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Research paper

Year-to-year variability in xylem and phloem traits of co-existing *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia*

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The xylem and phloem anatomy of co-existing tree species provides valuable information on how different tree species face climate change and adjust their vascular structure to local weather conditions. We examined and compared annual ring widths and conduit size in earlywood and early phloem in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* in a sub-Mediterranean site during the period 2019–2021. The selected xylem and phloem traits were correlated with monthly weather conditions (precipitation and temperature). We found that phloem increment widths and conduits in earlywood and early phloem in the studied tree species showed different trends in terms of interannual variability and in relation to local weather conditions. In *F. ornus*, May conditions affected xylem traits, while June conditions phloem traits. In *Q. pubescens*, winter and March precipitation was related to phloem development. In *O. carpinifolia*, xylem ring width was positively correlated with June precipitation, while early phloem conduits were negatively affected by April temperature. Only two consistent patterns were detected across the species and years studied: wider xylem increments compared with phloem increments, and wider earlywood vessels compared with early phloem sieve tubes. Statistically significant differences were observed among species across all years for the size of xylem and phloem conduits and the hydraulic conductivity of earlywood vessels, which indicates great differences in the calculated hydraulic conductivity among the tree species. To summarize, hydraulic conductivity of earlywood vessels in *Q. pubescens* was on average for all 3 years 10.4-times and 114-times larger than in *F. ornus* and *O. carpinifolia*, respectively. High interannual variability and species-specific sensitivity of xylem and phloem traits to precipitation and temperature confirm high plasticity and different radial growth strategies of the studied tree species to ensure optimal functioning under local weather conditions.

Keywords: anatomy, early phloem, earlywood, European hop-hornbeam, manna ash, pubescent oak, sieve tube, sub-Mediterranean, vessel.

Introduction

The sub-Mediterranean region is characterized by dry and hot summers and fairly harsh winters (Joffre and Rambal 2011) and has been recognized as a significant climate change hotspot (Ramírez-Valiente et al. 2022, Lazoglou et al. 2024). The region is expected to become more vulnerable due to frequent and severe extreme conditions and climate-related natural hazards, such as droughts, forest fires and heatwaves, which will cause significant challenges to the performance of trees and forest ecosystems (Pachauri et al. 2014, Köhl et al. 2020). How trees respond and adapt to these changes depends on species-specific structural and/or physiological adjustments to maintain the functional balance among tree organs and tissues responsible for water acquisition, transport and transpiration, while also preserving carbon gain, which is important for growth and for supporting stress response mechanisms (Bréda et al. 2006, Sterck et al. 2008). The structural characteristics of vascular tissues (xylem and phloem) in relation to local environmental conditions are, therefore, a reflection of the phenotypic plasticity of tree species (Valladares et al. 2007) and can be considered to be a proxy for tree functional responses and resilience to stress factors (Sass-Klaassen et al. 2016, Tornos-Estupiña et al. 2023).

Xylem and phloem anatomical traits of co-existing tree species provide valuable information on how different tree species face climate change (Tang et al. 2022, Shtein et al. 2023, Gričar et al. 2024). Although xylem and phloem tissues are connected by ray parenchyma cells (Pfautsch et al. 2015, Sevanto et al. 2018), their central roles in the tree differ. The xylem of angiosperms has three basic functions: long-distance water transport, mechanical support of the plant body, and storage of water and nutrients (Pratt et al. 2007). Phloem is essential to tree function, acting as the long-distance transport system for photoassimilates and signaling molecules that support actively growing tissues and regulate overall tree growth and development (Dinant and Lemoine 2010). It

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also plays a critical role in induced defense responses by translocating defensive metabolites and signals from stress-affected tissues (van Bel et al. 2013, Gómez-Gallego et al. 2025). Numerous processes occurring within the phloem are therefore vital for tree responses to both abiotic and biotic environmental challenges. Environmental constraints such as drought can impair phloem function (Dannoura et al. 2019); however, trees generally strive to maintain phloem transport homeostasis for as long as possible, as this function is fundamental to their survival (Salmon et al. 2019). As the role of phloem tissue is essential for tree vulnerability and responses to various stress factors, it is crucial to understand better the structural and physiological changes of phloem tissue in different tree species and environments (Savage et al. 2016, Sevanto 2018).

