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Comparative analysis of wood anatomy of European larch, Norway spruce, and European beech in mixed and monoculture stands under contrasting climatic conditions

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ABSTRACT

We present a tree-ring and wood-anatomical study of less widespread European larch (*L. decidua*) growing in mixed a monoculture stands with the economically important Norway spruce (*P. abies*) and European beech (*F. sylvatica*) under identical meteorological conditions in the Czech highlands. Tree responses to drought were assessed by comparing two contrasting periods: Control period (2009–2010) and a Dry period (2017–2018). We analysed tree-ring widths (*TRW*), early- and latewood widths (*EWW/LWW*), lumen area (*LA*), cell wall thickness (*CWT*), cell density (*CD*), relative conducting area (*RCTA*), hydraulically weighted mean cell diameter (D_h), and the potential hydraulic conductivity (K_p). A significant reduction in radial growth (51.8 %) was observed during the Dry period, with spruce and beech showing the greatest decline in monocultures, while larch exhibited mostly non-significant changes. Although *TRW* did not differ significantly between mixtures and monocultures within species, notable variations emerged at the wood-anatomical level. Tree species generally showed reduced anatomical variability and more stable water conductivity mostly in mixed stands under dry conditions. However, drought impacts were more pronounced in larger trees and denser stands, suggesting that forest structure can amplify vulnerability to water stress. Species-specific drought responses were distinct: larch showed no anatomical changes; spruce exhibited the greatest reduction in latewood lumen area and cell wall thickness; and beech reduced lumen area while increasing cell density, enhancing water transport efficiency under prolonged drought.

1. Introduction

Currently, spruce monocultures are facing an intensified challenge from ongoing climate change in Central Europe region (Marozau et al., 2021; Ponocná et al., 2016). With rising temperatures and uneven distributions of precipitation, forests are experiencing more frequent and severe seasonal water deficits (Pendergrass and Knutti, 2018; Trnka et al., 2011), which are having a significant impact on tree growth and forest productivity (De Micco et al., 2019). Previous studies on economically important European tree species, such as Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.), have extensively described the links between tree-ring width, wood structure, and specific events (Arnič et al., 2021, 2022; Castagneri et al., 2017; Gričar et al., 2015, 2024; Hajek et al., 2016). These studies confirmed that water stress during the dry period negatively influenced the anatomical traits and properties of the xylem and hydraulic conductivity, leading to reduced efficiency in water transport and increased vulnerability to embolism in trees xylem (Arnič et al., 2021, 2022; Castagneri et al., 2017; Gričar et al., 2015, 2024; Hajek et al., 2016). The currently rapid decline of spruce monocultures, mostly in lower altitudes (Hartl-Meier et al., 2014; Hlásny et al., 2021), has created a newfound potential and renewed attention to less widespread conifers such as the European larch (*Larix decidua* Mill.; Bolte et al., 2009). Although larch is the third most common conifer in Czech forests,

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representing 3.9 % of the total forest area (eAgri.cz. 2022), it has been neglected in systematic studies, possibly based on old assumptions of its non-native status in the majority of the Czech Republic. However, recent scientific palaeobotanical evidence proved its native status throughout the Czech landscape (Dudová and Szabó, 2022; Pokorný et al., 2024). European larch is a deciduous conifer characteristic with a deep root system that allows it to reach soil water from deeper layers (Tichý, 1949; Vyskot, 1985). Significantly high larch canopy transmittance allows throughfall and sunlight to reach the forest floor and provides a benefit to other tree species (and non-wood plants, as well) growing beneath its canopy (Fellner et al., 2016). These notable differences from other European conifers motivated an investigation into its responses to environmental changes, as well as its potential influence on the growth and adaptability of other commercially significant tree species.

In general, the wood anatomy of larch and spruce are difficult to distinguish. However, larch can be differentiated from spruce based on the following characteristics: i) the transition from earlywood to latewood is less abrupt in spruce; ii) the heartwood is indistinct in spruce and iii) larch forms biseriate bordered pits in radial walls of the tracheids. Beech, as diffuse-porous angiosperm tree species, is characterised by the numerous pores - vessels of similar size that are evenly grouped and distributed in earlywood but solitary in latewood (Hoadley, 1990; Schweingruber, 1990). Toward the latewood boundary, however, pore size and frequency decline sharply, producing a characteristic transition from a narrow to a wide latewood band with a distinctly darker shade (Hoadley, 1990). Consequently, the methodology of analyzing the entire tree ring in diffuse-porous species has become a well-established practice in dendrochronological research, as evidenced by study of Zimmermann et al. (2021).

In the context of tree acclimation to climatic variability, the cambium regulates hydraulic properties of conduits (Tyree and Zimmermann, 2002), which is reflected in changes in the appearance of typical tree rings (De Micco et al., 2016; Fonti et al., 2013). Trees efficiently transport water through large earlywood conduits. When water becomes limited, trees not only reduce the risk of embolism by creating narrower latewood conduits but also enhance mechanical support through denser wood formation. Latewood, characterized by smaller conduits and thicker cell walls, thus serves both a hydraulic safety function and a crucial mechanical function, increasing the structural integrity of the tree under stressful conditions (Battipaglia et al., 2014; De Micco et al., 2008). This physiological activity leading to acclimation of the size and quantity of conduits and the type of interconnections as xylem plasticity (Pittermann et al., 2006). Understanding the wood anatomy and hydraulic efficiency of trees is essential for comprehending how different species acclimatise and survive rapid environmental changes and extremes (Balzano et al., 2020).

With ongoing climate change, it is crucial to focus more carefully on studying the potential benefits of mixed forests as a possible strategy to facilitate ecological stability, forest ecosystem vitality, and consequently sustainable forest management (Hanewinkel et al., 2013). Building on these findings, the interdisciplinary national project QK21010335 was established to evaluate the production potential of European larch in mixed stands. The project aims to assess how stand structure, social status, species composition, and stand characteristics influence larch performance in Czech forests under climate change impacts. To the best of our knowledge, there is a significant gap in evaluating wood-anatomical features under changing climate conditions across variations of mixed forests containing European larch. This paper, as part of the project output, aims to fill these knowledge gap by examining larch's response to dry conditions in both monoculture and mixed stands, thereby advancing our understanding of its role in forest ecosystems under changing climatic conditions. We present the response of wood-anatomical features during the meteorological dry period and a more favourable period across different larch-spruce-beech mixtures in the highlands of the Czech Republic. The objective of this study is to compare the radial growth and wood anatomical responses of European larch, Norway spruce and European beech across varying mixtures and monocultures, with a particular focus on drought period, and to investigate whether larch-containing mixtures are less affected by drought. We hypothesize that i) water stress during the dry period influences the anatomical traits and properties of European larch xylem, and ii) the differences between the observed periods will be less pronounced in mixed stands than in monocultures.

