Biologia (2025) 80:1125–1142
https://doi.org/10.1007/s11756-024-01693-7

ORIGINAL ARTICLE

Intra-annual dynamics of stem circumference variation and water status of four coniferous tree species (*Pinus sylvestris, Picea abies, Larix decidua* and *Abies alba)* under warmer and water-limited conditions

Adriana Leštianska[1] · Peter Fleischer Jr[1,2] · Katarína Merganičová[3,4] · Peter Fleischer Sr[1,2] · Katarína Střelcová[1]

Received: 16 October 2023 / Accepted: 16 April 2024 / Published online: 7 May 2024
© The Author(s) 2024

Abstract

In the paper, the intra-annual growth patterns and tree water balance of four different tree species (*Pinus sylvestris*, *Picea abies*, *Larix decidua* and *Abies alba*) were examined. Seasonal radial increment, tree water deficit (ΔW) and maximum daily shrinkage (MDS) were derived from the records obtained using high-resolution digital band dendrometers. The study area was located in Arboretum Borová hora (350 m a. s. l., Zvolen valley, Central Slovakia) characterised by a warmer climate (*Picea abies*) and warmer and drier climate (*Abies alba*, *Larix decidua*, *Pinus sylvestris*) compared to the sites of tree origins. Monitored species exhibited remarkably distinct growth and water balance patterns over the 2015 growing season characterised with the highly above normal temperature and uneven precipitation distribution. *A. alba* exhibited smooth continuous growth least affected by varying environmental conditions. Of all analysed species, only *A. alba* showed significant positive correlations of radial growth and ΔW with temperature and global radiation, despite environmental water limitations. The lowest cumulative growth, lower negative values of ΔW and greater MDS of *L. decidua* indicate a higher water limitation of this species. The results showed more pronounced sensitivity of *P. sylvestris* to increased temperature and drought. All monitored variables of environmental conditions, except precipitation, significantly influenced MDS values of all studied tree species. Based on 30 variables describing radial stem growth patterns and water status we identified large inter-species variability and discrete species-specific groups, while the indicators of growth and water status of *L. decidua* and *P. sylvestris* were similar and the most different patterns were observed between *A. alba* and *L. decidua*. The behaviour of *P. abies* was closer to *A. alba* than to the other two species.

Keywords Climate-tree physiology relation · Dendrometer · Tree water balance

Introduction

Future climate projections indicate an increase in the frequency and severity of climatic extremes at global and regional scales (Seneviratne et al. 2021), which may affect species distributions and compositions, functionality and stability of ecosystems. Tolerance to extreme climatic conditions is the outcome of various combinations of physiological, anatomical, and morphological adjustments (Lindner et al. 2010). Forests growing outside their natural environmental conditions belong to most sensitive ecosystems. Altitude is one of the most important factors influencing the spatio-temporal patterns of vegetation responses, including tree growth (Mäkinen et al. 2002). The growth of trees at high altitudes in Central Europe is primarily influenced by temperature (Frank and Esper

✉ Adriana Leštianska
adriana.lestianska@tuzvo.sk

[1] Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 24, 960 01 Zvolen, Slovakia

[2] Research Station of Tatra National Park, Tatranská Lomnica 14066, 05960 Vysoké Tatry, Slovakia

[3] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Prague 6, Suchdol 16500, Czech Republic

[4] Department of Biodiversity of Ecosystems and Landscape, Slovak Academy of Sciences, Štefánikova 3, P.O.Box 25, 81499 Bratislava, Slovakia

2005). Hence, an increase in temperature has usually a positive impact on tree growth at such sites (Rozenberg et al. 2020). However, at lower altitudes, where moisture conditions are driving factors (Mäkinen et al. 2002), adverse effects of rising temperatures, linked to summer droughts, are noticeable (Rozenberg et al. 2020). While many studies have examined morphological and physiological adaptations of species to water availability (Benavides et al. 2019), there is limited knowledge about interspecific variations in growth sensitivity.

Temperate tree species periodically increase their radial stem dimensions during growing seasons depending on environmental variables. Daily stem circumference changes are the cumulative results of the formation of new xylem cells (physiological growth) and reversible elastic changes of stem tissues caused by water inflow (stem swelling or expansion) and water outflow (stem shrinkage) (Daudet et al. 2005; De Swaef et al. 2015). Stem shrinkage represents tissue elasticity, and is a function of wood density, i.e. it is species-specific (Zweifel et al. 2014). The timing of the diurnal dynamics of stem tissue water depletion and replenishment depends on actual environmental conditions, transpiration and sap flow (Perämäki et al. 2001; Zweifel et al. 2006). Currently, a widely used method in the research of climate-tree water balance-growth relations is based on monitoring of stem circumference changes using automatic dendrometers. Non-destructive continuous observations of stem circumference changes using high precision dendrometers provide time series of fluctuations in tree water reserves at different time scales, from minute changes to seasonal tree growth in relation to changes in environmental conditions (Leštianska et al. 2015, 2020, 2023; Oberhuber et al. 2015; Zweifel et al. 2021). These analyses enable us to deduce growth rates and identify patterns of intra- and inter-annual growth variability in response to changing environment.

One way of investigating water changes in plant tissues and relative plant water content in relation to its hydration state at high temporal resolution is to use the tree water deficit (ΔW) (Hinckley and Lassoie 1981; Zweifel 2016). ΔW is known as tree water deficit-induced stem shrinkage and it is an indicator of the absolute stem water deficit (Dietrich et al. 2018). ΔW allows accounting for accumulated water deficits also over an extended period of drought (from few days to months) (Zweifel et al. 2005; Dietrich et al. 2018).

Another stem water indicator derived from stem circumference changes is maximum daily shrinkage (MDS) (e.g. Zweifel et al. 2005; Ehrenberger et al. 2012), which quantifies the reduction in stem radius over 1 calendar day (Deslauriers et al. 2007), and hence, it is an indicator of tree plasticity to respond to current air and soil conditions (Giovannelli et al. 2007). ΔW and MDS are currently often used in ecophysiological research to assess drought stress because they are mainly driven by a combination of atmospheric and soil conditions (Zweifel et al. 2016; Dietrich et al. 2018).

Assessing the species-specific response of stem size to climate presents challenges as it necessitates uniform site and stand conditions to isolate the influence of climate accurately. In our research, we conducted a comparison of changes in the stem circumference between species that were growing at the same site situated in warmer and drier conditions compared to their natural habitats. The selected coniferous species for this study included *Picea abies L.* Karst, *Abies alba* Mill., *Pinus sylvestris* L., and *Larix decidua* Mill., all of which are native in central Europe.

The Norway spruce (*Picea abies*) holds great economic significance in Europe. It has been extensively cultivated across various climatic conditions, demonstrating its adaptability to environment (Caudullo et al. 2016). Nevertheless, it is widely acknowledged that spruce is vulnerable to drought that can have a considerable impact on its growth rates and overall health (Boden et al. 2014). Silver fir (*Abies alba*) is primarily found in the mountain ranges of the Alps and Carpathians and its ecotypes show great variation in the resistance to frost, drought and shading. Climate change is believed to have had an adverse impact on the growth performance of fir populations in Europe in recent decades (Battipaglia et al. 2009). Scots pine (*P. sylvestris*) is an evergreen conifer with a broad Euro-Siberian distribution. It is a moderately drought-sensitive species. Despite its effective water-saving mechanisms, it exhibits sensitivity to climate fluctuations (Bouriaud and Popa 2009) and its productivity may decline at exposed locations with water deficit, as pine is commonly found at dry sites. European larch (*Larix decidua*) is characteristic of mountainous regions of the Carpathians and the Alps (Danek et al. 2017). At lower altitudes, it is considered a non-native species, which is why studies on larch growth in such areas are less prevalent. *Larix decidua* is considered a light-demanding, pioneer tree species that does not show significant decline related to climate change and thrives on soils with high water supply (Keller et al. 1997). However, several studies (e.g. Lévesque et al. 2013; Schuster and Oberhuber 2013; Dyderski et al. 2018) indicate that it is significantly sensitive to soil water deficit.

The key questions of our work address the intra-annual stem circumference variation patterns in relation to species and environmental conditions. Intra-annual variations are still not completely understood, because analyses of fine-resolution intra-annual stem growth dynamics across species, sites and years are demanding. The main aim of this paper is to evaluate the intra-annual growth and water status of four coniferous tree species and identify possible climate-growth patterns interactions. Based on band dendrometer records (BDR) we aim to i) identify the intra-annual growth patterns of each tree species, aiming to gain insights into the impact of atmospheric and soil conditions, ii) identify the

environmental factors that drive tree growth and tree water status of tree species, iii) identify species-specific irreversible and reversible changes in stem circumference under changing environmental conditions. To fulfill these intentions, we used a unique dataset of short-term atmospheric and edaphic measurements as well as radial measurements from stem dendrometers installed on the trees of four coniferous species (*Picea abies*, *Abies alba*, *Pinus sylvestris* and *Larix decidua*) that were planted at the same site located in warmer and drier conditions than their natural habitats. The year 2015 characterised by dry periods and above normal temperature during the growing season serves as a model year to examine how trees may cope with predicted climatic changes in future. We hypothesised that selected tree species showed different physiological reactions to water availability due to differences in their water management and storage strategies in the stem. Additionally, we also hypothesised that the differences in growth and water regime patterns would be more distinct between different tree species than between trees of the same species.

Material and methods

Study site and tree species

The research was carried out in the Arboretum of Technical University in Zvolen, located in Central Slovakia (48°35′N, 19°07′E, altitude 353 m a.s.l). This facility serves the purpose of conserving the gene pool of the Carpathian dendroflora ex situ (Lukáčik 2015). The study area represents common upland forest communities in Central Slovakia. The climate at the site is temperate with average annual air temperature 8.2 °C and annual precipitation total 651 mm. During the growing season (April–September), a long-term average temperature is 14.7 °C and the total precipitation is 377 mm (calculated from long-term data obtained from a nearby meteorological station in Sliač, situated at an altitude of 313 m a.s.l. and provided by the Slovak Hydrometeorological Institute (SHMI), representing a period of 1961–1990). Cambisol is a dominant soil type there (https://geo.enviroportal.sk/atlassr). The description of the climatic conditions of the origin of the studied species (Fig. 1) was derived from CRUTEM4 datasets (Jones et al. 2012) and Panoply software.

Four research plots, each representing a single species, namely Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), European larch (*Larix decidua*) and Silver fir (*Abies alba*) were selected within the Arboretum area to ensure similar environmental conditions at all plots. The selected provenances of the four tree species currently grow in conditions that are generally warmer for *Picea abies*, and warmer and drier for *Pinus sylvestris*, *Larix decidua* and *Abies alba* compared to their original natural habitats (Fig. 1). For this study, a total of 20 trees (five adult trees at each plot) of approximately the same age of around 50 years were selected. The descriptive statistics of their tree circumferences at breast height are provided in Table 1.