In this respect, much less is known about phloem anatomy, which, apart from a few species, still represents a gap in our understanding of the ability of tree species to adapt the structure of secondary vascular tissues to local environmental conditions (Gričar 2024). In the case of *Picea abies* and *Fagus sylvatica*, high interannual variability and sensitivity of phloem to precipitation and temperature has been found. Moreover, the positive or negative responses to temperature and precipitation were species- and site-specific and largely depended on the local weather conditions (water availability) at the three temperate sites (Gričar et al. 2024). Deciduous tree species with different types of wood porosity (ring-porous and diffuse porous) often coexist in forests and woodlands, although it is unclear how the porosity affects the acclimatization potential of xylem and phloem conduits to climate change. In our preliminary study of leaf phenology and seasonal radial growth in three coexisting deciduous tree species (*Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia*), we confirmed different timing of leaf phenology and radial growth patterns among the studied species, which resulted in different size of xylem and phloem conduits (Gričar et al. 2020*b*). Differences between diffuse-porous *O. carpinifolia* and ring-porous *F. ornus* and *Q. pubescens* were observed mainly in the timing of leaf development and seasonal radial growth patterns in spring. In ring-porous *Q. pubescens* and *F. ornus*, stem radial growth began more than a month before bud swelling, whereas in diffuse-porous *O. carpinifolia*, these two events occurred almost simultaneously. Additionally, earlywood vessels were largest in the ring-porous species, while in the sieve cells of the early phloem, no relationship was found between cell size and wood porosity (Gričar et al. 2020*b*). This research was performed during only one growing season, i.e., 2019, which did not permit more detailed comparison of conducting properties in xylem and phloem among the three sub-Mediterranean tree species in relation to weather conditions. However, other studies have clearly demonstrated the effect of drier conditions on phloem anatomy in different deciduous tree species (Kiorapostolou and Petit 2018, Dannoura et al. 2019, Gričar et al. 2024).

Here, we examined and compared annual ring widths and conduit size in earlywood and early phloem in three deciduous tree species (*F. ornus*, *Q. pubescens* and *O. carpinifolia*) during the period 2019–2021. In addition, the weather effect (temperature, precipitation) on the selected xylem and phloem traits was analyzed. We hypothesized that, although the size and potential conductivity of earlywood vessels and size of early phloem sieve tubes depend on species-specifics, ring-porous species (*F. ornus* and *Q. pubescens*) show similar year-to-year trends and relations to the selected weather factors. The study was carried out on Podgorski Kras, a sub-Mediterranean site in Slovenia, where the proportion of selected deciduous tree species has increased in recent decades on previously deforested and denuded karst areas (Ferlan et al. 2016). Although the economic value of these trees is currently very limited, their ecological importance for these areas has been recognized and will most likely increase in Central Europe due to climate change (Buras and Menzel 2019).

Materials and methods

Study site description

The study was conducted on Podgorski Kras (45°32′56.3″N, 13°54′36.1″E, 430 m a.s.l.), a karst region in SW Slovenia. The site was abandoned ∼30 years ago and, since then, the grasslands have been slowly overgrown by trees and shrubs. The vegetation is uneven, characterized by patches of woody plants interspersed by grassy gaps (meadows and pastures). Woody plant encroachment is composed of various mid- and late succession species, whereby pubescent oak (*Quercus pubescens* Willd.), manna ash (*Fraxinus ornus* L.) and European hophornbeam (*Ostrya carpinifolia* Scop.) are the dominant deciduous tree species growing in either pure or mixed stands. In addition, black pine (*Pinus nigra* Arnold.) spreads from nearby afforested stands. The average height of the tree layer is 8–12 m, while the mean cover of woody species is ∼55%. The vegetation of the site is mid-successional, consisting of species of the former successional stage [calcareous grassland (*Carici humilis–Centaureetum rupestris* Ht. 1931)] and of species of the potential natural vegetation of the area (*Ostryo carpinifoliae–Quercetum pubescentis* Ht. 1950) (Ferlan et al. 2016).