2. Materials and methods

2.1. Characteristic of research plots

The *TRW* and wood-anatomical features were measured along of tree-rings series of two coniferous species, European larch (*Larix decidua* Mill.) and Norway spruce (*Picea abies* [L.] Karst.), as well as one broadleaf species, European beech (*Fagus sylvatica* L.), growing in various of four mixtures and three monoculture forests (see Table 1) in the lower-altitude highlands of Drahanská vrchovina (approx. 500 m a.s. l.) in the Czech Republic. The samples were taken in seven permanent research plots of middle-aged forest stands designed to emphasize the same meteorological conditions as well as the wide range of spruce-larch-beech mixtures and monoculture stands (Fig. 1, Table 1). The study area was managed by University Forest Enterprise Masaryk Forest in Křtiny and no intervention was applied to the research plots for the last 15 years. This region is located within Nemoral-Continental vegetation region (Preislerová et al., 2024) and is characterized by a moderately warm and dry climate with an annual mean temperature of 7.5 °C, an annual mean humidity of 75–85 %, and annual amount of precipitation of 600–800 mm (1961–2000; slpkrtiny.cz. 2002; Tolasz et al., 2007). The soil type is oligotrophic cambisol formed on acid granodiorite (slpkrtiny.cz. 2002; Tomášek, 2007).

2.2. Plot measurements and tree sampling

The diameter at breast height (DBH) of all trees at the research plots was measured using a diameter measuring tape, while the height (H) of 10 trees per plot and species was measured using a VERTEX LASER. The spatial positions of the trees (x–y coordinates) were recorded using the Field-Map system (IFER, Czech Republic) to precisely specify tree species composition (Table 1), determine competition indices – defined as the sum of competition from the five most competitive neighbouring trees, following Hegyi (1974) – and calculate the social area, as described Nagel (1999), by assessing the spatial influence of a tree based on its size and the competitive overlap with neighbouring trees within a certain distance (Table 1 in Supplementary). A total of 40 larches, 40 spruces, and 40 beeches of medium age (10 samples per species from each site) were cored with a 5-mm increment borer (Haglöf Sweden, Långsele, Sweden). Priority was given to trees representing the majority of the forest stand during tree selection for coring. Suppressed and dominant trees were excluded to ensure a more representative sampling of average growth conditions and tree characteristics within the stand. The wooden cores were taken at the breast height (1.3 m) from the north side of the trunk and stored in a compound of ethanol, glycerine, and distilled water (von Arx et al., 2016).

2.3. Microclimate and selection of study periods

Using data from the E-OBS data version 25.0e (Cornes et al., 2018), we obtained gridded daily temperature and precipitation data for the investigated location specified by the coordinates 49.3499°N, 16.7499°E. To minimize potential age-related effects in trees, we focused on data from the last 15 years, identifying two distinct periods: a favourable period (Control, 2009–2010) and a dry period (Dry, 2017–2018). The Control period was characterized by higher mean annual precipitation (708 mm) and a lower mean annual temperature (7.8 °C), while the Dry period experienced reduced precipitation

Table 1
Research plots characteristics. *BA* represents the sums of tree basal areas at 1.3 m, *n* Trees represents the number of trees per hectare, *SDI* represents Stand Density Index according to Pretzsch (2009) and Reineke (1933), and *MSII* represents Mean Species Intermingling Index according to Füldner (1996). *Other tree species* represents an admixture of species such as *Pinus sylvestris*, *Betula pendula*, *Quercus* spp., *Carpinus betulus*, *Fraxinus excelsior*, *Tilia* spp., *Salix* spp.

Research plot			Age	Area	BA	n Trees	SDI	MSII	Mean DBH	Mean Height	Forest Type	Coordinates
Acronym	Composition of tree species [%]		[years]	[ha]	[m²/ha]	[n/ha]			[cm]	[m]	*	
L	Larch	99	62	0.09	72.66	652	886	0.03	29.9	26.77	Fagetum oligo-mesotrophicum	49.315271
	Other tree species	1			0.57				17.3			16.791965
S	Spruce	96	42	0.09	71.71	809	675	0.11	23.2	21.47	Fagetum oligo-mesotrophicum	49.315903
	Other tree species	4			2.80				18.1			16.784972
B	Beech	92	58	0.09	55.31	1288	855	0.19	19.6	21.73	Fagetum mesotrophicum	49.314322
	Other tree species	8			5.13				15.9			16.780634
SL	Spruce	75	58	0.09	50.20	499	743	0.41	33.8	27.71	Fagetum mesotrophicum	49.313660
	Larch	25			16.44				28.0	25.14		16.781260
BL	Beech	71	58	0.09	51.09	1008	901	0.32	21.5	15.66	Fagetum mesotrophicum	49.314431
	Larch	25			15.73				31.4	27.63		16.781064
	Other tree species	4			5.23				22.9			
SB	Spruce	52	70	0.09	31.72	530	676	0.40	34.8	24.06	Fagetum oligo-mesotrophicum	49.313442
	Beech	48			29.54				25.1	19.97		16.783537
SLB	Spruce	32	80	0.12	19.84	494	745	0.62	33.6	21.15	Fagetum oligo-mesotrophicum	49.315875
	Larch	31			19.47				35.5	19.39		16.766475
	Beech	29			18.45				26.4	16.28		
	Other tree species	8			4.90				29.9			

* According to Czech Forest Ecosystem Classification (Viewegh et al., 2003).

Fig. 1. Geographical location of a) the Czech Republic within Europe (green), b) highlands of Drahanská vrchovina in the Czech Republic (red) and c) permanent research plots. A circle represents spruce, a square represents beech, and an asterisk represents larch. A combination of symbols indicates a mixed-species plot (Mapy.cz. 2024).