Environmental data

Meteorological data: global radiation (GR, $W.m^{-2}$), air temperature (AT, °C), relative air humidity (RH, %), precipitation (P, mm) were recorded with an automatic meteorological station (EMS Brno, CZ) installed at an open area near research plots (from 80 to 150 m from plots). Vapour pressure deficit (VPD, Pa) was calculated based on relative humidity and air temperature records. Monthly climate characteristics (average, totals) were derived from the measured meteorological data of air temperature and precipitation, and compared with the long-term averages representing the period 1961–1990 calculated from the data measured at the climatological station Sliač (313 m a.s.l.) provided by SHMI. The assessment of the abnormality of the current weather was carried out according to the methodological instructions of SHMI (Lapin et al. 1988).

Soil water potential (SWP, bar) was measured at three different depths (15, 30 and 50 cm) under forest canopy at each study plot using gypsum blocks and MicroLog SP3 (EMS Brno, CZ). Average daily SWP values per plot calculated from all depths were used for further analyses. All measurements (meteorological and soil water potential data) were recorded at 20-min intervals and processed to represent a daily level.

Dendrometer records and their analyses

To characterise intra-annual radial growth patterns, high-resolution automatic band dendrometers (model DRL 26, EMS Brno, CZ, accuracy ± 0.01 mm) were used to monitor 20 sample trees of *Abies alba*, *Pinus sylvestris*, *Picea abies* and *Larix decidua* (i.e. five trees per species). The dendrometers were installed on stems at a height 2.0–2.5 m from stem base in April 2015, after carefully smoothing and removing the outermost bark layer. Stem circumferences were measured at 20 min intervals. The measurements lasted from April 15 to October 19, 2015 capturing the growing season.

Dendrometer records were analysed using two methods: (i) a daily cycle approach and (ii) a stem cycle approach. Both approaches involve dividing the data into three distinct phases based on stem dynamics: stem contraction (phase 1), expansion (phase 2), and stem circumference increment (phase 3) (Downes et al. 1999; Deslauriers et al. 2003). The daily approach operates on 24-h scale (from 0:00 to 0:00). In our study, one day was represented by 72 stem circumference values, each recorded every twenty minutes.

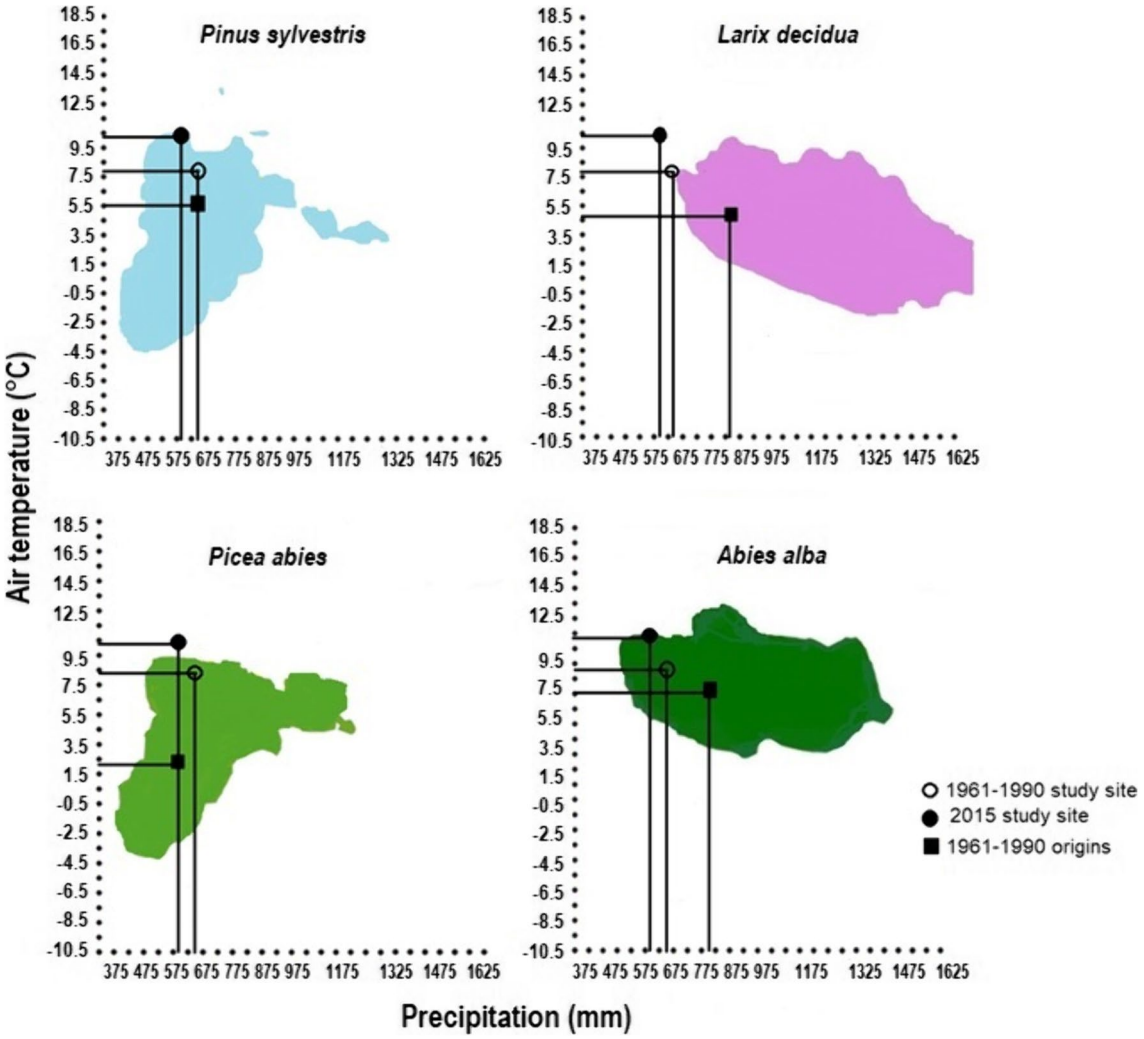


Fig. 1 Tree-species specific requirements on annual climate parameters (coloured areas) derived from Kölling (2007) compared with local long-term values (empty circles), local values representing the year 2015 (filled circles), and values representing the sites of their origins (squares)

Table 1 Descriptive statistics of stem circumferences (cm) measured at 1.3 m above ground at the beginning of 2015

		Stem circumference (cm)			
Tree species	Number of trees	Minimum	Maximum	Mean	Standard deviation
P. sylvestris	5	73.7	100.0	89.0	10.0
L. decidua	5	74.6	101.5	89.2	9.6
P. abies	5	76.7	85.3	80.7	6.5
A. alba	5	75.0	121.5	94.4	12.3

The stem cycle approach describes stem dynamics independently of individual calendar days and operates on a time scale different from 24 h. A contraction phase refers to the period between the maximum and subsequent minimum values of BDR. An expansion phase is the period between the BDR minimum and the subsequent maximum value. An increment phase is a part of the expansion phase that occurs when the stem size exceeds the previous absolute maximum and continues until it reaches the subsequent maximum. According to Deslauriers et al. (2007), the difference between the expansion maximum and the previous maximum represents the positive stem circumference variation (ΔR^+, mm). If the maximum of the previous cycle was not exceeded, a zero or a negative value of ΔR (ΔR^-, mm) was assigned. The duration (h, hours) of each phase was derived from the dendrometre records. From diurnal BDR we determined if the positive (ΔR^+) and negative (ΔR^-) stem circumference variations occurred on a particular calendar day. Subsequently, we counted the occurrences of ΔR^+ and ΔR^- within predefined 15-day intervals.

Seasonal circumference increment was calculated as a difference between the BDR values at the end and the start of the season.

Tree water deficit (ΔW, mm) as an indicator of tree water status indicator was assessed using dendrometer records that were de-trended for growth following the method by Ehrenberger et al. (2012). It was determined by calculating the difference in stem size recorded by dendrometers at a specific time point and the stem size under fully hydrated conditions (ΔW = 0), which is estimated from the growth line (Oberhuber et al. 2015).

Maximum daily shrinkage (MDS, mm) reflects the daily cycle of water uptake and loss. It refers to the difference between daily maximum and minimum stem circumferences and is used to quantify the proportion of water taken during the night compared to the amount of water lost from elastic cambial and phloem tissues during the day (Deslauriers et al. 2007).

The identification of stem cycles from BDR, duration of each phase of stem dynamics, and the quantification of ΔW, MDS and ΔR was performed using custom routines developed in the "DendrometeR" R package (van der Maaten et al. 2016).

Statistical analyses

The Spearman rank-correlation coefficients were calculated to explore the relationships between daily values of environmental variables: global radiation (GR), precipitation (P), relative air humidity (RH), vapour pressure deficit (VPD), mean (ATmean), minimum (ATmin) and maximum (ATmax) air temperature, and soil water potential (SWP), and stem characteristics extracted from BDR (tree water deficit (ΔW), maximum daily shrinkage (MDS), and stem circumference variation (ΔR)).

The correlations between the time series of daily BDR values of individual trees within single trees species (Table 3b) and the average curves of different species (Table 3a) were calculated using the normalized cross-correlation approach. To describe the tree radial growth pattern and stem water status in more detail, another 30 variables were derived from BDR (Table 2) beside the mentioned indicators (ΔR, ΔW, MDS). Principal component analysis (PCA) was applied to all variables to assess the differences and similarities between four coniferous species. PCA was performed in the R environment using "factoextra" package and "ggplot2" for data visualization (Kassambara and Mundt 2020). We used four methods: "daily.stats", "cycle.stats", "smooth.spline function" and "ΔW" to process the data. Daily values were calculated with "daily.stats" (marked D in Table 2), while "cycle.stats" was used to identify the magnitude of three distinct phases (contraction, expansion and growth, marked as C in Table 2) within stem cycles in dendrometerR package (van der Maaten et al. 2016).

Results

Environmental conditions during the study period

The courses of meteorological characteristics (daily global radiation totals, daily mean temperature, relative humidity, vapour pressure deficit, and daily precipitation totals) between April 15 and October 19, 2015 are depicted in Fig. 2. The local daily mean relative air humidity varied between 45 and 100% (Fig. 2). The monthly mean relative air humidity in the period was 79 ± 8%. Rain events were unevenly distributed (Fig. 2). The onsite meteorological data representing the year 2015 were compared with the long-term normal (1961–1990) from the nearest meteorological station (Sliač, 313 m a.s.l., 3.5 km from the study area of Borová hora). The average air temperature (16.9 °C) and the precipitation total (412 mm) during the observed period (April–October) of the year 2015 exceeded the long-term normal by 2.2 °C and 4%, respectively (Fig. 3). All monthly air temperatures in the assessed period exceeded the long term monthly normals, while the maximum difference was observed in August (+4.4 °C) (Fig. 3).

High monthly precipitation total (99 mm, 155% of the long-term normal) was recorded in July (Fig. 3), although most of the rain events occurred within few days at the end of July (Fig. 2). The longest period without precipitation lasting for approximately 40 days started on June 10 and finished on July 19, 2015 (Fig. 2). During 20 days in this period, the daily mean air temperature exceeded 20 °C, causing a notable decrease of soil water potential (Fig. 2). The vapour pressure deficit reached maximum values in July (17.7 hPa). The daily totals of global radiation reached the highest values in June and July (Fig. 2). A similar dry and warm period started in the middle of August and continued until late September.

