD of *J. excelsa* remained high until October when SWC sharply increased with the first rain events. Therefore, *C. libani* was able to recover from high TWD with humid air induced by minor rain events and cooler temperatures only (eventually with the help of deep taproots), whereas *J. excelsa* needed also more humidity in the soil to show the same response. This finding was statistically further supported by a closer relationship between TWD and VPD of *C. libani* than of *J. excelsa* (Fig. 8 in Annex) and a closer relationship between TWD and SWC of *J. excelsa* than of *C. libani* (Table 2, Güney et al. 2020). The different determining weights of VPD and SWC on TWD have been discussed for other species before (Ehrenberger et al. 2012; Zweifel et al. 2005) and the closer VPD dependency of TWD indicates a closer coupling to air conditions which was shown to disappear with increasing drought stress. We interpret these results as a better ability of *C. libani* to deal with the prevailing conditions compared with *J. excelsa*. However, this finding is in contrast to the higher number of annual growth hours of *J. excelsa* compared with *C. libani* which indicates that both species have special abilities indicating a good drought tolerance.

The annual course of MDS showed no species-specific differ-ences. MDS was highest during July and August for both species and years, indicating that gas exchange was maintained during the hottest and driest months. Heavily drought stressed trees were found to minimize their daily shrinkage and swelling dynamics (Zweifel et al. 2007) and thus show very low MDS only. However, normalized MDS was significantly higher in *C. libani* than in *J. excelsa* during summer 2014. Since *C. libani* showed a significantly higher stem growth than *J. excelsa* during the year 2014, this confirms our hypotheses that species that are able to maintain higher MDS during dry periods are able to grow more. Nevertheless, we interpret that both species, despite the different growth responses, were not yet at the edge of their capability to remain physiologically active.

4.4 Do we cover the full story?

Despite the fact that almost all investigated growth indicators point towards a better performance of *C. libani*, we critically ask

whether this might hold under more severe drought conditions predicted for the near future when the species are pushed towards their physiological capability to survive. Studies using plant water potentials and the related wilting point by Genc et al. (2005) showed a higher survival rate of *J. excelsa* under drought stress than *C. libani*. It appears that *J. excelsa* is able to maintain physiological processes under extreme conditions but at a very low growth rate. This ability to downregulate physiology may have led to the poorer growth performance in this study but may also indicate a more conservative (growth) strategy (Moran et al. 2017) bearing the potential to survive even more extreme conditions. This could also explain why *J. excelsa* is found in arid regions with total annual precipitation occasionally as low as 250 mm (Fontaine et al. 2007; Gültekin and Gültekin 2007), whereas *C. libani* is reported to grow in areas with > 430 mm annual precipitation only (Boydak 2003; Durkaya et al. 2013). The ability to grow more during the cold season could be a further advantage of *J. excelsa* over *C. libani* in drier and hotter environments.

5 Conclusions

In our study, almost all the physiological indicators measured point towards *C. libani* which, compared with *J. excelsa*, grew more under increased temperatures and VPD and recovered faster from tree water deficit-induced stem shrinkage under higher VPD already, whereas *J. excelsa* needed rain and higher SWC to resume growth. However, there remains the question whether *J. excelsa* with its conservative way of keeping physiological processes low during hottest and driest periods might increase its probability to survive at the cost of a generally lower growth performance. One clue to such an argument is based on the ability of *J. excelsa* to grow more hours per year than its neighboring tree species. More studies under more extreme conditions and including aspects of tree mortality are needed to follow up on this question.

Compliance with ethical standards

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

Annex

Table 4 Average tree ring width for the period 2005–2014 (TRW, based on extracted tree cores), annual stem radius increase (SRI) based on dendrometer measurements, and averaged annual values for daily GRO$_{rate}$ (rate of irreversible growth), tree water deficit (TWD), and maximum daily shrinkage (MDS) for *Juniperus excelsa* and *Cedrus libani* during 2013 and 2014