(498 mm) and elevated mean annual temperature (9.1 °C). For reference, the long-term mean annual temperature (1951–2000) was 7.3 °C, with an average precipitation of 563 mm (Fig. 2).

To support the determination of our study periods based on local meteorological data, we reviewed climate information provided by the Reports on the State of Forests and Forest Management (2008, 2009, 2010, 2016, 2017 & 2018) delivered by the Ministry of Agriculture of the Czech Republic. These reports declare that, between 2016 and 2018, weather in the Czech Republic was characterised by significant temperature and precipitation extremes, which what aligns with findings of Moravec et al. (2021) and Salomón et al. (2022). According to their studies, the years 2017 and 2018 were widely recognized in Europe as a period marked by seasonal drought and multiple heatwaves, which significantly impacted forests. The transition from 2016 and 2017 in Czech Republic was marked by relatively low snow cover, followed by an exceptionally warm spring and a significant dry period in southern Czechia during May and June. The year 2018 become the warmest year in the Czech Republic since the beginning of meteorological observations, with a mean annual temperature of 9.7 °C, exceeding the long-term normal by 1.8 °C. In contrast, precipitation was strongly below average, with an annual total of 519 mm, representing 75 % of the long-term norm. After a warm January, colder weather followed in February and March, but by April, temperatures rapidly rose to summer levels and remained above average throughout the summer months. The combination of high temperatures and low precipitation led to severe drought, further exacerbated by the dry growing seasons of previous years (eAgri.cz. 2017, 2018, 2019).

The determined Control period, the Czech Republic was

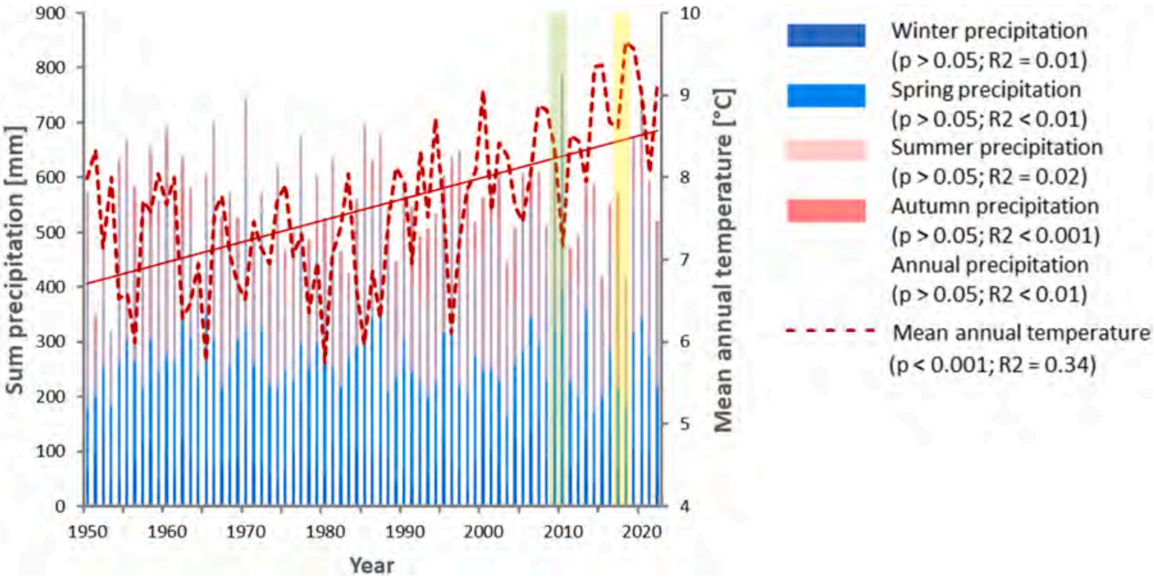

Fig. 2. Graphical representation of Climate diagram showcasing long-term regional precipitation data with stacked columns for seasonal precipitation, alongside the mean annual temperature represented by a red dashed line, including corresponding linear trends and highlighted Control (green) and Dry (yellow) periods.

characterised by favourable temperature and precipitation. In 2008, the autumn months from October to December experienced normal precipitation, with only November slightly below average. The year 2009 was marked by prolonged snow cover and a warm spring. From mid-June to early August, intense precipitation events occurred, while October brought a rapid onset of cold weather and snowfall. Most months of 2009 remain within normal temperature ranges, with the annual precipitation above average. The winter of 2009/2010 was relatively cold, with persistent snow cover even in lower elevations. In 2010, a very wet and warm summer dominated. Spring that year offered favourable temperature and precipitation conditions, and the growing season of 2010 was generally beneficial for the health of forest stands (eAgri.cz. 2009, 2010, 2011).

To validate the ecological valence of the studied tree species in relation to the determined Control and Dry periods, we consulted the European Atlas of Forest Tree Species (European Commission, 2020). According to this resource, the temperature and precipitation condition during 2009–2010 align with the typical ecological range of all investigated species. In contrast, the temperature and precipitation during the Dry period fall near or beyond ecological valence of these species (European Commission, 2020).

2.4. TRW measurements

The surfaces of 120 wooden cores (from bark to pith) were cut with WSL sledge microtome and scanned by Canon CanoScan LiDE 300 at 1200 dpi resolution for tree-ring widths (*TRW*) measurements. Tree-ring measurements were subsequently obtained using the CooRecorder & CDendro software (Cybis, Saltsjöbaden, Sweden). Cross-dating of tree-ring series was performed on 8–10 samples per species from each site using the COFECHA software with series intercorrelation 0.5–0.8 (Fig. 1 in Supplementary; Holmes, 1983).

2.5. Microsection processing

Microsections were processed from a selected 60 wooden cores, five samples of each tree species from each research plot (Bryukhanova and Fonti, 2013). Microsections were prepared from approximately last 15 years by separating 3–4 cm segment from wood core according to Gärtner et al. (2015) and von Arx et al. (2016). Sections were viewed using a Zeiss Axio Imager A.2 light microscope (Carl Zeiss Microscopy, White Plains, NY, USA), and the images were acquired using a Zeiss Axiocam 712 colour camera (Carl Zeiss Microscopy GmbH, Jena, Germany).