Stem growth and tree water status derived from BDR

Rapid radial growth occurred from late May to late June irrespective of species. Temporal species-specific stem circumference variations and seasonal stem circumference increments derived from BDR exhibited substantial differences between tree species (Figs. 4 and 5). The most intensive radial growth was found for *A. alba*. Both *A. alba* and *P. abies* followed a similar pattern in stem circumference variations with low fluctuations over the season. *P. sylvestris* and *L. decidua* showed pronounced fluctuations in the seasonal courses of their stem circumferences (Fig. 4). The largest

Table 2 Variables describing radial stem growth pattern and water status derived from band dendrometre records used in principal component analysis, where D indicates *daily.stats*, C *cycle.stats*, S *smooth.spline* and ΔW *tree water deficit* applied methods. Early, mid and late stages of the growing season refer to 1st, 2nd and 3rd equally long parts of the study period

No	Variable	Unit	Applied method
1	Cumulative time of expansion in the growing season	hours	D
2	Cumulative time of contraction in the growing season	hours	D
3	Cumulative time of radial increment in the growing season	hours	D
4	Number of cycles per season	number	C
5	Average time of daily expansion	hours	D
6	Average time of daily contraction	hours	D
7	Average time of daily radial increment	hours	D
8	Average time of a cycle	hours	C
9	Average amplitude of expansion	mm	C
10	Average amplitude of contraction	mm	C
11	Average amplitude of radial increment	mm	C
12	Average amplitude of a cycle	mm	C
13	Circumference increment in early stage of growing season	mm	C
14	Circumference increment in mid-stage of growing season	mm	C
15	Circumference increment in late stage growing season	mm	C
16	Total circumference increment during growing season	mm	C
17	Relative circumference increment in early stage of growing season	%	C
18	Relative circumference increment in mid stage of growing season	%	C
19	Relative circumference increment in late stage of growing season	%	C
20	Average stem water deficit per day	mm	ΔW
21	Average circumference increment per cycle	mm	C
22	Average maximum daily shrinkage (MDS)	mm	D
23	Number of complete stem cycles per growing season	number	C
24	Cumulative stem water deficit	mm	ΔW
25	Cumulative maximum daily shrinkage (MDS)	mm	D
26	Cumulative residuals of BDR deviation from spline function	mm	S
27	Cumulative sum of radial growth	mm	D
28	Average MDS in early stage of growing season	mm	D
29	Average MDS in mid stage of growing season	mm	D
30	Average MDS in late stage of growing season	mm	D

seasonal increment was recorded for *A. alba* (13.6 ± 4.2 mm) followed by *P. sylvestris* (8.8 ± 2.5 mm), and *P. abies* (5.8 ± 1.4 mm). *L. decidua* had the lowest radial increment (4.9 ± 2.9 mm) (Figs. 4 and 5).

Despite large absolute differences in stem circumference temporal development (Fig. 4), the inter-species cross-correlations of BDR were high ($R^2 = 0.79–0.98$, $p < 0.05$, Table 3a). Intra-species cross-correlations of stem circumference variations were higher, since the average cross-correlation values exceeded $R^2 = 0.90$ for all species except for *L. decidua* which exhibited contrasting growth responses of individual trees (Table 3b).

Positive stem circumference variations (ΔR^+) dominated in *A. alba* during the whole season, except for early September. In *P. abies* ΔR^+ dominated in the first half of the growing season. Higher proportions of negative stem circumference variations (ΔR^-) with similar temporal distribution patterns were recorded for *P. sylvestris* and *L. decidua* (Fig. 6).

Daily averages and seasonal cumulative values of tree water deficit (ΔW) (Fig. 7) increased in the following order: *A. alba* (-0.1 mm, -12.5 mm), *P. abies* (-0.2 mm, -37.4 mm), *P. sylvestris* (-0.7 mm, -123.8 mm), and *L. decidua* (-1.0 mm, -195.4 mm). Lower values of daily ΔW for *P. sylvestris* and *L. decidua* were recorded during the longer rainless period in July and from the middle of August until October (Fig. 7). Species specific maximum daily shrinkage and seasonal cumulative shrinkage were the highest for *L. decidua* (0.34 mm, 64.4 mm) followed by *P. sylvestris* (0.33 mm, 62.5 mm), *P. abies* (0.16 mm, 30.4 mm) and *A. alba* (0.15 mm, 27.4 mm). The lowest values of ΔW of *P. abies* and *A. alba* were at the beginning of the season (Fig. 7). Close to zero values of ΔW occurred after precipitation events, while in the case of *P. sylvestris* and *L. decidua* they usually lasted only few days (Fig. 7) despite the fact that high values of SWP remained for much longer time (Fig. 2).

Peak values of MDS generally occurred in mid-July, which coincided with low precipitation totals (Fig. 8). *L.*

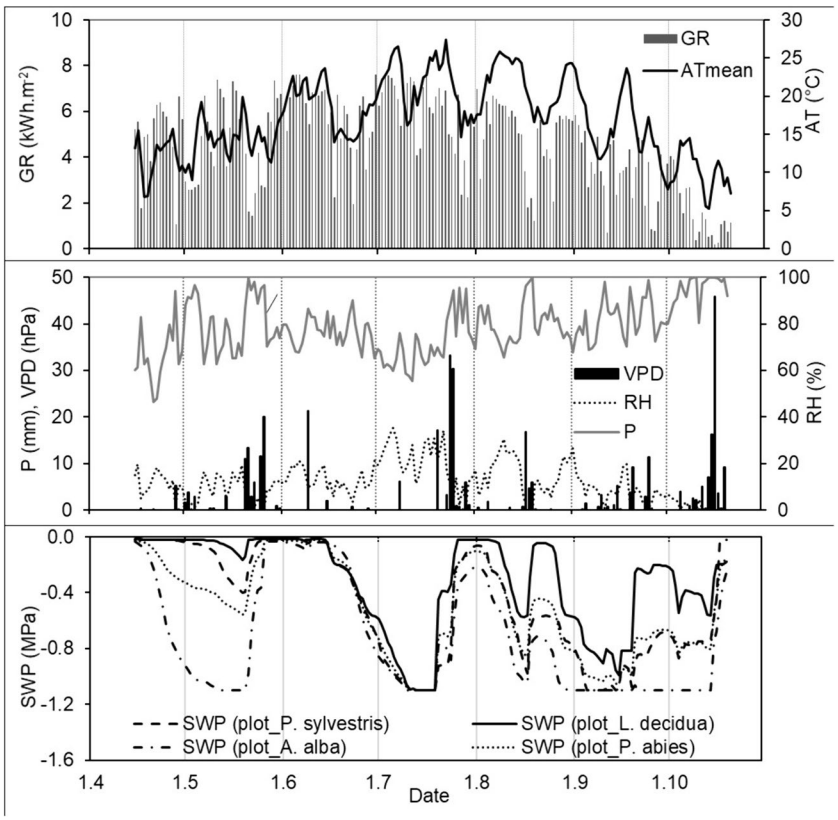


Fig. 2 Seasonal courses of daily mean air temperature (AT) and daily totals of global radiation (GR), daily precipitation (P), daily mean relative air humidity (RH), daily mean vapour pressure deficit (VPD), and soil water potential (SWP) at individual plots during the growing season of 2015

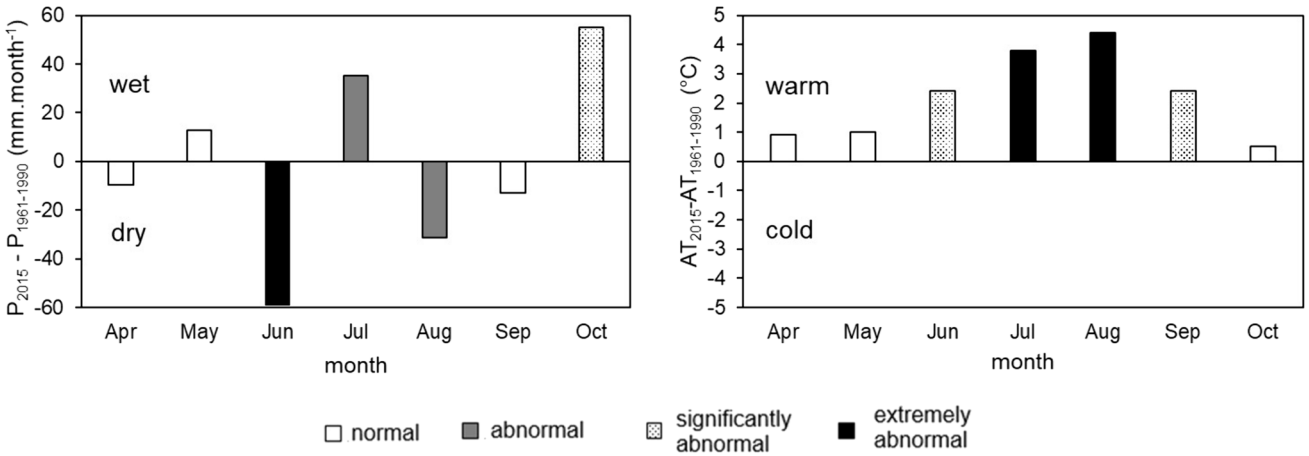


Fig. 3 Anomalies of local monthly precipitation totals (left) and of local monthly average air temperature values (right) for the period of April to October in the year 2015 in comparison to long-term monthly means representing the period 1961–1990

decidua and *P. sylvestris* were more sensitive to moisture conditions indicated by pronounced changes in daily dehydration/rehydration, while *P. abies* and *A. alba* showed higher drought resistance (Figs. 7 and 8).