The climate at the study site is sub-Mediterranean and well supplied with rainfall. However, the shallow limestone soils and the frequent wind reduce the effect of high precipitation, which leads to a high proportion of deep percolation loss of soil water and frequent summer droughts (Ferlan et al. 2016). In all 3 years studied (2019–2021), over 1100 mm of annual precipitation was recorded on the plot, with the lowest amount in 2021 (1147 mm), when 26.8% and 19.7% less rainfall occurred than in 2019 (1568 mm) and 2020 (1430 mm), respectively (Figure 1). Weather conditions during the period of radial growth of the selected tree species (i.e., March–August; Gričar et al. 2020*b*) were comparable in 2019 and 2021, but different in 2020. The driest months, with precipitation below 50 mm, were March and June in 2019 and 2021, and April in 2020. The wettest month, with precipitation above 150 mm, was May in 2019 and 2021, and June in 2020. In 2019 and 2021, the average monthly temperature was above 20 °C in the period June–August, and in 2020 in July and August. The climatic data were obtained from the nearby climate station belonging to the Slovenian Environment Agency (ARSO).

The Standardized Precipitation Evapotranspiration Index (SPEI) was used to assess drought severity at the study site for the period 2019–2021. SPEI integrates precipitation and potential evapotranspiration (PET), the latter calculated using Heargreaves' equation. The monthly SPEIs were computed using the SPEI package in R (Beguería et al. 2014). SPEI calculations showed that in the years 2019–2021, there were 9 months considered wet, of which 8 months were moderately wet and one was very wet (November 2019). Three wet

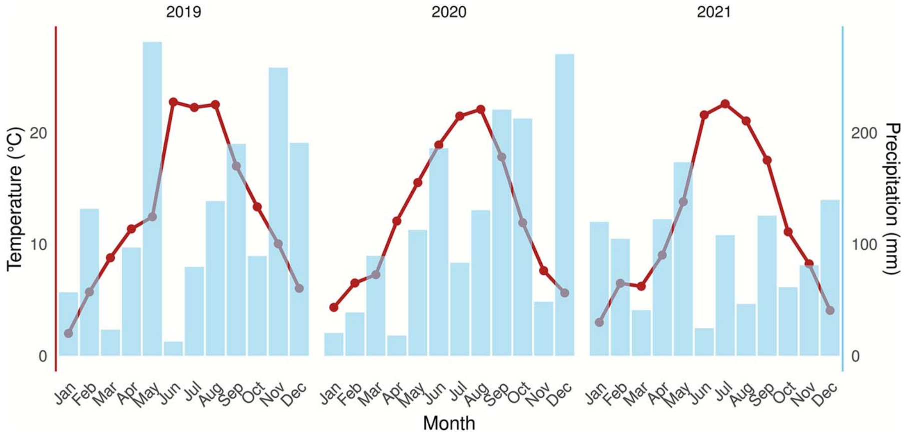

Figure 1. Mean monthly temperatures (red lines) and the monthly sum of precipitation (blue bars) for the years of sampling (2019–2021) on Podgorski Kras.

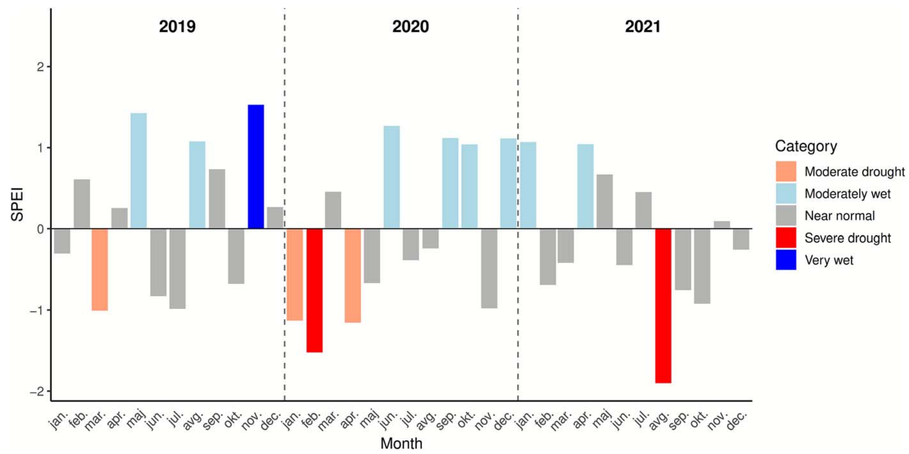

Figure 2. Monthly standardized precipitation-evapotranspiration index (SPEI) in the period 2019–2021. SPEI values above 1 indicated moderately wet months and above 1.5 very wet months, while values below −1 indicated moderate drought and below −1.5 months with severe drought (Danandeh Mehr et al. 2020).