2.6. Measurement and analysis of wood-anatomical features

The wood-anatomical features were measured from panoramic pictures of permanent microsections via image software ImageJ (Rasband, 1997). We measured vessel lumen areas (*LA*) for beech and tracheid lumen areas (*LA*) and the cell wall thickness (*CWT*) for conifers only. Using radial *CWTs* and cell *LAs*, we determined the earlywood width (*EWW*) and latewood width (*LWW*) of conifer tree rings, applying Mork's definition as the basis for our calculations (Denne, 1989). Cell density (or frequency distribution of vessels; *CD*) as the number of conduit cells per square mm and the relative conducting area (*RCTA*) representing the percentage of the cumulative conductive area within the analysed area were calculated (Arnič et al., 2022). Based on the *LAs* we also calculated the hydraulically weighted mean cell diameter (D_h) using equivalent circle diameters D_i (Sperry et al.; 1994), and the potential hydraulic conductivity (K_p) based on Hagen-Poiseuille's law, where D_i is the diameter of each measured cell i, ρ is density of water (998.2 kg m^{-3}), η is water viscosity (1.002 × 10–9 MPa s) both at 20°C, and *AA* is the analysed area (m^{2}) of each segment (Kotowska et al., 2021; Zimmermann, 1983). In the case of conifers, a series of cells in radial rows – min. 40 cells for *EW* and min. 30 cells for *LW* were selected as analysed area (*AA*). In beech, the area between two rays was selected (Fig. 3).

Data obtained from the year 2009, 2010, 2017, and 2018 were analysed collectively by defined periods using IBM SPSS Statistics, Statistica.pro, and MS Excel, employing Univariate Analysis of Variance (UNIANOVA) and one-way ANOVA. We used Tukey's HSD and Duncan post-hoc tests, appropriate for different sample sizes, to verify differences between the groups when ANOVA P-values were significant (<0.05). To complement these analyses and better capture the combined effects of structural and environmental factors, we additionally implemented linear mixed-effects models. These models included stand density, tree DBH, and period (Control vs. Dry) as fixed effects, with interaction terms (e.g., Stand Density × Period, DBH × Period) used to explore how stand structure might modulate drought effects. Random effects were included to account for plot-level variability. This approach allowed us to compare direct treatment effects through ANOVA with

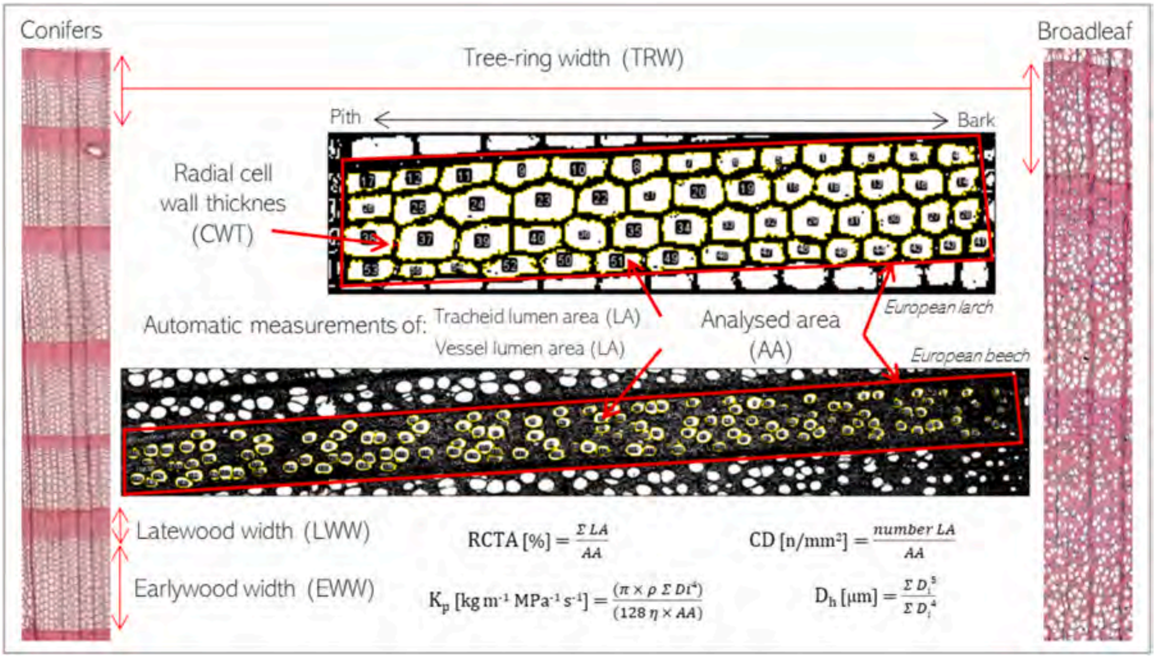

Fig. 3. Measurements of *TRW* and wood-anatomical features: in conifers, the number and lumen area (*LA*) of tracheids, cell wall thicknesses (*CWT*) in the radial direction, and earlywood (*EWW*) and latewood (*LWW*) widths of analysed area (*AA*) were measured. In broadleaf, the number and lumen area of vessels (*LA*) and analysed area (*AA*) were measured. In both, the relative conducting area (*RCTA*), cell density/vessel frequency (*CD*), hydraulically weighted mean cell diameter (D_h) and the potential hydraulic conductivity (K_p) of wood segments were calculated.

more complex, structure-sensitive responses through mixed models. While ANOVA highlights broad, group-level differences, the mixed-effects framework quantifies relative influence of structural covariates. Models were implemented in R (v4.3.1) using the lmerTest package (Kuznetsova et al., 2017). Model performance was evaluated using both marginal and conditional R^2 values.

3. Results

3.1. Radial growth

We observed a significant decrease in radial growth between the Control (2009–2010) and the Dry (2017–2018) periods across all research plots with beech contribution and nearly all plots with spruce contribution. Larches exhibited a significant decrease only in the plot with presence of beech (BL; Fig. 4). The smallest growth reduction between periods was observed in larch monoculture (L; 19 %), while the largest reduction occurred in beech monoculture (B; 62 %). On average, larch reduced its growth by 43 %, beech by 50 %, and spruce by 62 % during the Dry period. No significant differences in growth rates within each tree species among the study plots were observed during the Dry period.