Tree ID	TRW (μm)	SRI (μm)		GRO$_{rate}$ (μm day^{-1})		TWD (μm)		MDS (μm)	
		2013	2014	2013	2014	2013	2014	2013	2014
Juniperus excelsa									
J1	494	397	141	0.86 ± 4	0.32 ± 2	122 ± 67	156 ± 90	88 ± 39	96. ± 43
J2	181	78	0	0.16 ± 2	0.0	363 ± 192	313 ± 115	55 ± 31	49 ± 24
J3	121	109	0	0.19 ± 3	0.0	220 ± 132	221 ± 73	50 ± 28	47 ± 20
J4	138	140	86	0.22 ± 2	0.21 ± 3	295 ± 156	239 ± 114	54 ± 23	48 ± 19
J5	657	502	1070	1.38 ± 6	2.98 ± 9	108 ± 70	83 ± 64	53 ± 30	50 ± 26
Mean	318	245	259	0.56 ± 3	0.70 ± 3	277 ± 137	254 ± 105	59 ± 27	58 ± 23
Cedrus libani									
C1	468	232	511	0.47 ± 3	1.35 ± 8	171 ± 86	162 ± 107	64 ± 31	72 ± 43
C2	482	318	1178	0.70 ± 4	2.71 ± 9	119 ± 75	90 ± 99	60 ± 37	72 ± 50
C3	640	280	1216	0.55 ± 4	3.08 ± 9	200 ± 123	123 ± 84	93 ± 54	85 ± 51
C4	785	308	1182	0.69 ± 4	3.22 ± 9	126 ± 74	96 ± 69	69 ± 40	64 ± 38
Mean	593	284	1021	0.60 ± 4	2.59 ± 9	155 ± 82	131 ± 75	72 ± 38	75 ± 41

Table 5 Results of the two-part model for GRO$_{rate}$ of *Juniperus excelsa* and *Cedrus libani*. Zero GRO$_{rate}$ was modeled using the logit function, and positive GRO$_{rate}$ (non-zero values) was modeled with the generalized linear model (GLM) function. Coefficients that are statistically significant are indicated by an asterisk

Juniperus excelsa

Variables	Two-part model Logit			
	Coef.	Std. Err	z	p value
Constant	− 10.696	2.086	− 5.130	< 0.001*
T_{max}	0.038	0.053	0.740	0.462
Pp	0.033	0.016	2.130	0.033*
SWC	− 0.021	0.017	− 1.230	0.219
RH	0.111	0.025	4.520	< 0.001*
GR	0.033	0.043	0.770	0.439
VPD	0.097	0.093	1.060	0.291
	GLM			
Constant	0.606	0.963	0.630	0.529
T_{max}	− 0.005	0.039	− 0.140	0.891
Pp	0.011	0.008	1.500	0.133
SWC	0.012	0.014	0.080	0.937
RH	0.003	0.015	0.180	0.855
GR	0.063	0.038	1.630	0.103
VPD	− 0.070	0.067	− 1.050	0.293

R^2-pseudo = 0.21; p = 0.000 < 0.05

Cedrus libani

Variables	Two-part model Logit			
	Coef.	Std. Err	z	p value
Constant	− 16.345	2.700	− 6.050	< 0.001*
T_{max}	0.128	0.057	2.240	0.025*
Pp	− 0.004	0.014	− 0.300	0.760
SWC	0.037	0.019	1.900	0.058
RH	0.148	0.029	5.080	< 0.001*
GR	− 0.029	0.046	− 0.630	0.530
VPD	0.212	0.097	2.180	0.029*
	GLM			
Constant	− 4.578	2.042	− 2.240	0.025*
T_{max}	0.156	0.046	3.410	0.001*
Pp	− 0.005	0.014	− 0.370	0.710
SWC	0.049	0.0164	2.960	0.003*
RH	0.042	0.022	1.880	0.060
GR	− 0.028	0.040	− 0.690	0.488
VPD	0.002	0.078	0.020	0.984