The differences in growth responses and water status characteristics between trees and species were further analysed by principal component analysis (PCA) (Fig. 9). The derived 30 variables describing growth patterns and water status in details (Table 2) were distributed in 2D space of two first components (Fig. 9). Closer distances between variables indicate higher correlations between them (e.g. variables 14–15, 13–16, for variable description see Table 2). The PCA results revealed that the first component accounted for 52.9% of the total variance in the analysed data, while the second component explained additional 14.6%. The first component primarily represented tree water deficit characteristics. In contrast, the second component was predominantly influenced by

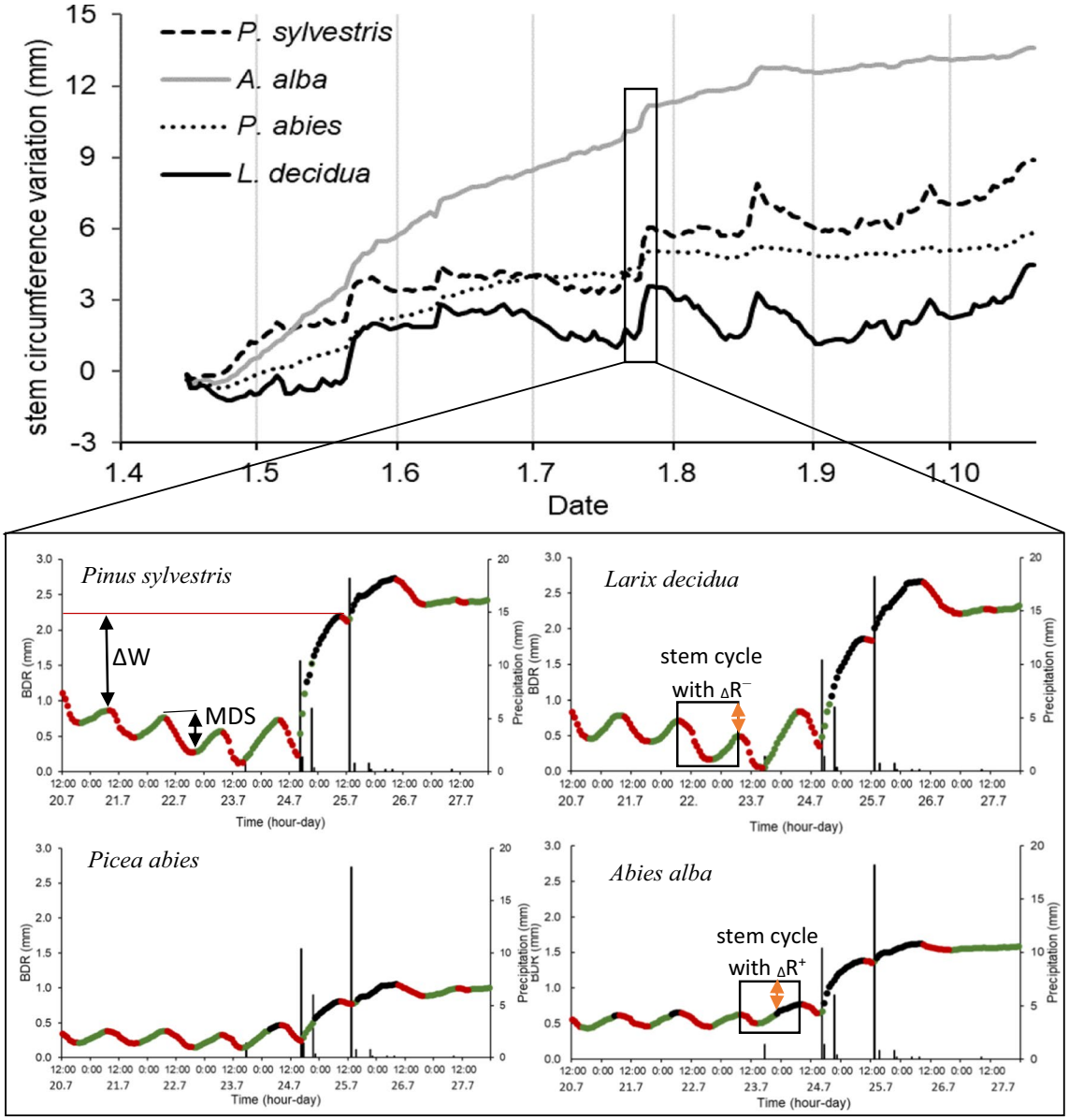


Fig. 4 Courses of stem circumference changes of *P. sylvestris*, *L. decidua*, *P. abies* and *A. alba* from April 15 to October 19 in the year 2015. Each line represents an average from 5 trees of the same species. Detailed figures show the period with no rainfall (20–23 July 2015) followed by the short rainy interval (24–26 July 2015) and indicate distinct phases of the stem cycle: contraction (red), expansion (green) and increment (black), using hourly data points. Maximum daily shrinkage (MDS) represents the variance between the highest and lowest values of stem size recorded within a day. Tree water deficit (ΔW) indicates the difference between the actual stem size and the growth line (red lines) that represents the stem size under fully hydrated circumstances. The positive stem circumference variation (ΔR^+, indicated by the orange error in the detailed figure for *A. alba*) was calculated when the stem circumference exceeded the previous morning maximum. The negative stem radial variation (ΔR^-, indicated by the orange error in the detailed figure for *L. decidua*) was calculated when the previous cycle maximum was not reached

variables derived from the maximum daily shrinkage. In the PCA biplot, four distinct clusters emerged, each corresponding to different tree species. The cluster labelled 'F', representing *A. alba*, is prominently positioned on the right. This positioning is influenced by variables V13 to V16, which denote growth metrics. Additionally, variables V20 and V24, associated with tree water deficit, played a significant role in shaping this cluster. The cluster corresponding to *L. decidua* was formed on the opposite side of the biplot. This species exhibited a contrasting growth pattern and water status when compared to *A. alba*. The *P. sylvestris* cluster showed a positive correlation with variables V28, 27, 29, 25, 26, 22, 11, and 12, which describe the maximum daily shrinkage. The *P. abies* cluster located

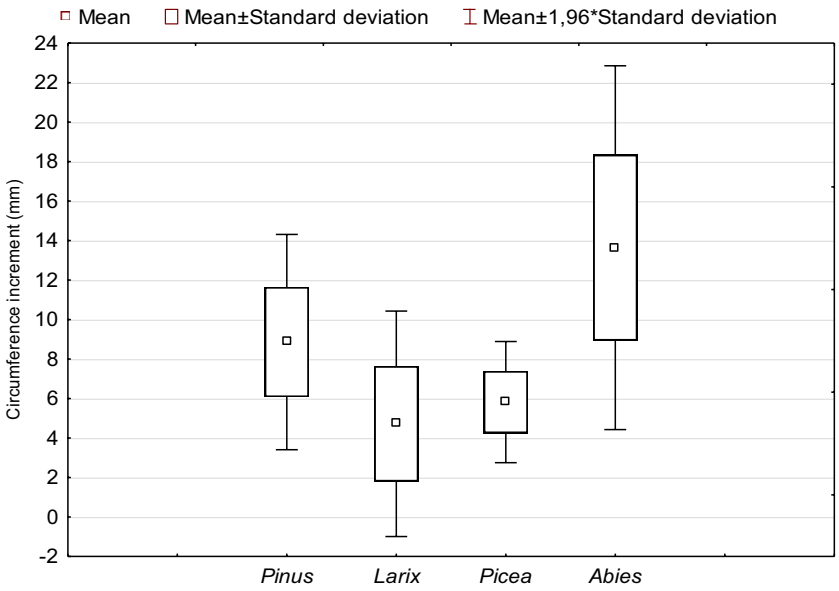


Fig. 5 Tree species specific seasonal circumference increments in the growing season (April–October) of the year 2015. Box plots represent the mean, standard deviation, and 95% variation range of increment values ($p > 0.05$), with $n = 5$ for individual species

Table 3 a) Inter-species and b) intra-species cross-correlations between stem band dendrometre records

Species	a)				b)				
	R^2				R^2				
	P. sylvestris	*L. decidua*	*P. abies*	*A. alba*	No. of trees	Min	Max	Mean	Std
P. sylvestris	1.00	-	-	-	5	0.93	0.99	0.97	0.016
L. decidua	0.82	1.00	-	-	5	0.14	0.99	0.67	0.295
P. abies	0.93	0.85	1.00	-	5	0.96	0.99	0.98	0.012
A. alba	0.95	0.79	0.98	1.00	5	0.90	0.99	0.97	0.035

in the first quadrant is mainly influenced by growth related variables V17 and V21.

Stem circumference characteristics and environmental conditions

Spearman correlation coefficients revealed significant impacts of monitored environmental factors on daily changes of positive stem circumference variation (ΔR^+) and tree water status (ΔW, MDS) during the studied period from April 15 to October 19, 2015 (Table 4). ΔR^+ of all tree species positively correlated with all atmospheric characteristics and negatively with SWP (Table 4). ΔR^+ of all species was significantly correlated with characteristics related to water regime (RH, P, VPD, SWP), while more significant relationships were found for *L. decidua* and *P. sylvestris* than for *P. abies* and *A. alba*. The strongest positive correlation of ΔR^+ to precipitation was revealed for *P. sylvestris*. *P. abies* had the highest correlation coefficient between ΔR^+ and SWP.

In the case of ΔW, the highest positive correlations were found between ΔW and SWP for all species (Table 4), while the highest and lowest values were recorded for *L. decidua* and *A. alba*, respectively. Significant negative correlations of ΔW to ATmean, ATmin, ATmax and VPD were obtained only for *P. sylvestris* and *L. decidua*. In the case of *A. alba* and *P. abies*, ΔW showed a positive correlation with GR. ΔW positively correlated with air temperature characteristics (ATmean, ATmin, ATmax) only in the case of *A. alba*.

All four species revealed highly significant relationships between MDS and environmental variables, whereby air temperature (mean, min, max) showed the highest positive correlations with MDS of all species. MDS of all species was positively correlated with global radiation, while the lowest value of the correlation coefficient was found for *P. sylvestris*. Significant and high positive values of correlation coefficients were also revealed between MDS and VPD for all species. The results showed that MDS was negatively correlated to RH and SWP, while *P. sylvestris* was found to be the most sensitive to SWP values and the other monitored species were more sensitive to relative air humidity (Table 4). No significant correlations were found between MDS and precipitation (Table 4).

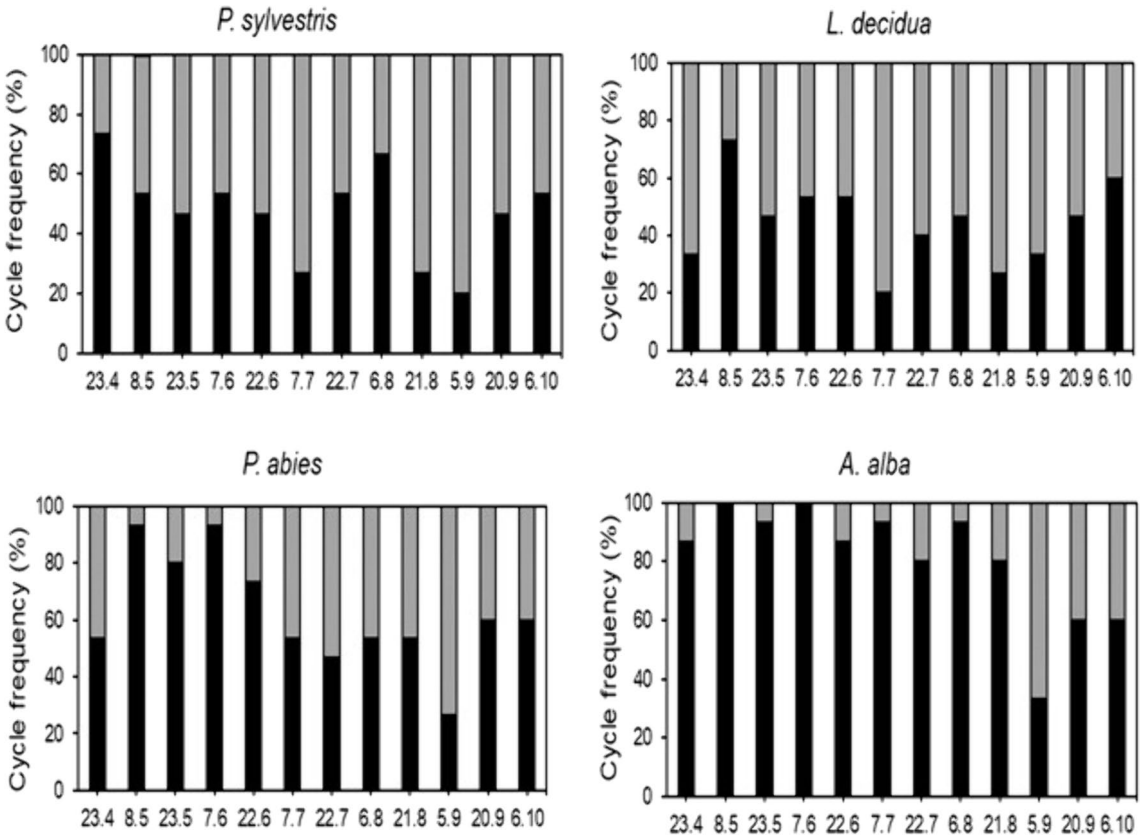


Fig. 6 Frequency of positive (ΔR^+) and negative (ΔR^-) stem circumference variations in 15-day intervals of band dendrometre records (BDR). Black columns (ΔR^+) indicate that the previous day maximum BDR was exceeded on the given day. Grey columns (ΔR^-) indicate that the maximum BDR of the previous day was not reached. Bars of the histogram represent 15-day intervals and dates on x axis refer to the middle of each interval