In larches, a significant reduction of *EWW* by 0.53 mm and *LWW* by 0.54 mm was found only in the BL plot during the Dry period (Table 2 in Supplementary). During both periods, strong correlation was observed between *TRW* and *EWW* (r = 0.86–0.97) and between *TRW* and *LWW* (r = 0.66–0.93). Spruce exhibited a significant reduction in EWW (by 0.66–1.19 mm) during the Dry period across most plots, except for the SB plot, while LWW did not differ significantly (Table 2 in Supplementary). Strong positive correlation was observed between *TRW* and *EWW* during both the Control period (r = 0.86–0.99) and the Dry period (r = 0.83–0.98). In contrast, the correlation between *TRW* and *LWW* was slightly negative in the SB and SLB plots (r = -0.03 to −0.35) and positive in the S and SL plots (r = 0.14–0.48) during the Control period. During the Dry period, a positive correlation between *TRW* and *LWW* was found for spruce (r = 0.28–0.78).

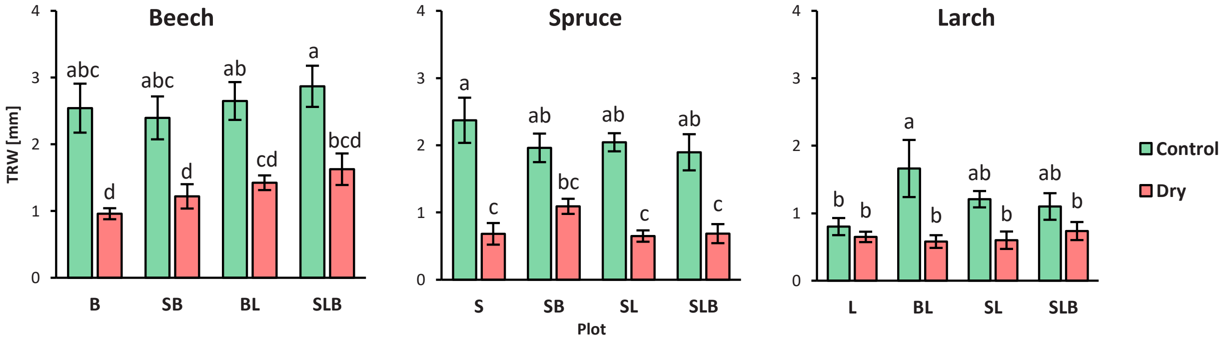

Fig. 4. Bar plots showing differences in mean tree-ring widths (y-axes) between the Control (green bars) and the Dry (red bars) periods across research plots (x-axes; see Table 1). The bars depict standard errors and letters a significant difference between periods and plots for particular species. Tukey’s HSD test, Alpha = 0.05 was used.

3.2. *Wood-anatomical features*

For larch, the mean *EW LA* varied from 981.3 to 1208.5 μm^2 in the Control period and from 978.8 to 1251.9 μm^2 in the Dry period; the mean *LW LA* varied from 77.9 to 96.9 μm^2 in the Control period and from 62.3 to 94.3 μm^2 in the Dry period (Fig. 5). Surprisingly, there was no significant reduction in *EW LA* and *LW LA* between both observed periods. The mean *EW CWT* for larch varied among the investigated plots from 6.3 to 9.6 μm in the Control period and from 7.3 to 9.2 μm in the Dry period; mean *LW CWT* varied from 11.4 to 13.8 μm in the Control period and from 9.5 to 13.8 μm in the Dry period (Fig. 5). The mean *EW CD* of larch varied from 472.7 to 537.7 n/mm^2 in the Control period and from 459.6 to 559.9 n/mm^2 in the Dry period; the mean *LW CD* varied from 1112.2 to 1417.5 n/mm^2 in the Control period and from 1127.6 to 1353.6 n/mm^2 in the Dry period. No significant differences in *CD* of larch were observed between study periods (Table 3 in Supplementary).

For spruce, the mean *EW LA* varied from 412.0 to 616.0 μm^2 in the Control period and from 418.0 to 604.7 μm^2 in the Dry period; the *LW LA* varied from 75.6 to 110.7 μm^2 in the Control period and from 64.3 to 83.5 μm^2 in the Dry period (Fig. 5). The mean *EW CWT* for spruce varied from 7.3 to 8.9 μm in the Control period and from 7.1 to 8.5 μm in the Dry period; the *LW CWT* varied from 9.1 to 10.8 μm in the Control period and from 8.1 to 9.2 μm in the Dry period (Fig. 5). No significant difference in *EW CWT* of spruce was observed between both compared periods, but *LW CWT* was reduced by 12.6 % in the Dry period. For spruce, the mean *EW CD* varied from 852.2 to 1021.4 n/mm^2 in the Control period and from 924.3 to 1103.4 n/mm^2 in the Dry period. The mean *LW CD* varied from 1567.4 to 1760.3 n/mm^2 in the Control period and from 1870.5 to 2001.3 n/mm^2 in the Dry period. No significant differences in *CD* of spruce were observed between observed periods (Table 3 in Supplementary).

Beech's mean *LA* varied from 1632.6 to 1860.0 μm^2 in the Control period and from 1356.9 to 1678.0 μm^2 in the Dry period (Fig. 5). Beech mean *CD* varied from 116.5 to 124.8 n/mm^2 in the Control period and from 146.0 to 174.4 n/mm^2 in the Dry period (Fig. 5). A significant increase in *CD* of 24.0 % was observed in the Dry period, the highest increase was in monoculture (B). No significant differences were observed between plots within particular periods.

3.3. *Water conductivity*

The range of mean *EW RCTA* for larch was 50.3–56.7 % in the Control period and 53.8–56.8 % in the Dry period. The mean *LW RCTA* for larch varied from 8.6 % to 10.9 % in the Control period and from 7.5 % to 12.5 % in the Dry period with no significant differences between plots (Fig. 2 in Supplementary). Similarly, we did not observe significant differences in D_h and K_p between research plots containing larch or between the two investigated periods (Table 2).

For spruce, the mean *EW RCTA* varied from 42.2 % to 53.6 % in the Control period and from 40.2 % to 54.6 % in the Dry period, and the mean *LW RCTA* of spruce varied from 11.9 % to 18.0 % in the Control period and from 11.8 % to 14.9 % in the Dry period. The lowest *RCTA* was observed in the spruce monoculture (S), with no significant differences between the two observed periods (Fig. 2 in Supplementary). Similarly, no significant difference in D_h was observed between periods and plots. However, a significant difference in K_p was found between monoculture (S) and SB forest during the Dry period (SB; Table 2).