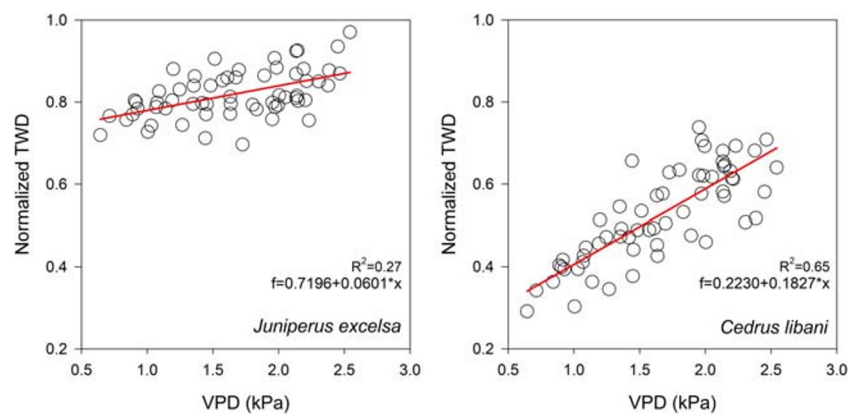R^2-pseudo = 0.23; p = 0.000 < 0.05
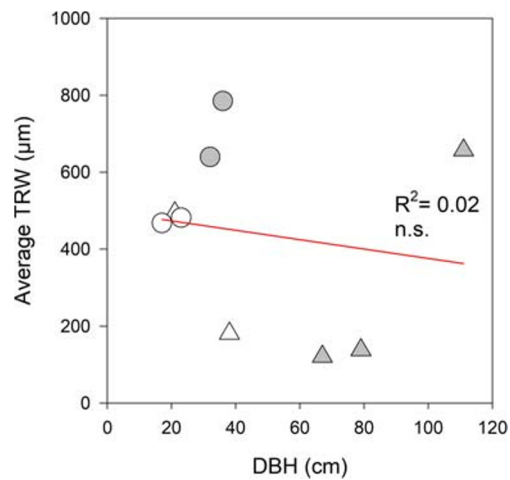
Fig. 7 Linear regression between diameter at breast height (DBH) and average tree ring width (TRW) for the period 2005–2014 (based on tree cores) showing no significant relationship at the 0.05 level. Triangles= *Juniperus excelsa*; Circles: *Cedrus libani*. White symbols and grey symbols indicate suppressed and co-dominant trees, respectively

Fig. 8 Relationship between averaged daily vapor pressure deficit (VPD) and normalized tree water deficit (TWD) in *Juniperus excelsa* (left) and *Cedrus libani* (right) during August 1 to September 30, 2013. Linear regressions were significant at the $p < 0.001$ level

References

Abbasnia M, Toros H (2019) Analysis of long-term changes in extreme climatic indices: a case study of the Mediterranean climate, Marmara Region, Turkey. In: Meteorology and climatology of the Mediterranean and Black Seas. Springer, In, pp 141–153. https://doi.org/10.1007/978-3-030-11958-4_9

Akkemik Ü (2006) Tree-ring data in last 300 years of Turkey: signatures of drought-record over the years. Sci Echoes 3:34–40

Aldea J, Bravo F, Vázquez-Piqué J, Rubio-Cuadrado A, del Río M (2018) Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands. Agric For Meteorol 256: 220–230. https://doi.org/10.1016/j.agrformet.2018.03.013

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP, Wolf A, Ziaco E, Pacala S (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532. https://doi.org/10.1126/science.aab1833

Arndt SK, Livesley SJ, Merchant A, Bleby TM, Grierson PF (2008) Quercitol and osmotic adaptation of field-grown Eucalyptus under seasonal drought stress. Plant Cell Environ 31:915–924

Aussenac G (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. Ann For Sci 59:823–832. https://doi.org/10.1051/forest:2002080

Avsar MD, Tonguc F (2003) Evaluation of growth potential of Crimean juniper (Juniperus excelsa Bieb.) seedlings for the first growing season under Tekir Forest nursery conditions in Kahramanmaras, Turkey. J Environ Biol 24(2):155–159

Baquedano F, Castillo F (2007) Drought tolerance in the Mediterranean species Quercus coccifera, Quercus ilex, Pinus halepensis, and Juniperus phoenicea. Photosynthetica 45:229

Barraclough AD, Zweifel R, Cusens J, Leuzinger S (2019) Disentangling the net: concomitant xylem and over-bark size measurements reveal the phloem-generated turgor signal behind daytime stem swelling in the mangrove Avicennia marina. Funct Plant Biol 46:393–406

Basaran S, Tolunay D, Makineci E, Basaran MA, Kavgacı A, Çetin A, Kaçar S, Baş N (2008) Determining the actual state of Cedar Research Forest Elmali by GIS based digital maps. South-West Anatolia Forest Research Institute report, Antalya, p 331

Belotti F, Deb P, Manning WG, Norton EC (2015) twopm: two-part models. Stata J 15:3–20

Boydak M (2003) Regeneration of Lebanon cedar (Cedrus libani A. Rich.) on karstic lands in Turkey. For Ecol Manag 178:231–243. https://doi.org/10.1016/S0378-1127(02)00539-X