months were recorded in 2019, four wet months in 2020 and 2 months in 2021. In 2020, three wet months were tracked in the period September–December, while in 2021 in the period January–April. Furthermore, SPEI values showed that 5 months were considered dry, of which 3 months were regarded as moderately dry and 2 months severely dry (in February 2020 and August 2021). Three dry months were detected in spring 2020, one in March 2019 and one in August 2021 (Figure 2).

Xylem and phloem anatomy

At the beginning of each of the growing seasons (2019–2021), six dominant or codominant trees per species were selected, without any visible injuries on the tree stem surface. The mean characteristics of the sampled individuals are presented in Table 1. From March until September in the period 2019–2021, microcores of 2.4 mm in diameter and 2 cm in length were collected using a Trephor tool (Rossi et al. 2006) on the same dates on which leaf phenological observations were performed. The microcores were taken in stems at 0.7–1.7 m above the ground following a helical pattern and separated by 3–5 cm to avoid wound effects. Each microcore contained phloem, cambium and the two to three youngest xylem rings. Immediately after removal, the microcores were put in 70% ethanol. In the laboratory, the samples were further processed for preparation of transverse sections stained with safranin and Astra blue for light microscopy (see Prislan et al. (2022) for details).

From the samples taken at the end of each growing season (August–September), two cross-sections of sufficient quality of phloem, cambial and xylem tissues per tree per species were selected for anatomical analysis. The final widths of xylem and phloem increments were measured along three radial rows of cells (parallel to the rays) and then averaged (Figure 3). To assess the species-specific differences in conduit size, the tangential and radial diameters, as well as the area of five randomly selected earlywood vessels were measured in each of the cross-sections and mean values were calculated (in total 10 earlywood vessels). Similarly, in phloem, the tangential and radial diameters and lumen area of five randomly selected sieve tubes of early phloem were measured in each of the cross-sections and mean values calculated (in total 10 early phloem sieve tubes). To meet the criteria of random selection, we defined a rectangular area in the youngest xylem/phloem adjacent to the cambium in the image analysis system. In this area, the first five random points that fell on conduits in xylem/phloem marked the cells that we measured. All observations and measurements of tissues were performed with an image analysis system consisting of an Olympus BX51 (Tokyo, Japan) light microscope, a PIXElink, PL-A66Z digital

Table 1. Characteristics of the sampled trees.

	Fraxinus ornus	*Quercus pubescens*	*Ostrya carpinifolia*
DBH (cm)	13.7 ± 2.4	19.4 ± 3.7	13.6 ± 2.6
H (m)	9.3 ± 1.1	9.7 ± 1.3	9.7 ± 1.1
Tree age (years)	46.1 ± 5.2	55.3 ± 9.8	49.6 ± 4.4

Mean values ± standard deviation. DBH—diameter at breast height; H—tree height.