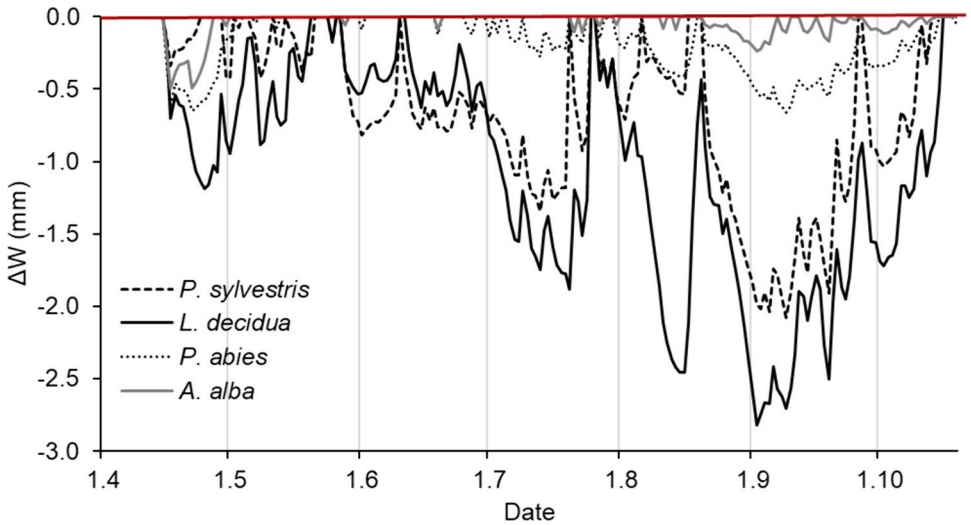


Fig. 7 Mean species-specific tree water deficit (ΔW, mm) from April 15 to October 19, 2015. The solid red line indicates the stem size under the fully hydrated conditions

Discussion

Tree growth is controlled by a multitude of factors, with climate being one of the most crucial. Climate envelope models visualise the current distribution of plant species, as demonstrated by Kölling (2007). Despite some limitations this approach has a potential to estimate future species spatial distribution and their sensitivity under changing climate (Walentowski et al. 2017). Our study was performed under conditions that are projected for coming

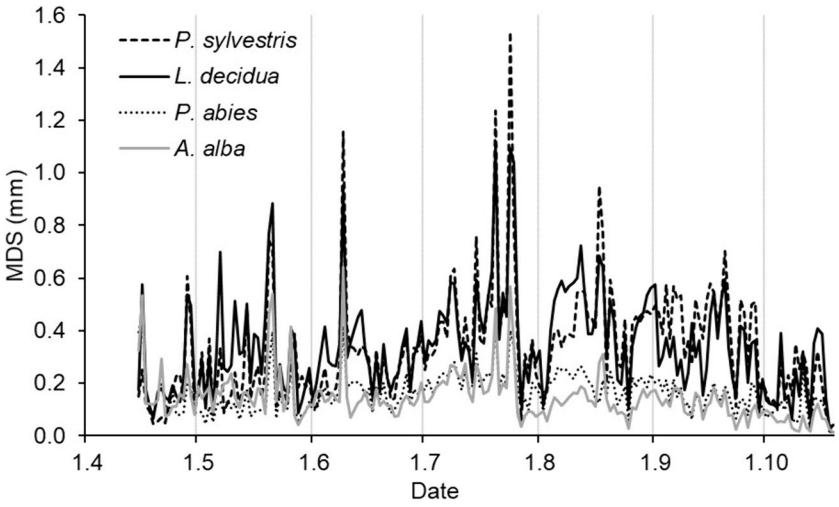


Fig. 8 Mean species-specific maximum daily shrinkage (MDS, mm) from April 15 to October 19, 2015

Table 4 Spearman rank-correlation coefficients for the relationships between daily environmental variables (GR = global radiation; AT_{mean} = mean air temperature; AT_{min} = minimum air temperature; AT_{max} = maximum air temperature; RH = relative air humidity; P = precipitation; VPD = vapour pressure deficit; SWP = soil water potential) and positive stem circumference variation (ΔR^+), maximum daily shrinkage (MDS) and daily water deficit (ΔW) of *P. abies, P. sylvestris, L. decidua* and *A. alba*

		GR	ATmean	ATmin	ATmax	RH	P	VPD	SWP
Pinus sylvestris	ΔR^+	-0.237**	-0.187**	-0.024	-0.214**	0.325***	0.458***	-0.335***	0.239***
	ΔW	-0.088	-0.316***	-0.235**	-0.322***	0.118	0.246***	-0.244***	0.619***
	MDS	0.152*	0.517***	0.568***	0.476***	-0.092	0.141	0.301***	-0.527***
Abies Alba	ΔR^+	0.154*	0.162*	0.198**	0.109	0.111	0.297***	-0.016	0.221**
	ΔW	0.219**	0.213**	0.220**	0.158*	0.033	0.167*	0.069	0.233**
	MDS	0.358***	0.404***	0.297***	0.410***	-0.370***	0.003	0.437***	-0.012
Picea abies	ΔR^+	0.101	0.007	0.057	-0.038	0.179*	0.241***	-0.125	0.411***
	ΔW	0.221**	0.052	0.044	0.007	0.087	0.093	-0.030	0.465***
	MDS	0.395***	0.620***	0.571***	0.606***	-0.343***	-0.067	0.546***	-0.169*
Larix decidua	ΔR^+	-0.179*	-0.068	0.052	-0.087	0.311***	0.345***	-0.254***	0.170*
	ΔW	0.106	-0.244***	-0.257***	-0.252***	0.071	0.083	-0.183*	0.684***
	MDS	0.353***	0.619***	0.611***	0.581***	-0.223**	0.085	0.460***	-0.269***

Significance levels: *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

decades as the mean temperature in the analysed growing season of 2015 exceeded the long-term value by + 2.4 °C. Higher annual air temperatures were observed also in the preceding (2014: + 2.8 °C; 2013: + 1.5 °C; 2012: + 1.7 °C) as well as in the following years (2016: + 1.7 °C, 2017: + 1.1 °C, 2018: + 2.8 °C). In addition, the meteorological drought in the year 2015 was identified as one of the most severe droughts since the summer event of 2003, affecting a large part of continental Europe (Ionita et al. 2017; Laaha et al. 2017) including Slovakia (Fendeková et al. 2017). The responses of stem radial growth and water status to environmental conditions in 2015 reflected the position of environment with regard to species-specific climate envelopes illustrated in Fig. 1. Notably, the highest sensitivity was found for *L. decidua,* followed by *P. abies*, and *P. sylvestris*. The weakest response was revealed for *A. alba*, for which both the long-term (1961–1990) and the 2015 climatic conditions occurred inside the species climate envelope (Fig. 1).

Monitored species exhibited remarkably different growth patterns over the 2015 growing season characterised by the highly above normal temperature and uneven precipitation distribution (Figs. 2 and 3). *Larix decidua* showed the lowest cumulative growth (Fig. 4). We assume that the limited growth of *L. decidua* at the studied site resulted from environmental conditions that occurred outside the climatic envelope of the species causing its higher stress and stimulating strong individual tree responses. Although *L. decidua* has been shown to develop a specific drought avoidance strategy by osmotic adjustment resulting from the accumulation of solutes (Anfodillo et al. 1998), it was found to be sensitive to water stress when growing at dry

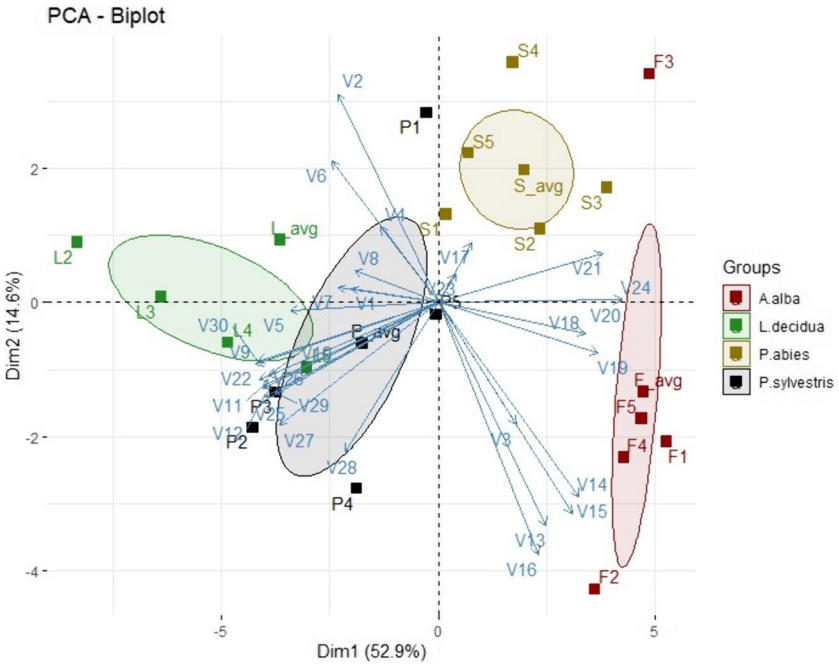


Fig. 9 Species-specific responses of stem circumference variations analysed by principal component analysis. Abbreviations in labels: $V_{1–30}$variables describing growth patterns and water status listed in Table 2; $F_{1–5}$–fir trees (*A. alba*); F_avg–average value for fir; $S_{1–5}$–spruce trees (*P. abies*); S_avg–average value for spruce; $P_{1–5}$–pine trees (*P. sylvestris*); P_avg–average value for pine; $L_{1–5}$–larch trees (*L. decidua*); L_avg–average value for larch

and low elevation sites (Eilmann and Rigling 2012; Danek et al. 2021), especially during summer months, which was also confirmed by our results (Figs. 4 and 10). The weak adjustability of *L. decidua* to drought is possibly related to its deciduous habit and/or anisohydric strategy due to which high transpiration rates are maintained under long-lasting drought events (Leo et al. 2013) finally causing the impairment of tree water status (Bréda et al. 2006).