Bray EA (1993) Molecular responses to water deficit. Plant Physiol 103: 1035–1040

Brinkmann N, Eugster W, Zweifel R, Buchmann N, Kahmen A (2016) Temperate tree species show identical response in tree water deficit but different sensitivities in sap flow to summer soil drying. Tree Physiol 36:1508–1519

Camarero JJ, Olano JM, Parras A (2010) Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytol 185: 471–480. https://doi.org/10.1111/j.1469-8137.2009.03073.x

Carus S (2004) Increment and Growth in Crimean Juniper (Juniperus excelsa Bieb.) Stands in Isparta—Sütcüler Region of Turkey. J Biol Sci 4:173–179

Cuny HE, Rathgeber CBK, David F et al (2015) Woody biomass production lags stem-girth increase by over one month in coniferous forests. Nat Plants 1:15160. https://doi.org/10.1038/nplants.2015.160

Daudet F-A, Améglio T, Cochard H, Archilla O, Lacointe A (2005) Experimental analysis of the role of water and carbon in tree stem diameter variations. J Exp Bot 56:135–144

De Swaef T, De Schepper V, Vandegehuchte MW, Steppe K (2015) Stem diameter variations as a versatile research tool in ecophysiology. Tree Physiol 35:1047–1061

Deslauriers A, Morin H, Urbinati C, Carrer M (2003) Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Quebec (Canada). Trees 17:477–484. https://doi.org/10.1007/s00468-003-0260-4

Deslauriers A, Anfodillo T, Rossi S, Carraro V (2007) Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees. Tree Physiol 27:1125–1136

Dietrich L, Zweifel R, Kahmen A (2018) Daily stem diameter variations can predict the canopy water status of mature temperate trees. Tree Physiol 38(7):941–952

Downes G, Beadle C, Worledge D (1999) Daily stem growth patterns in irrigated Eucalyptus globulus and E. nitens in relation to climate. Trees 14:102–111

Drew DM, Downes GM (2009) The use of precision dendrometers in research on daily stem size and wood property variation: a review. Dendrochronologia 27:159–172. https://doi.org/10.1016/j.dendro.2009.06.008

Durkaya B, Durkaya A, Makineci E, Ülküdür M (2013) Estimation of above-ground biomass and sequestered carbon of Taurus Cedar (Cedrus libani L.) in Antalya, Turkey. Iforest 6:278–284. https://doi.org/10.3832/ifor0899-006

Ehrenberger W, Rüger S, Fitzke R, Vollenweider P, Günthardt-Goerg M, Kuster T, Zimmermann U, Arend M (2012) Concomitant dendrometer and leaf patch pressure probe measurements reveal the effect of microclimate and soil moisture on diurnal stem water and leaf turgor variations in young oak trees. Funct Plant Biol 39: 297–305

Epron D (1997) Effects of drought on photosynthesis and on the thermo-tolerance of photosystem II in seedlings of cedar (Cedrus atlantica and C. libani). J Exp Bot 48:1835–1841

Fisher M, Gardner AS (1995) The status and ecology of a Juniperus excelsa subsp. polycarpos woodland in the northern mountains of Oman. Vegetatio 119:33–51

Fontaine M, Aerts R, Özkan K, Mert A, Gülsoy S, Süel H, Waelkens M, Muys B (2007) Elevation and exposition rather than soil types determine communities and site suitability in Mediterranean mountain forests of southern Anatolia, Turkey. For Ecol Manag 247(1–3):18–25

Garnier E, Berger A (1986) Effect of water stress on stem diameter changes of peach trees growing in the field. J Appl Ecol:193–209

Genc M, Deligöz A, Gültekin H (2005) Stress resistance of the Juniperus oxycedrus and J. foetidissima, J. excelsa, Pinus nigra subsp. pallasiana, Cedrus libani and Picea orientalis seedlings. Ladin Sempozyumu, 20-22 Ekim 2005, Trabzon, Book of abstracts, pp 474–482

Giovannelli A, Deslauriers A, Fragnelli G, Scaletti L, Castro G, Rossi S, Crivellaro A (2007) Evaluation of drought response of two poplar clones (Populus× canadensis Mönch 'I-214'and P. deltoides Marsh.'Dvina') through high resolution analysis of stem growth. J Exp Bot 58:2673–2683

Gričar J, Jagodic Š, Prislan P (2015) Structure and subsequent seasonal changes in the bark of sessile oak (*Quercus petraea*). Trees 29:747–757