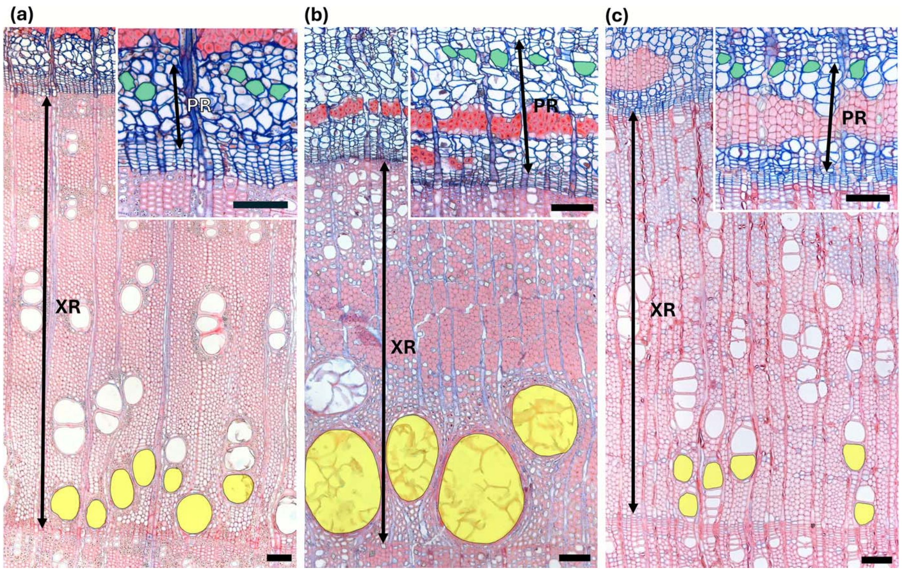

Figure 3. Cross-sections of xylem and phloem increments in (a) *Fraxinus ornus*, (b) *Quercus pubescens* and (c) *Ostrya carpinifolia*. The area of earlywood vessels is marked with yellow; the area of early phloem sieve tubes is marked with green. XR—the youngest xylem increment; PR—the youngest phloem increment. Scale bars = 100 μm.

camera and the NIS-Elements Basic Research V.2.3 image analysis program (Tokyo, Japan).

Theoretical vessel hydraulic conductance (Kh) was calculated following (Nonweiler 1975), which corrects for elliptical vessel shape. Lumen area (LA, m^2) was measured directly from cross-sectional images, while radial (Rr) and tangential (Rt) radii (m) from the same vessel were used to derive shape parameters (perimeter and eccentricity).

$$Kh = \frac{LA \cdot m^2}{\nu \cdot k}$$

where m is the mean hydraulic radius, k is a shape correction factor, and ν is the dynamic viscosity of water at 20 °C (1.002×10^{-3} Pa·s 1.002×10^{-3} Pa·s).

Conductivity of the early phloem sieve tubes was not calculated since in such a case the entire surface of the conducting phloem area would need to be taken into account. The data underlying this article are available in DiRROS repository (Gričar et al. 2025).

Statistical analysis

Differences in xylem and phloem anatomical features, i.e., annual ring width, conduit diameter and lumen area, and hydraulic conductivity (Kh) of earlywood vessels, were assessed and compared among the three selected species (*Fraxinus ornus* [FO], *Quercus petraea* [QP] and *Ostrya carpinifolia* [OC]) and years 2019–2021. Due to deviations from normality and homoscedasticity, non-parametric tests were used. To assess the year-to-year variability effects induced due to weather conditions, a Kruskal–Wallis test (K-W) with year as a factor was applied for each species and each measured feature separately. When significant differences were detected, post-hoc comparisons were conducted using Dunn's test with a Bonferroni correction. The same approach was used to detect differences among tree species; here, K-W was used for each investigated year separately. Data were analyzed using R environment (R Core Team 2024).

Results

Increment widths

In the xylem, the average values of increment widths for all 3 years were largest for *F. ornus* and smallest for *O. carpinifolia*. However, xylem ring widths among and within species varied between years (Table 2, Figure 4). Intra-annual variation in the xylem ring widths was species-specific (Figure 4). In 2019, *F. ornus* exhibited significantly wider xylem increments than the other two species, while in 2020, *Q. pubescens* had significantly wider xylem increments than the other two species. In 2021, no statistically significant differences in xylem ring width were found among the three species (Table 2). Within an individual species, the xylem increment in *F. ornus* was widest in 2019, when it was 51.1% and 63.0% wider than in 2021 and 2020, respectively (Figure 4). In *Q. pubescens*, the xylem increment was widest in 2020, when it was 14.1% and 31.0% wider than in 2019 and 2021, respectively. In *O. carpinifolia*, the xylem increment was the widest in 2019, when it was 10.5% and 47.1% wider than in 2021 and 2020, respectively.

Table 2. Results of Dunn post-hoc tests comparing xylem and phloem traits.