L. decidua as well as *P. abies* have been suggested to be sensitive to reduced soil moisture availability, especially at xeric and mesic sites across the European Alps situated at low to mid-elevations (e.g. Lévesque et al. 2013; Danek et al. 2021). Based on Heres et al. (2014), and Morán-Lopéz et al. (2014), *P. abies* performance and recruitment are highly threatened by increased aridity. Compared to *L. decidua*, *P. abies* is generally considered a more drought-sensitive species, because it is shallow-rooted and more conservative concerning its water use (Anfodillo et al. 1998). It has also been shown that *L. decidua* regulates stomatal conductance more strongly than *P. abies* during atmospheric drought (Peters et al. 2019). At the same time, relative ΔW was consistently larger in *L. decidua* (Fig. 7), while MDS in study trees of *P. abies* reached much lower values compared to *L. decidua* (Fig. 8). This indicates a more anisohydric behaviour of *L. decidua* under severely limiting soil moisture conditions (Bréda et al. 2006) and high sensitivity of *L. decidua* to drought (Eilmann and Rigling 2012; Lévesque et al. 2014). *P. abies* has a better water-saving strategy than *L. decidua* (Anfodillo et al. 1998). In several studies (e.g. Oberhuber et al. 2015; Peters et al. 2019) *P. abies* exhibited an isohydric behaviour, thus minimizing the risk of hydraulic failure via timely stomatal closure, consequently strongly reducing sap flow and reduction of excessive water losses. According to Střelcová et al. (2013), stomatal closure under advanced drought may cause a decrease in the response of *P. abies* to meteorological parameters, and soil water availability becomes the main limiting factor for transpiration. In our study, in the advancing drought, when soil water potential reached low values, ΔW of *P. abies* did not respond proportionally to changes in evaporation conditions (Table 4). The use of internal water storage is a significant factor affecting the sap flow variability of *P. abies* (Preisler et al. 2022). Utilization of internal stem water reserves makes *P. abies* in the short term less dependent on soil water content. Water stored in xylem and phloem tissues can meet tree transpiration demands for about a week (Čermák et al. 2007). However, without sufficient refilling, internal water storage cannot support transpiration for a longer period without the risk of xylem cavitation. It is possible that *P. abies* did not utilize stem water reserves for transpiration during the drier year 2015, likely because of much lower sap flow (i.e. closed stomata) and lower requirements for stored trunk water. Similarly, Schäfer et al. (2018) observed a decrease in ΔW values of *P. abies* with the increasing drought. This anomaly was likely due to reduced transpiration rates driven by high evaporative demands and exhausted soil water reserves. We presume that this was the main reason why ΔW was small during the extreme drought in 2015.

Both *L. decidua* and *P. sylvestris* grew in cascades separated by plateaus representing stagnation periods (Fig. 4), which can be explained by SWP decline during rainless periods (Fig. 2). The remarkable plateau in BDR of *P. sylvestris*

and *L. decidua* (Fig. 4) observed during June and July 2015 corresponded with the prevalence of negative stem radial variations (ΔR^-) in R^+/R^- ratios (Figs. 4 and 6). Positive stem radial variations (ΔR^+) dominated in *A. alba* and partly in *P. abies* mostly at the beginning of the growing season, which agrees with Deslauriers et al. (2007). The increase of circumference became evident after "water storage cells" were rehydrated following precipitation events, which is in accordance with Zweifel et al. (2005) and Vieira et al. (2013). ΔR^+ of all species was correlated with characteristics related to water regime (RH, P, VPD, SWP), while for *L. decidua* and *P. sylvestris* all relationships were significant. The strongest positive correlation of ΔR^+ to precipitation was revealed for *P. sylvestris*. *P. abies* had the highest correlation coefficient between ΔR^+ and SWP. It indicates that *P. sylvestris* reacts more to atmospheric conditions while *P. abies* is more responsive to soil moisture. Notable stem shrinkages (ΔR^-) observed in our study do not mean there was no radial growth at the same time. It suggests that the amplitude of stem shrinkage due to the net loss of stem water content exceeded the real stem circumference increment. Water consumption by plants depends not only on the water content in the soil but also on the water content in plant tissues. Primarily, plants draw water from the soil to meet their demands. With the decreasing soil water content in rainless periods, the physiological water scarcity in the plant body is observed and the plant growth is slowed down.

The fact that *P. sylvestris* was more responsive species than *A. alba* or *P. abies* was unexpected because the actual climatic conditions of *P. sylvestris* occurred within the species-specific envelope (Fig. 1). Besides, this species is known to be drought resistant. This is attributed to its relative isohydric strategy, which involves efficient stomatal control to reduce transpiration and prevent water losses (Irvine et al. 1998). *P. sylvestris* is known to be well protected against drought due to its embedded stomata and pronounced waxy layer on the epidermis (Krakau et al. 2013). However, its sensitivity to increased temperatures and drought has been a cause for concern regionally (Galiano et al. 2010). *P. sylvestris* was more sensitive to higher temperatures and was particularly responsive to ATmax (Table 4). Our results may therefore also be related to the generally higher vulnerability of *P. sylvestris* to longer summer drought periods and higher mean temperatures, as observed in many regions (Weber et al. 2010). This idea is substantiated by the fact that the dry year covered in this study belongs to those with well-documented summer droughts, such as 2003 (Merlin et al. 2015) or 2015 (Ionita et al. 2017). Our results unveiled that the drought-avoidance strategy of *P. sylvestris* might not be sufficient to counterbalance the negative impacts of climate change. Our study thereby confirms that in the Carpathian Mountains pine will be threatened by more frequent droughts in future, which is in accordance with Bouriaud and Popa (2007). A long-term reduction in *P. sylvestris* growth since 1950 has already been observed in multiple studies (Heres et al. 2014; Morán-Lopéz et al. 2014). Close relationships of radial stem growth derived from BDR to atmospheric and soil water status were previously reported for *P. sylvestris* at xeric sites (Oberhuber and Gruber 2010) and for a drought-prone mixed coniferous forest (Oberhuber et al. 2014).

In contrast, *A. alba* exhibited smooth continuous growth least affected by varying environmental conditions in spite of the lowest SWP values during the season (Fig. 2). Hence, *A. alba* was the most resistant tree species to changed conditions defined by increased temperature and periodical droughts. This supports the results of Vitali et al. (2017) who presented *A. alba* as an adaptive species to changing conditions, especially drought. Due to this, fir is often considered as a prospective species under climate change (Lindner et al. 2008), since fir productivity should not be adversely affected by increasing temperature (Bošeľa et al. 2018; Usoltsev et al. 2019). Of all analysed species, only *A. alba* showed significant positive correlations of radial growth and tree water deficit (ΔW) with temperature and global radiation (Table 4). Even under low SWP, *A. alba* did not show remarkable stem shrinkage and performed intense growth (Figs. 2 and 4).

MDS of all tree species showed similar responses to all monitored environmental variables (Table 4). During the longer period characterized by a lack of soil water in the rainless period or during the period with a low amount of precipitation, MDS decreased (Figs. 2 and 8) due to the insufficient tissue rehydration during the night. In general, the transpiration of trees depends not only on VPD, which reflects air temperature and relative air humidity, but also on radiation (Penman 1948). Stem shrinkage and expansion typically follow a diurnal pattern with a minimum stem radius in the afternoon and a maximum stem radius in the early morning. It is proportional to the loss of water from elastic tissues and can cover up to 100% of the transpired water on a cloudy day (Zweifel and Häsler 2001). However, high VPD accelerates sap flow, particularly under sufficient soil water content (Flo et al. 2021). In general, small MDS values indicate 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 value may indicate a day with little light or a day with closed stomata and thus limited transpiration and assimilation (Güney et al. 2020). On the contrary, large MDS values indicate days with open stomata and thus large transpiration and high assimilation (Güney et al. 2020). All monitored variables of environmental conditions, except precipitation, significantly influenced MDS values of all studied tree species (Table 4), which agrees with other studies (Herzog et al. 1995). The strong correlation of

MDS with VPD indicates a close coupling of transpiration, sap flow and diurnal stem shrinkage (Steppe et al. 2006). As reported by Dietrich et al. (2018), while MDS is an indicator of tree water status under conditions of sufficient water availability, it is not a reliable indicator of tree water status over longer time intervals involving drought periods. During a dry period when SWP progressively decreases, tree water potential does not fully recover during night-time, which in turn slows down the rehydration of elastic stem tissues. In such cases, the tissues may not be completely refilled during the night and thus, the stem remains in a partly shrunk state (Zweifel et al. 2001).

As Dietrich et al. (2018) pointed out, ΔW describes daily canopy water potential better than MDS during longer periods of stem shrinkage. ΔW is closely related to drought and is affected mainly by a combination of atmospheric and soil conditions (Oberhuber et al. 2015; Zweifel 2016). Low values of tree water deficit indicate water stress. ΔW values during the dry year 2015 were driven primarily by soil water potential, which was also confirmed in other studies (Ježík et al. 2015; Leštianska et al. 2020). Our data showed that SWP affected ΔW of *P. sylvestris* and *L. decidua* more strongly than ΔW of *P. abies* (Table 4). This outcome most likely indicates that in the short term, the use of water stored in the living tissues of the bark makes *P. abies* less dependent on the current water availability in the soil, which is consistent with the results of Turcotte et al. (2011). We observed lower values of ΔW for *P. sylvestris* and *L. decidua* suggesting higher water stress of these species. This was supported also by higher correlation values ($r = 0.62$ and 0.68, respectively) between ΔW and SWP for *P. sylvestris* and *L. decidua* than for *P. abies* and *A. alba* ($r = 0.47$ and 0.23, respectively) (Table 4).

PCA based on 30 variables describing radial stem growth pattern and water status (Table 2) and 20 individual trees identified discrete species-specific groups (Fig. 9) and hence large inter-species variability (Fig. 9). High intra-species cross-correlation values (Table 3) confirmed uniform growth responses of the studied trees of the same species except for *L. decidua,* which showed very variable seasonal courses of BDR of individual trees (Table 3b). Generally, we can state that the indicators of growth and water status of *L. decidua* and *P. sylvestris* were similar (Fig. 9). The most different patterns were observed for *A. alba* and *L. decidua*. The behaviour of *P. abies* was closer to *A. alba* than to the other two species. According to Carpenter and Brock (2006), the increasing variance in respective system processes serves as a decisive symptom of approaching a critical threshold. The most uniform response was observed for *A. alba* indicating least stressful conditions for this species. Relatively high resilience of *A. alba* to climate change has already been pointed out by other studies (Bouriaud and Popa 2009; Latreille et al. 2017). Research outcomes suggest that silver fir could be better suited for the future European climate, as it grew well during the mid-Holocene period under warmer conditions than what we have been experiencing today (Ruosch et al. 2016). According to Bošela et al. (2014), there has been a notable increase in the radial growth of silver fir across the entire Western Carpathian region after its recovery from the period of severe growth decline during 1970–1980 (Büntgen et al. 2014). Although our study did not examine population-level responses, it clearly indicated that Silver fir was generally more resistant and resilient to drought events and is therefore a suitable alternative to *P. abies* or *L. decidua*.