The mean *RCTA* of beech varied from 18.8 % to 22.4 % in the Control period and from 21.7 % to 28 % in the Dry period. A significant increase of *RCTA* by 18.0 % was observed in the Dry period compared to the Control period, with the highest values in beech monoculture (B). The only research plot with no observed change between periods was a mixture of all tree species (SLB; Fig. 2 in Supplementary). We observed no significant differences in D_h and K_p of beech between compared periods. However, during the Dry period, the lowest D_h and K_p were found in the mixture of all tree species (SLB), while the highest were observed in the beech-spruce (SB; Table 2).

Model performance was generally strong, with marginal R^2 values reaching as high as 0.91 for some anatomical traits and conditional R^2 up to 0.96 (Table 4 in Supplementary). Drought consistently reduced K_p and D_h across species, more so than stand density or DBH. Denser stands and larger trees exhibited lower K_p and *LA*, particularly under dry conditions. Interaction terms between stand structure and drought period (e.g., DBH × Period, Stand Density × Period) were included in the models. The interaction between Stand Density and DBH was statistically significant for *LA* and K_p, and marginally significant for D_h, whereas other interactions did not reach statistical significance. Among the mixtures, beech-containing types, particularly spruce–beech (SB) mixture tended to show higher K_p and D_h values, while the more complex three-species (SLB) combination showed no consistent advantage (Table 5 in Supplementary).

4. Discussion

4.1. *Species-specific radial growth and wood-anatomical responses to drought*

We investigated *TRW* and wood-anatomical traits in European larch, Norway spruce, and European beech trees in various forest from monocultures to mixed stands under a favourable Control and stressful Dry meteorological periods. *TRW* analysis revealed a significant radial increment reduction (51.8 %) for spruce and beech during the Dry period, underscoring how growth dynamics reflect tree responses to environmental stress. The observed decline suggests prioritization of water conservation over growth during drought through mechanisms like reduced sap flow, stomatal closure, and lowered carbon assimilation (Arnič et al., 2021; Castagneri et al., 2017; Hajek et al., 2016; Zeppel et al., 2013).

Larch showed the lowest, non-significant *TRW* reductions, consistent with previous findings of Sasani et al. (2021), suggesting a hydraulically safer wood and anisohydric behavior that allows continued transpiration and photosynthesis under drought. Anatomical parameters such as *CWT* showed minor changes, primarily in the beech-larch (BL) stand, while *EW* and *LW LA* remained stable. These findings align with studies reporting larch's insensitivity to drought and its ability to maintain open stomata under low leaf water potentials (Sasani et al., 2021; Carrer et al., 2017). The overall stability in *CD*, *RCTA*, D_h, and K_p further supports the idea that larch anatomy remains resilient under short-term drought, potentially due to drought legacy effects persisting longer in conifers (Anderegg et al., 2015; Huang et al., 2018). Our first hypothesis - that water stress during the Dry period would influence the anatomical properties of larch xylem - was therefore not fully confirmed.

In contrast, spruce exhibited a marked decline in *LW LA* (by 20.3 %) and *LW CWT* (by 12.6 %), indicating narrower rings with reduced hydraulic efficiency during drought. This matches known seasonal sensitivity of tracheid formation to water stress (Plomion et al., 2001; Fajstavr et al., 2019). *EW LA* also decreased, reflecting climatic influences from both the previous autumn and current growing seasons as declare Castagneri et al. (2015), (2017) and Gričar et al. (2015). The reduction in *LA* helps regulate the risk of embolism during drought (Bryukhanova and Fonti, 2013). The difference in response between spruce *EW CWT* (non-changed) and *LW CWT* (decreased) between periods, highlights the complex dynamics of xylem development. This contrasts with Montwé et al. (2014) and Tsalagkas et al. (2024), who found that drought-treated spruce formed *LW* cells with relatively thicker walls than irrigated trees. Water conductivity variables (*CD*, *RCTA*, D_h and K_p) decreased in most spruce stands, though not significantly. Strong *TRW* – *EWW* correlations and weak *TRW* – *LWW* links suggest that earlywood and latewood in conifers should be analyzed separately to better understand physiological responses (Hoadley, 1990; Schweingruber, 1990; Piermattei et al., 2020).