Parameter	Comparison	2019	2020	2021
AEP	FO–OC	***	**	**
	FO–QP	***	***	***
	OC–QP	**	***	***
AEV	FO–OC	***	***	***
	FO–QP	***	***	***
	OC–QP	***	***	***
Kh_X	FO–OC	***	***	***
	FO–QP	***	***	***
	OC–QP	***	***	***
PRW	FO–OC	**	***	**
	FO–QP	***	***	***
	OC–QP	ns	*	**
XRW	FO–OC	*	ns	ns
	FO–QP	*	***	ns
	OC–QP	ns	***	ns

AEP—lumen area of early phloem sieve tubes; AEV—earlywood vessel lumen area; Kh-X—hydraulic conductivity of earlywood vessels; PRW—widths of annual phloem increments and XRW—widths of annual xylem increments among species (FO—*Fraxinus ornus*; QP—*Quercus pubescens* and OC—*Ostrya carpinifolia*) for the years 2019–2021. Significance levels are indicated as follows: ns = not significant, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

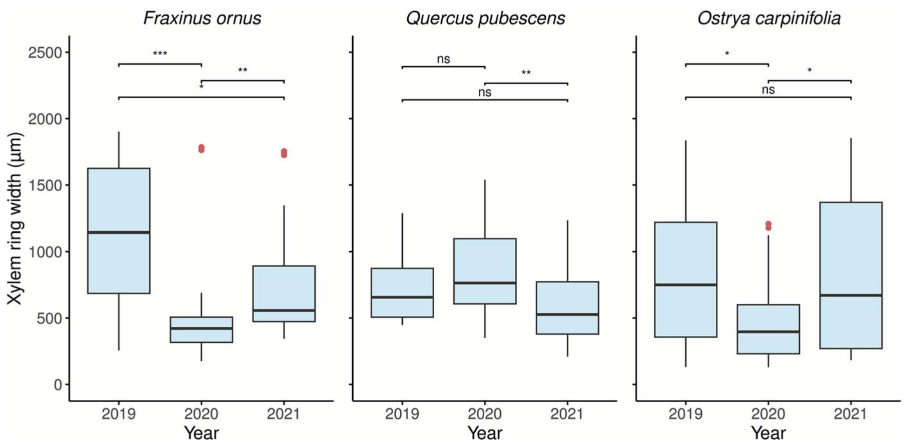

Figure 4. Widths of annual xylem increments in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* on Podgorski Kras in the period 2019–2021. The significances of differences in xylem increments among species are indicated as follows: ns = not significant, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

In the phloem, the average values of increment widths for all 3 years were largest for *Q. pubescens* and smallest for *F. ornus*. Except for *O. carpinifolia* and *Q. pubescens* in 2019, in all other cases statistically significant differences in the values of phloem ring width among species were found between years (Table 2). Within an individual species, in *F. ornus*, the phloem increment was widest in 2019, when it was 1.9% and 18.2% wider than in 2021 and 2020, respectively (Figure 5). In *Q. pubescens*, the phloem increment was widest in 2020, when it was 4.4% and 5.6% wider than in 2021 and 2019, respectively. In *O. carpinifolia*, the phloem increment was widest in 2019, when it was 4.2% and 6.5% wider than in 2021 and 2020, respectively (Figures 4 and 5).

The tendency of interannual variation in widths was also different within the same species in phloem and xylem. The only general pattern that could be observed in all species and in all years was a consistently wider xylem increment compared with that of phloem. Thus, in *F. ornus*, the xylem increment was on average 79.0% greater than the phloem increment, 62.8% in *Q. pubescens* and 66.0% in *O. carpinifolia*.

Size of conduits in earlywood and early phloem

Our analyses showed that statistically significant differences could be observed among species across all years for the size of xylem and phloem conduits and the hydraulic conductivity of earlywood vessels (Table 2). Differences in the size of the xylem and phloem conduits were detected in all species, with earlywood vessels being considerably larger than early phloem sieve tubes, i.e., 94.7% larger in *Q. pubescens*, 97.6% in *F. ornus* and 80.0% in *O. carpinifolia* (Figures 6 and 7). In the xylem, the largest earlywood vessels were found in *Q. pubescens* and the smallest in *O. carpinifolia*, while in the phloem the largest phloem sieve tubes were found in *Q. pubescens* and the smallest in *F. ornus*. On average, earlywood vessels in *Q. pubescens* were 67.4% and 89.9% larger than in *F. ornus* and *O. carpinifolia*, respectively. Furthermore, early phloem sieve tubes in *Q. pubescens* were on average 15.7% and 27.7% larger than in *O. carpinifolia* and *F. ornus*, respectively.