Conclusions

The present study examined intra-annual stem circumference variation patterns of four coniferous tree species (*Larix decidua, Picea abies, Pinus sylvestris* and *Abies alba*) using high-resolution dendrometer data considering both tree water status and radial growth in relation to environmental conditions. The study focused on the year 2015 when the mean temperature in the analysed growing season exceeded the long-term value and the meteorological drought was identified as one of the most severe droughts since the summer 2003 affecting a large part of Europe including Slovakia. Monitored species were growing at the same site situated at a lower elevation in warmer and drier conditions compared to their natural habitats and were exposed to similar microclimatic conditions above and below ground. The analyses revealed profound differences in seasonal growth and tree water balance patterns between the coniferous species. ΔW indicated different strategies of water status regulation of anisohydric and isohydric species. *L. decidua* showed the lowest cumulative growth probably due to the most adverse climatic conditions that occurred outside its climatic envelope as well as the impairment of tree water status related to its anisohydric strategy. Significantly lower negative values of tree water deficit and greater MDS of *L. decidua* indicate a higher water limitation of this species. The fact that *P. sylvestris* was a more responsive species than *A. alba* or *P. abies* was unexpected. However, our results are in agreement with a growing number of regional studies that report a more pronounced sensitivity of *P. sylvestris* to increased temperatures and drought. Of all analysed species, only *A. alba* showed substantial growth due to significant positive correlations of radial increment and tree water deficit with temperature and global radiation, despite environmental water limitations. Based on derived 30 variables describing radial stem growth patterns and water status we identified discrete species-specific groups and large inter-species variability. The patterns differed most

between *A. alba* and *L. decidua*, while the behaviours of *P. abies* and *A. alba* were similar. Although our study did not examine population-level responses, it indicated that *A. alba* was generally more resistant and resilient to drought and therefore seems to be a suitable alternative to *P. abies* or *L. decidua*. The observations from the year 2015 provided us with insights about how different tree species can cope with the increased occurrence of dry periods and above-normal air temperature. However, to generalize the obtained outcomes, longer data series are needed since the effect of consecutive dry years might drastically change the capacity of individual trees and tree species to recover from drought events.

Acknowledgements The study was supported by research grants of the Slovak Research and Development Agency APVV-19-0340, APVV-18-0347, APVV-18-0390, APVV-21-0224, APVV-21-0412, the Slovak Grant Agency for Science no. VEGA 1/0285/23 and by grant "EVA4.0", No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDEEVA4.0.

Funding Open access funding provided by The Ministry of Education, Science, Research and Sport of the Slovak Republic in cooperation with Centre for Scientific and Technical Information of the Slovak Republic

Data availability The data presented in this study are available on request from the corresponding author.

Declarations

Ethics approval The authors declare that the research meets ethical standards applicable to the research discipline.

Consent to participate All authors approved the participation.

Consent for publication All authors agree with the contents of the manuscript and gave final approval for publication.

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

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Anfodillo T, Rento S, Carraro V, Furlanetto L, Urbinati C, Carrer M (1998) Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in *Larix decidua* Miller, *Picea abies* (L.) Karst and *Pinus cembra* L. Ann For Sci 55(1–2):159–172. https://doi.org/10.1051/forest:19980110

Battipaglia G, Saurer M, Cherubini P, Siegwolf RTW, Cotrufo MF (2009) Tree rings indicate different drought resistance of a native (*Abies alba* Mill.) and a non-native (*Picea abies* (L.) Karst.) species co-occurring at a dry site in Southern Italy. Forest Ecol Manag 257:820–828. https://doi.org/10.1016/j.foreco.2008.10.015

Benavides R, Scherer-Lorenzen M, Valladares F (2019) The functional trait space of tree species is influenced by the species richness of the canopy and the type of forest. Oikos 128(10):1435–1445. https://doi.org/10.1111/oik.06348

Boden S, Kahle HP, Wilpert KV, Spiecker H (2014) Resilience of Norway spruce (*Picea abies* (L.) Karst) growth to changing climatic conditions in Southwest Germany. For Ecol Manage 315:12–21. https://doi.org/10.1016/j.forego.2013.12.015

Bošela M, Petráš R, Sitková Z, Priwitzer T, Pajtík J, Hlavatá H, Sedmák R, Tobin B (2014) Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. Environ Pollut 184:211–221. https://doi.org/10.1016/j.envpol.2013.08.036

Bošeľa M, Lukáč M, Castagneri D, Sedmák R, Biber P, Carrer P et al (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. Sci Total Environ 615:1460–1469. https://doi.org/10.1016/j.scitotenv.2017.09.092

Bouriaud O, Popa I (2007) Site and species influence on tree growth response to climate in Vrancea Mountains. Proc Rom Acad 9(1):63–72

Bouriaud O, Popa I (2009) Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. Trees 23(1):95–106. https://doi.org/10.1007/s00468-008-0258-z

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–544. https://doi.org/10.1051/forest:2006042

Büntgen U, Tegel W, Kaplan JO, Schaub M, Hagedorn F, Bürgi M, Brázdil R, Helle G, Carrer M, Heussner KU, Hofmann J, Kontic R, Kyncl T, Kyncl J, Camarero JJ, Willy T, Esper J, Liebhold A (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. Front Ecol Environ 12:100–106. https://doi.org/10.1890/130089

Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. Ecol Lett 9:311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x

Caudullo G, Tinner W, de Rigo D (2016) *Picea abies* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds.) European Atlas of Forest Tree Species 114–116:e012300

Čermák J, Kučera J, Bauerle WL, Phillips N, Hinckley TM (2007) Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. Tree Physiol. 27(2):181–198. https://doi.org/10.1093/treephys/27.2.181

Danek M, Chuchro M, Walanus A (2017) Variability in Larch (*Larix Decidua* Mill.) Tree-ring growth response to climate in the polish Carpathian Mountains. Forests 8(10):354. https://doi.org/10.3390/f8100354

Danek M, Chuchro M, Danek T (2021) Extreme growth reaction of larch (Larix decidua Mill.) from the Polish Sudetes and Carpathians: spatial distribution and climate impact. Trees 35:211–229. https://doi.org/10.1007/s00468-020-02029-z

Daudet FA, 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. https://doi.org/10.1093/jxb/eri026
De Swaef T, De Schepper V, Vandegehuchte MW, Steppe K (2015) Stem diameter variations as a versatile research tool in ecophysiology. Tree Physiol 35(10):1047–1061. https://doi.org/10.1093/treephys/tpv080
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, Rossi S, Anfondillo T (2007) Dendrometer and intra-annual tree growth: what kind of information can be inferred? Dendrochronologia 25:113–124. https://doi.org/10.1016/j.dendro.2007.05.003
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. https://doi.org/10.1093/treephys/tpy023
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. https://doi.org/10.1007/PL00009752
Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Glob Chang Biol 24:1150–1163. https://doi.org/10.1111/gcb.13925
Ehrenberger W, Rüger S, Fitzke R, Vollenweider P, Günthardt-Goerg MS, 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(4):297–305. https://doi.org/10.1071/Fp11206
Eilmann B, Rigling A (2012) Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiol 32:178–187. https://doi.org/10.1093/treephys/tps004
Fendeková M, Danáčová Z, Gauster T, Labudová L, Fendek M, Horvát O (2017) Analysis of hydrological drought parameters in selected catchments of the southern and eastern Slovakia in the years 2003, 2012 and 2015. Acta Hydrologica Slovaca 18(2):135–144
Flo V, Martínez-Vilalta J, Mencuccini M, Granda V, Anderegg WRL, Poyatos R (2021) Climate and functional traits jointly mediate tree water-use strategies. New Phytol 231(2):617–630. https://doi.org/10.1111/nph.17404
Frank D, Esper J (2005) Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps. Dendrochronologia 22:107–121. https://doi.org/10.1016/j.dendro.2005.02.004
Galiano L, Martínez-Vilalta J, Lloret F (2010) Drought-induced multifactor decline of scots pine in the pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems 13:978–991. https://doi.org/10.1007/s10021-010-9368-8
Giovannelli A, Deslauriers A, Fragnelli G, Scaletti L, Castro G, Rossi S, Crivellaro A (2007) Evaluation of drought response of two poplar clones (Populus x canadensis Monch "I-214" and P. deltoides Marsh. 'Dvina') through high resolution analysis of stem growth. J Exp Bot. 58(10):2673–2683. https://doi.org/10.1093/jxb/erm117
Güney A, Zweifel R, Türkan S, Zimmermann R, Wachendorf M, Güney CO (2020) Drought responses and their effects on radial stem growth of two co-occurring conifer species in the Mediterranean mountain range. Ann For Sci 77(105). https://doi.org/10.1007/s13595-020-01007-2
Heres AM, Voltas J, Lopez BC, Mart Nez-Vilalta J (2014) Drought-induced mortality selectively affects Scots pine trees that show limited intrinsic water-use efficiency responsiveness to raising atmospheric CO_2. Funct Plant Biol 41(3):244–256. https://doi.org/10.1071/FP13067
Herzog KM, Häsler R, Thum R (1995) Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. Trees 10:94–101. https://doi.org/10.1007/BF00192189
Hinckley T, Lassoie J (1981) Radial growth in conifers and deciduous trees: a comparison. Mitt Forstlichen Bundesversuchsanstalt 142:17–56
Ionita M, Tallaksen LM, Kingston DG, Stagge JH, Laaha G, Van Lanen HAJ, Scholz P, Chelcea SM, Haslinger K (2017) The European 2015 drought from a climatological perspective. Hydrol Earth Syst Sci 21(3):1397–1419. https://doi.org/10.5194/hess-21-1397-2017
Irvine J, Perks MP, Magnani F, Grace J (1998) The response of *Pinus sylvestris* to drought: Stomatal control of transpiration and hydraulic conductance. Tree Physiol 18:393–402. https://doi.org/10.1093/treephys/18.6.393
Ježík M, Blaženec M, Letts MG, Ditmarová Ľ, Sitková Z, Střelcová K (2015) Assessing seasonal drought stress response in Norway spruce (*Picea abies* (L.) karst.) by monitoring stem circumference and sap flow. Ecohydrol 8(3):378–386. https://doi.org/10.1002/eco.1536
Jones PD, Lister DH, Osborn TJ, Harpham C, Salmon M, Morice CP (2012) Hemispheric and large-scale land surface air temperature variations: An extensive revision and an update to 2010. J Geophys Res 117:D05127
Kassambara A, Mundt F (2020) factoextra: Extra and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0.7. https://CRAN.R-project.org/package=factoextra
Keller T, Guiot J, Tessier L (1997) Climatic effect of atmospheric CO2 doubling on radial tree growth in South Eastern France. J Biogeogr 24(6):857–864. https://doi.org/10.1046/j.1365-2699.1997.00140.x
Kölling C (2007) Klimahüllen für 27 Baumarten. AFZ-DerWald 62(23):1242–1245
Krakau UK, Liesebach M, Aronen T, Lelu-Walter MA, Schneck V (2013) Scots Pine (Pinus sylvestris L.). In: Pâques LE (ed.) Forest tree breeding in Europe. Current state-of-the-art and perspectives. Springer, Dordrecht Chapter 6:267–323
Laaha G, Gauster T, Tallaksen LM, Vidal J-P, Stahl K et al (2017) The European 2015 drought from a hydrological perspective. Hydrol Earth Syst Sci 21(6):3001–3024. https://doi.org/10.5194/hess-21-3001-2017
Lapin M, Faško P, Kveták Š (1988) Metodický predpis 3–09–1/1 Klimatické normály, Slovenský hydrometeorologický ústav Bratislava 25 s
Latreille A, Davi H, Huard F, Pichot Ch (2017) Variability of the climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients. For Ecol Manage 396:150–159. https://doi.org/10.1016/j.foreco.2017.04.012
Leo M, Oberhuber W, Schuster R, Grams TEE, Matyssek R, Wieser G (2013) Evaluating the effect of plant water availability on inner-alpine coniferous trees based on sap flow measurements. Eur J For Res 133:691–698. https://doi.org/10.1007/s10342-013-0697-y
Leštianska A, Merganičová K, Merganič J, Střelcová K (2015) Intra-annual patterns of weather and daily radial growth changes of Norway spruce and their relationship in the Western Carpathian mountain region over a period of 2008–2012. J For Sci 61(7):315–324. https://doi.org/10.17221/24/2015-JFS