Gültekin H, Gültekin Ü (2005) Natural distribution, biology and ecology of some Juniper (*Juniperus* L.) species in Turkey (in Turkish with English abstract). Batı Akdeniz Ormancılık Araştırma Müdürlüğü Dergisi 7

Gültekin H, Gültekin Ü (2007) Türkiye'deki ardıç (*Juniperus* L.) türlerinin silvikültür teknikleri. Doğu Akdeniz Ormancılık Araştırma Müdürlüğü. DOA Dergisi 13:69–111

Güney A, Kerr D, Sökücü A, Zimmermann R, Küppers M (2015) Cambial activity and xylogenesis in stems of *Cedrus libani* A. Rich at different altitudes. Bot Stud 56:20. https://doi.org/10.1186/s40529-015-0100-z

Güney A, Küppers M, Rathgeber C, Şahin M, Zimmermann R (2017) Intra-annual stem growth dynamics of Lebanon Cedar along climatic gradients. Trees 31:587–606. https://doi.org/10.1007/s00468-016-1492-4

Güney A, Zweifel R, Türkan S, Zimmermann R, Wachendorf M, Güney CO (2020) High-resolution stem radius changes of *Juniperus excelsa* and *Cedrus libani* from the Taurus Mountain range of SW-Turkey. Zenodo repository. [Dataset]. V1. https://doi.org/10.5281/zenodo.3978175

Hinckley TM, Lassoie JP (1981) Radial growth in conifers and deciduous trees: a comparison. Mitteilungen der Forstliche Bundesversuchsanstalt Wien 142:17–56

Hinckley TM, Lassoie JP, Running SW (1978) Temporal and spatial variations in the water status of forest trees. For Sci 24:a0001–z0001

Hsiao TC, Acevedo E, Fereres E, Henderson D (1976) Water stress, growth and osmotic adjustment. Philos Trans R Soc Lond B Biol Sci 273:479–500

Ilek A, Kucza J, Morkisz K (2016) Hygroscopicity of the bark of selected forest tree species. Iforest 10:220

Kuhn M (2012). The caret package. R Foundation for Statistical Computing, Vienna, Austria. URL https://cran.r-project.org/package=caret.

Ladjal M, Huc R, Ducrey M (2005) Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. Tree Physiol 25:1109–1117

Ladjal M, Deloche N, Huc R, Ducrey M (2007) Effects of soil and air drought on growth, plant water status and leaf gas exchange in three Mediterranean cedar species: *Cedrus atlantica, C. brevifolia* and *C. libani*. Trees 21:201–213. https://doi.org/10.1007/s00468-006-0112-0

Lazzarin M, Zweifel R, Anten N, Sterck FJ (2018) Does phloem osmolality affect diurnal diameter changes of twigs but not of stems in Scots pine? Tree Physiol 39:275–283

Lockhart JA (1965) An analysis of irreversible plant cell elongation. J Theor Biol 8:264–275

Mencuccini M, Hölttä T, Sevanto S, Nikinmaa E (2013) Concurrent measurements of change in the bark and xylem diameters of trees reveal a phloem-generated turgor signal. New Phytol 198:1143–1154

Mencuccini M, Salmon Y, Mitchell P, Höltta T, Choat B, Meir P, O'Grady A, Tissue D, Zweifel R, Sevanto S, Pfautsch S (2017) An empirical method that separates irreversible stem radial growth from bark water content changes in trees: theory and case studies. Plant Cell Environ 40:290–303

Moran E, Lauder J, Musser C, Stathos A, Shu M (2017) The genetics of drought tolerance in conifers. New Phytol 216:1034–1048

Morgan JM (1984) Osmoregulation and water stress in higher plants. Annu Rev Plant Physiol 35:299–319

Nuri O, Uysal M (2009) Usability of the Taurus Cedar and Crimean Pine in green belt afforestations in semiarid regions in Turkey: a case study in Konya Province Loros Mountain-Akyokus. Afr J Agric Res 4:1049–1057

Özkan K, Gulsoy S, Aerts R, Muys B (2010) Site properties for Crimean juniper (*Juniperus excelsa*) in semi-natural forests of south western Anatolia, Turkey. J Environ Biol 31(1):97

Ozturk T, Ceber ZP, Türkeş M, Kurnaz ML (2015) Projections of climate change in the Mediterranean Basin by using downscaled global climate model outputs. Int J Climatol 35:4276–4292

Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wohlgemuth T, Zweifel R, Dobbertin M (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Chang Biol 19:229–240

Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol 170:301–310. https://doi.org/10.1111/j.1469-8137.2006.01660.x

Rossi S, Deslauriers A, Anfodillo T, Carraro V (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152:1–12. https://doi.org/10.1007/s00442-006-0625-7

Saatcioglu F (1969) Silviculture I- Biological principles of silviculture (in Turkish). lstanbul University, Faculty of Forestry publications, p 323

Sass-Klaassen U, Leuschner H, Buerkert A, Helle G (2008) Tree-ring analysis of *Juniperus excelsa* from the northern Oman mountains. In: Proceedings of the Dendrosymposium 2007, May 3rd-6th 2007, Riga, Latvia, 2008. pp 83–90

Sevim M (1961) Bazı orman ağaçlarının kök sistemleri ve yetişme muhiti şartları ile münasebetleri. İstanbul Üniversitesi Orman Fakültesi Dergisi, pp 49-65

Tognetti R, Lasserre B, Di Febbraro M, Marchetti M (2019) Modeling regional drought-stress indices for beech forests in Mediterranean mountains based on tree-ring data. Agric For Meteorol 265:110–120. https://doi.org/10.1016/j.agrformet.2018.11.015

Touchan R, Xoplaki E, Funkhouser G, Luterbacher J, Hughes MK, Erkan N, Akkemik Ü, Stephan J (2005) Reconstructions of spring/summer precipitation for the Eastern Mediterranean from tree-ring widths and its connection to large-scale atmospheric circulation. Clim Dyn 25:75–98. https://doi.org/10.1007/s00382-005-0016-5

Tümen I, Hafızoğlu H (2003) Türkiye'de yetişen ardıç (*Juniperus* L.) türlerinin kozalak ve yaprak uçucu yağlarının bileşiminde bulunan terpen grupları. Bartın Orman Fakültesi Dergisi 5

Tyree M, Jarvis P (1982) Water in tissues and cells. In: Physiological plant ecology II. Springer, pp 35–77

van Emmerik T, Steele-Dunne S, Paget A, Oliveira RS, Bittencourt PR, Barros FV, van de Giesen N (2017) Water stress detection in the Amazon using radar. Geophys Res Lett 44:6841–6849

Vieira J, Rossi S, Campelo F, Freitas H, Nabais C (2013) Seasonal and daily cycles of stem radial variation of *Pinus pinaster* in a drought-prone environment. Agric For Meteorol 180:173–181

Vieira J, Rossi S, Campelo F, Freitas H, Nabais C (2014) Xylogenesis of *Pinus pinaster* under a Mediterranean climate. Ann For Sci 71:71–80. https://doi.org/10.1007/s13595-013-0341-5

Voelker SL, DeRose RJ, Bekker MF, Sriladda C, Leksungnoen N, Kjelgren RK (2018) Anisohydric water use behavior links growing season evaporative demand to ring-width increment in conifers from summer-dry environments. Trees 32:735–749

Willson CJ, Manos PS, Jackson RB (2008) Hydraulic traits are influenced by phylogenetic history in the drought-resistant, invasive genus *Juniperus* (Cupressaceae). Am J Bot 95:299–314

Yücedağ C, Gailing O (2013) Genetic variation and differentiation in *Juniperus excelsa* M. Bieb. populations in Turkey. Trees 27:547–554. https://doi.org/10.1007/s00468-012-0807-3

Zweifel R, Häsler R (2000) Frost-induced reversible shrinkage of bark of mature subalpine conifers. Agric For Meteorol 102:213–222

Zweifel R, Item H, Häsler R (2000) Stem radius changes and their relation to stored water in stems of young Norway spruce trees. Trees 15:50–57. https://doi.org/10.1007/s004680000072

Zweifel R, Zimmermann L, Newbery D (2005) Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiol 25:147–156

Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. J Exp Bot 57:1445–1459

Zweifel R, Steppe K, Sterck FJ (2007) Stomatal regulation by microclimate and tree water relations: interpreting ecophysiological field data with a hydraulic plant model. J Exp Bot 58(8):2113–2131

Zweifel R, Haeni M, Buchmann N, Eugster W (2016) Are trees able to grow in periods of stem shrinkage? New Phytol 211(3):839–849