In *F. ornus*, earlywood vessels were widest in 2019 and narrowest in 2020. In *Q. pubescens*, they were widest in 2019 and narrowest in 2021, and in *O. carpinifolia*, widest in 2021 and narrowest in 2019 (Figure 6). The difference between the xylem conduits size among the analyzed years was most significant in *Q. pubescens* (8.2–35.1%) and least in *O. carpinifolia* (2.5–2.8%). In *F. ornus*, early phloem sieve tubes were widest in 2021 and narrowest in 2019. In *Q. pubescens*, they were the widest in 2020 and the narrowest in 2019, and in *O. carpinifolia*, the widest in 2021 and the narrowest in

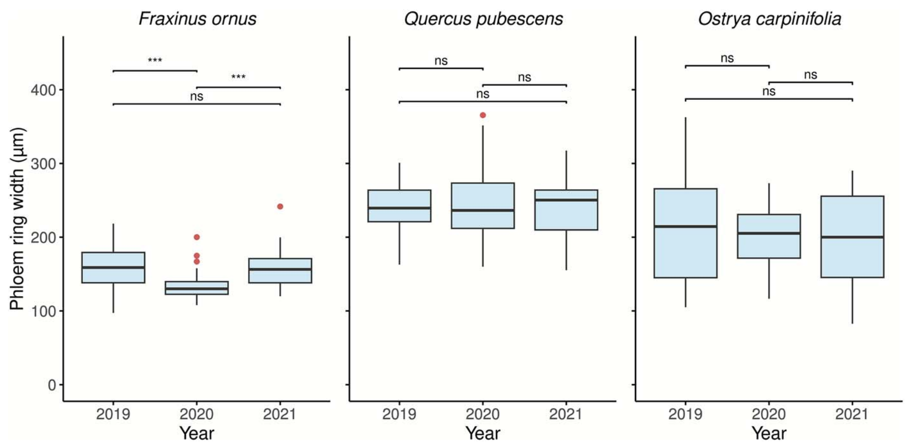

Figure 5. Widths of annual phloem increments in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* on Podgorski Kras in the period 2019–2021. The significances of differences in phloem increments among species are indicated as follows: ns = not significant, $^{***}P < 0.001$.

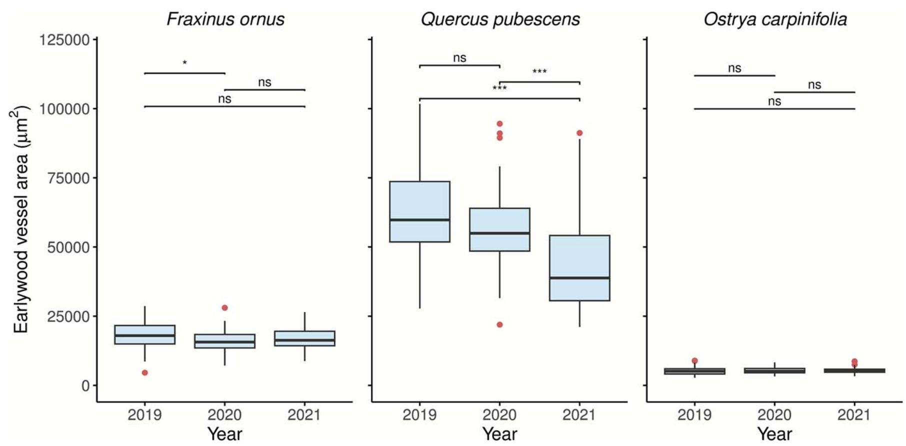

Figure 6. Earlywood vessel lumen area in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* on Podgorski Kras in the period 2019–2021. The significances of differences in earlywood vessel lumen area among species are indicated as follows: ns = not significant, $^{*}P < 0.05$, $^{***}P < 0.001$.