Leštianska A, Fleischer P Jr, Merganičová K, Fleischer P, Střelcová K (2020) Influence of warmer and drier environmental conditions on species-specific stem circumference dynamics and water status of conifers in submontane zone of Central Slovakia. Water 12(10):2945. https://doi.org/10.3390/w12102945

Leštianska A, Fleischer P Jr, Merganičová K, Fleischer P Sr, Nalevanková P, Střelcová K (2023) Effect of provenance and environmental factors on tree growth and tree water status of Norway Spruce. Forests 14(1):156. https://doi.org/10.3390/f14010156

Lévesque M, Saurer M, Siegwolf R, Eilmann B, Brang P, Bugmann H, Rigling A (2013) Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Glob Chang Biol 19(10):3184–3199. https://doi.org/10.1111/gcb.12268

Lévesque M, Rigling A, Bugmann H, Weber P, Peter Brang P (2014) Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric for Meteorol 197:1–12. https://doi.org/10.1016/j.agrformet.2014.06.001

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manag 259:698–709. https://doi.org/10.1016/j.foreco.2009.09.023

Lindner M, Garcia-Gonzalo J, Kolström M, Green T, Reguera R, Maroschek M, Seidl R, Lexer M, Netherer S, Schopf A (2008) Impacts of Climate Change on European Forests and Options for Adaptation. Report to the European Commission Directorate-General for Agriculture and Rural Development. European Forest Institute: Joensuu, Finland, p 173

Lukáčik I (2015) Arborétum Borová hora – história, súčasnosť a perspektívy. In: Lukáčik I, Sarvašová I (eds.) Dendroflóra strednej Európy – využitie poznatkov vo výskume, vzdelávaní a praxi. Dendroflora of Central Europe – utilization of knowledge in research, education and practice. Vydavateľstvo TU vo Zvolene 9–19

Mäkinen H, Nöjd P, Kahle HP, Neumann U, Tveite B, Mielikäinen K, Röhle H, Spiecker H (2002) Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. For Ecol Manag 171:243–259. https://doi.org/10.1016/S0378-1127(01)00786-1

Merlin M, Perot T, Perret S, Korboulewsky N, Vallet P (2015) Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For Ecol Manag 339:22–33. https://doi.org/10.1016/j.foreco.2014.11.032

Morán-López T, Poyatos R, Llorens P, Sabaté S (2014) Effects of past growth trends and current water use strategies on Scots pine and pubescent oak drought sensitivity. Eur J Forest Res 133:369–382. https://doi.org/10.1007/s10342-013-0768-0

Oberhuber W, Gruber A (2010) Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. Trees 24(5):887–898. https://doi.org/10.1007/s00468-010-0458-1

Oberhuber W, Gruber A, Kofler W, Swidrak I (2014) Radial stem growth in response to microclimate and soil moisture in a drought-prone mixed coniferous forest at an inner Alpine site. Eur J Forest Res 133(3):467–479. https://doi.org/10.1007/s10342-013-0777-z

Oberhuber W, Hammerle A, Kofler W (2015) Tree water status and growth of saplings and mature Norway spruce (*Picea abies*) at a dry distribution limit. Front Plant Sci 6:703. https://doi.org/10.3389/fpls.2015.00703

Penman HL (1948) Natural evaporation from open water, bare soil, and grass. Proc R Soc A193:120–146

Perämäki M, Nikinmaa E, Sevanto S, Ilvesniemi H, Siivola E, Hari P, Vesala T (2001) Tree stem diameter variations and transpiration in Scots pine: an analysis using a dynamic sap flow model. Tree Physiol 21(12–13):889–897. https://doi.org/10.1093/treephys/21.12-13.889

Peters RL, Speich M, Pappas C, Kahmen A, von Arx G, Graf Pannatier E, Steppe K, Treydte K, Stritih A, Fonti P (2019) Contrasting stomatal sensitivity to temperature and soil drought in mature alpine conifers. Plant Cell Environ 42(5):1674–1689. https://doi.org/10.1111/pce.13500

Preisler Y, Hölttä T, Grünzweig JM, Oz I, Tatarinov F, Ruehr NK, Rotenberg E, Yakir D (2022) The importance of tree internal water storage under drought conditions. Tree Physiol 42(4):771–783. https://doi.org/10.1093/treephys/tpab144

Rozenberg P, Chauvin T, Escobar-Sandoval M, Huard F, Shishov V, Charpentier J, Sergent A, Vargas-Hernandez JJ, MartinezMeier A, Pâques L (2020) Climate warming diferently afects Larix decidua ring formation at each end of a French Alps elevational gradient. Ann for Sci 77:54. https://doi.org/10.1007/s13595-020-00958-w

Ruosch M, Spahni R, Joos F, Henne PD, van der Knaap WO, Tinner W (2016) Past and future evolution of *Abies alba* forests in Europe - comparison of a dynamic vegetation model with palaeo data and observations. Glob Chang Biol 22(2):727–740. https://doi.org/10.1111/gcb.13075

Schäfer C, Thurm EA, Rötzer T, Kallenbach C, Pretzsch H (2018) Daily stem water deficit of Norway spruce and European beech in intra- and interspecific neighborhood under heavy drought. Scand J For Res 33(6):568–582. https://doi.org/10.1080/02827581.2018.1444198

Schuster R, Oberhuber W (2013) Drought sensitivity of three co-occurring conifers within a dry inner alpine environment. Trees 27(1):61–69. https://doi.org/10.1007/s00468-012-0768-6

Seneviratne SI, Zhang X, Adnan M et al (2021) Weather and Climate Extreme Events in a Changing Climate (Chapter 11). In: IPCC 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Eds. Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., et al Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press:1513–1766. https://doi.org/10.1017/9781009157896.013

Steppe K, De Pauw DJ, Lemeur R, Vanrolleghem PA (2006) A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. Tree Physiol 26(3):257–273. https://doi.org/10.1093/treephys/26.3.257

Střelcová K, Kurjak D, Lestianska A, Kovalčíková D, Ditmarová Ľ, Škvarenina J, Ahmed YAR (2013) Differences in transpiration of Norway spruce drought stressed trees and trees well supplied with water. Biol 68(6):1118–1122. https://doi.org/10.2478/s11756-013-0257-4

Turcotte A, Rossi S, Deslauriers A, Krause C, Morin H (2011) Dynamics of depletion and replenishment of water storage in stem and roots of black spruce measured by dendrometers. Front Plant Sci 2. https://doi.org/10.3389/fpls.2011.00021

Usoltsev V, Merganičová K, Konôpka B, Osmirko AA, Tsepordey IS, Chasovskikh VP (2019) Fir (*Abies* spp.) stand biomass additive model for Eurasia sensitive to winter temperature and annual precipitation. Cent Eur For J 65:166–172. https://doi.org/10.2478/forj-2019-0017

van der Maaten E, van der Maaten-Theunissen M, Smiljanić M, Rossi S, Simard S, Wilmking M, Deslauriers A, Fonti P, von Arx G, Bouriaud O (2016) DendrometeR: Analyzing the pulse of tree in R. Dendrochronologia 40:12–16. https://doi.org/10.1016/j.dendro.2016.06.001

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. https://doi.org/10.1016/j.agrformet.2013.06.009

Vitali V, Büntgen U, Bauhus J (2017) Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. Glob Change Biol 23(12):5108–5119. https://doi.org/10.1111/gcb.13774

Walentowski H, Falk W, Mette T, Kunz J, Bräuning A, Melnardus C, Zang Ch, Sucliffe L, Leuschner Ch (2017) Assessing future suitability of tree species under climate change by multiple methods: a case study in southern Germany. Ann For Res 60(1):101–126. https://doi.org/10.15287/afr.2016.789

Weber P, Bugmann H, Rigling A (2010) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. J Veg Sci 18(6):777–792. https://doi.org/10.1111/j.1654-1103.2007.tb02594.x

Zweifel R, Häsler R (2001) Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. Tree Physiol 21(9):561–569. https://doi.org/10.1093/treephys/21.9.561

Zweifel R, Item H, Häsler R (2001) Link between diurnal stem radius changes and tree water relations. Tree Physiol 21(12–13):869–877. https://doi.org/10.1093/treephys/21.12-13.869

Zweifel R, Zimmermann L, Newbery DM (2005) Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiol 25(2):147–156. https://doi.org/10.1093/treephys/25.2.147

Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth and water relations of trees: implication towards a growth mechanism. J Exp Bot 57:1445–1459. https://doi.org/10.1093/jxb/erj125

Zweifel R, Drew DM, Schweingruber F, Downes GM (2014) Xylem as the main origin of stem radius changes in Eucalyptus. Funct Plant Biol 41:520–615. https://doi.org/10.1071/FP13240

Zweifel R, Haeni M, Buchmann N, Eugster W (2016) Are trees able to grow in periods of stem shrinkage? New Phytol 211:839–849. https://doi.org/10.1111/nph.13995

Zweifel R, Sterck F, Braun S, Buchmann N, Eugster W, Gessler A et al (2021) Why trees grow in the dark. New Phytol 231:2174–2185. https://doi.org/10.1111/nph.17552

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.