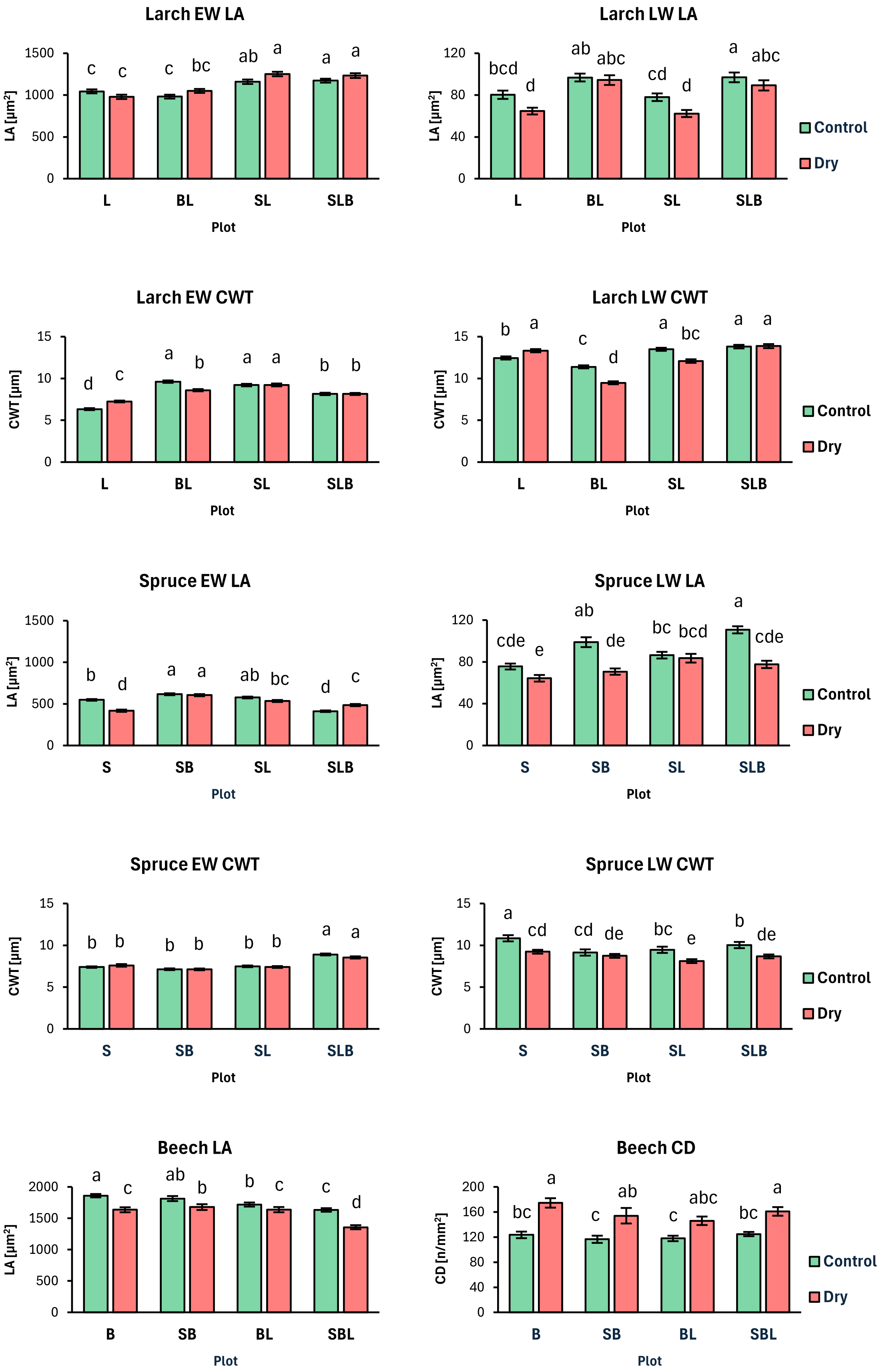

Fig. 5. Mean earlywood lumen area (*EW LA*), mean latewood lumen area (*LW LA*) in µm^2, mean earlywood cell wall thickness (*EW CWT*) and mean latewood cell wall thickness (*LW CWT*) in µm of coniferous species (y-axes). Mean lumen area (*LA*) in µm^2 and vessel frequency (*CD*) in n/mm^2 of beech (y-axes) in both the Control (green) and the Dry (red) period across all investigated plots (x-axes; see Table 1). The bars depict standard errors and letters a significant difference between periods and plots for particular species. Tukey's HSD test, Alpha = 0.05 was used.

Table 2

Statistical characteristics of the hydraulically weighted mean cell diameter (D_h) and the mean potential hydraulic conductivity (K_p) of larch (L), spruce (S), and beech (B) across all investigated plots during both observed periods. Letters depict a significant difference between periods and plots for particular species, and SD means standard deviation. The Tukey's HSD test, Alpha = 0.05 was used.

Species	Plot Acronym	D_h [μm]						K_p [kg m^{-1} MPa^{-1} s^{-1}]					
		Control p.			Dry p.			Control p.			Dry p.		
		Mean	SD	Homogenous groups	Mean	SD	Homogenous groups	Mean	SD	Homogenous groups	Mean	SD	Homogenous groups
L	**L**	40.10	5.48	*a*	40.65	5.79	*a*	18.12	6.72	*a*	19.42	8.46	*a*
	BL	41.45	3.52	*a*	40.61	4.59	*a*	19.18	6.50	*a*	21.55	7.49	*a*
	SL	42.91	4.36	*a*	43.62	4.96	*a*	22.63	6.41	*a*	24.27	5.96	*a*
	SLB	43.27	3.82	*a*	43.64	6.57	*a*	22.75	4.54	*a*	23.66	9.84	*a*
S	**S**	29.34	3.72	*ab*	26.22	6.00	*b*	9.51	3.33	*ab*	6.54	4.15	*b*
	SB	31.92	1.78	*a*	31.10	3.49	*ab*	12.16	1.75	*a*	11.93	4.10	*a*
	SL	30.47	2.88	*ab*	28.97	3.38	*ab*	10.41	3.73	*ab*	9.69	3.43	*ab*
	SLB	27.47	3.59	*ab*	28.51	4.60	*ab*	7.07	2.47	*b*	8.33	3.74	*ab*
B	**B**	57.87	3.63	*ab*	55.95	3.60	*ab*	21.28	4.39	*ab*	24.67	4.63	*ab*
	SB	59.34	7.06	*a*	59.48	5.02	*a*	20.28	6.85	*ab*	25.46	7.27	*a*
	BL	55.61	6.15	*ab*	57.75	3.57	*ab*	16.91	8.08	*b*	22.55	5.46	*ab*
	SLB	56.00	5.34	*ab*	52.38	4.25	*b*	17.85	6.20	*ab*	16.66	4.40	*b*

In beech, Dry-period anatomy showed a 10.2 % reduction in *LA* and an 18 % increase in *CD*, leading to significantly higher *RCTA*. While these changes enhance mechanical support, they may compromise water transport efficiency and prevent the onset of embolism under prolonged drought (Cochard et al., 2001; Arnič et al., 2021; Diaconu et al., 2016; Sass and Eckstein, 1995). These results align with previous findings showing vessel narrowing and consistent conductivity during dry years (Schuldt et al., 2016). According to Arnič et al. (2021), Beech's anatomical adjustments reflect both current and prior-season climate conditions. Given the diffuse-porous structure of beech, we followed the whole-ring analysis approach proposed by Zimmermann et al. (2021), instead of seasonally partitioned assessments that are more suitable for directly correlating with meteorological data.

Although wood anatomical traits such as *LA* and *CWT* reflected clear species-specific responses to drought, the inclusion of derived hydraulic parameters (e.g. K_p, *RCTA*) added valuable functional context. While based on simplified assumptions, these parameters help standardise comparisons of drought responses across species and site conditions by linking anatomical structure to potential hydraulic function, thereby enhancing our understanding of species-specific coping strategies under water stress. However, while separate ANOVA tests and clear reductions in *TRW* – particularly in spruce and beech – indicated a pronounced drought impact on growth and wood-anatomical traits, the fixed effect of drought period was not statistically significant in the linear mixed-effects models. This discrepancy may be attributed to the inclusion of structural variables such as stand density and DBH in the mixed models, which could have absorbed a portion of the variance otherwise explained by drought.

4.2. *Stand-specific radial growth and wood-anatomical response to drought*

Our second hypothesis – that differences between study periods would be less pronounced in mixed stands than in monocultures – was more strongly supported by wood-anatomical traits than by *TRW*s. However, interpreting mixture effects requires consideration of stand density and tree size (DBH), which significantly influenced growth responses, with tree size having a greater impact.

TRW analyses revealed no significant plot differences during the Dry period, but the strongest growth reductions occurred in spruce (by 71.2 %) and beech (by 62.2 %) monocultures (S, B). This aligns with studies showing greater drought resilience and lower mortality in mixed-species stands (e.g., Aldea, Ruiz-Peinado, 2022; Mölder and Leuschner, 2014; Vanhellemont et al., 2019; Vannoppen et al., 2019; Zamora-Pereira et al., 2021), although the benefits of species mixing remain context-dependent, influenced by e.g., species composition, microclimate, and site conditions.

During the Dry period, conifer monocultures had the lowest *LA* values. In spruce (S), *EW* and *LW LA* dropped by 10.3 % and 20.5 %, and in larch (L) by 11.3 % and 15.9 %, respectively. This reduction, coupled with a slight increase in *CWT*, indicates a shift toward safer, less efficient water transport under drought stress (Arnič et al., 2021; Diaconu et al., 2016; Sass and Eckstein, 1995). The potential influence of presence of European larch on enhancing water availability for other tree species during the Dry period was not clearly confirmed. Our findings did not show distinct differences in wood-anatomical features or water conductance between mixed stands containing larch and those without it. While plots were designed to minimize environmental variability, unmeasured site factors may still have influenced results. In contrast to conifers, beech during the Dry period exhibited the lowest values of *LA*, D_h and K_p in combination with relatively high growth in the spruce-larch-beech (SLB) mixed stand. This anatomical adjustment was accompanied by an increase in *CD*, which consequently helped stabilise *RCTA*. Conversely, beech in monoculture (B) experienced higher values of *LA, CD, RCTA,* D_h and K_p related to the lower increment.

Models including DBH, stand density, and period confirmed that drought reduced hydraulic efficiency across species, evidenced by declines in K_p and D_h. These changes reflect narrower conduits – a well-known adaptation to reduce embolism risk (Marciszewska and Tulik, 2013). Larger trees and those in denser stands, especially within the spruce-larch-beech (SLB) mixture, exhibited lower K_p and *LA*, likely due to greater hydraulic resistance and competition for water. Since DBH often correlates with tree hight, taller individuals face increased hydraulic resistance due to the longer path between roots and leaves. Moreover, denser stands intensify competition for water, further limits hydraulic efficiency (Scoffoni et al., 2016), as a strategy to safeguard water conductance and minimise cavitation risk under conditions of limited water availability (Arnič et al., 2021). Our findings support the idea that structural factors can amplify drought impacts. Among mixtures, only spruce-beech (SB) combinations maintained relatively high K_p and D_h under drought. In contrast, the three-species mixture (SLB) showed no clear anatomical advantage, suggesting that more species does not necessarily mean more resilience. These results align with previous research highlighting species-specific plasticity and possible facilitation between drought-tolerant species. For instance, some beech provenances are known to cope better with drought (Rose et al., 2009). These findings are further supported by ANOVA results, which showed significant period effects for several traits, highlighting drought as a primary driver of wood-anatomical variation across species (Bryukhanova and Fonti, 2013).

Complex interactions, including competition and facilitation among species with differing strategies, likely contributed to the observed patterns (Binkley, 2003; Bouillet et al., 2013; Boyden et al., 2005; Forrester et al., 2011; Pretzsch et al., 2010). For example, in mixed stands, inter-specific competition for water resources may disadvantage beech by allowing the more competitive spruce roots to displace beech roots from the topsoil horizons rich in bio-elements. Additionally, the lateral drift of beech litter into spruce-dominated areas may contribute to nutrient loss (Kelty, 1992), further affecting growth performance. These dynamics support previous findings that mixture effects are strongly site-dependent (Pretzsch et al., 2010). Both diversity and neighbour identity can modulate species responses to stress (Vanhellemont et al., 2019). From a management perspective, reducing stand density in drought-sensitive coniferous monocultures (Eilmann and Rigling, 2012) and promoting mixtures that sustain hydraulic function could enhance forest resilience. While our study focused on structural and anatomical factors, future research should also address the timing of drought, as spring deficits during xylem formation may have lasting effects (Basu et al., 2024).

5. Conclusion

This study evaluated the effects of drought on the radial growth and wood-anatomical traits of European larch, Norway spruce, and European beech growing in monocultures and mixed stands under similar climatic conditions in the Czech highlands. To the best of our knowledge, there is a lack of studies exploring such species combinations at the wood-anatomical level. The distinct functional traits of the studied species – the unique deciduous conifer larch, angiosperm beech, and evergreen conifer spruce – led to varying drought responses. During the Dry period, the narrow rings indicated stressful growing conditions that reduced lumen size and limited water-transport capacity, primarily in spruce late-wood, with *LAs* decreasing by 20.3 % and *CWTs* by 12.6 %. In contrast to spruce, larch exhibited stable wood-anatomical features, resulting in unaffected water conductivity. Beech's hydraulic acclimation to drought was characterised by a 10.2 % decrease in *LA* and an 18 % increase in *CD*, which resulted in enhanced water conductivity. In contrast to conifers, beech exhibited the most prone water conductance when grown in mixture with spruce and larch, a pattern that may be influenced by a greater tree age and stand density. Though clear patterns emerged, causality remains uncertain due to interacting biotic and abiotic factors. Further experimental studies are needed to clarify causal relationships.

CRediT authorship contribution statement

Viktória Pipíšková: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Angela Balzano:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Soham Basu:** Writing – review & editing, Methodology, Conceptualization. **Maks Merela:** Writing – review & editing, Methodology, Conceptualization. **Pavel Bednář:** Writing – review & editing. **Jan Světlík:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2025.126364.

Data Availability

Data will be made available on request.

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