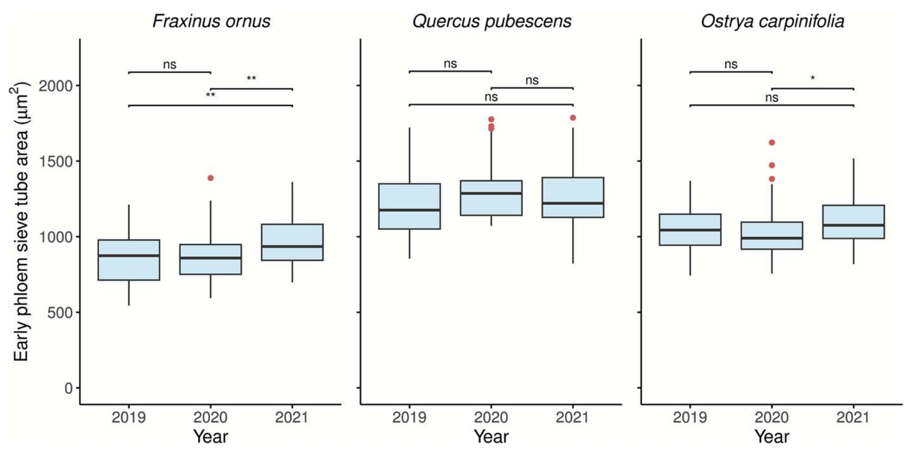

Figure 7. Lumen area of early phloem sieve tubes in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* on Podgorski Kras in the period 2019–2021. The significances of differences in earlywood vessel lumen area among species are indicated as follows: ns = not significant, $^{*}P < 0.05$, $^{**}P < 0.01$.

2020. The difference between the phloem conduits size among the analyzed years were most significant in *F. ornus* (6.5–8.1%) and least in *Q. pubescens* (5.4–8.5%) (Figure 7).

Due to the differences in the size of the earlywood vessels, their calculated hydraulic conductivity also significantly differed among the tree species (Figure 8, Table 2). The average values of calculated hydraulic conductivity for all 3 years were the largest for *Q. pubescens* and the smallest for *O. carpinifolia* (Figure 8). To summarize, the hydraulic conductivity of earlywood vessels in *Q. pubescens* was on average for all 3 years 10.4-times and 114-times larger than in *F. ornus* and *O. carpinifolia*, respectively.

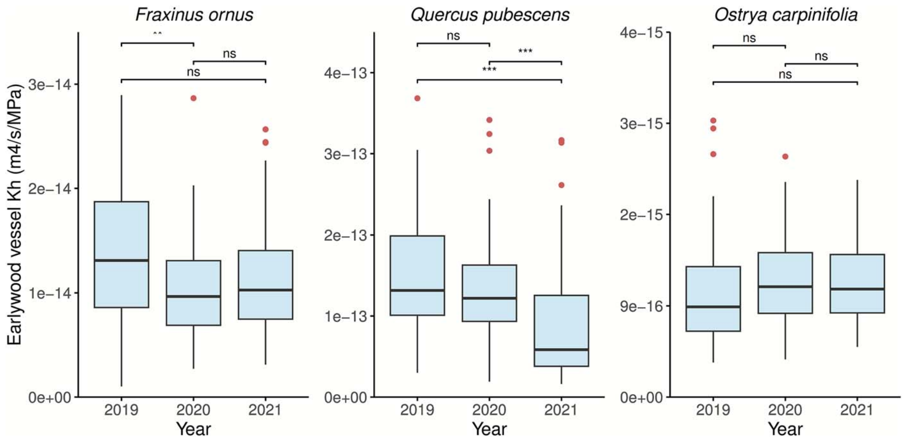

Figure 8. Hydraulic conductivity of earlywood vessels (Kh) in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia* on Podgorski Kras in the period 2019–2021. Due to differences in magnitude, the y-axes are scaled individually for each species. The significances of differences in earlywood vessel lumen area among species are indicated as follows: ns = not significant, ** $P < 0.01$, *** $P < 0.001$.

Weather–xylem/phloem relationship

Different weather drivers were found to correlate with the increment widths and the conduit traits across tree species (Figure 9). In *F. ornus*, May conditions, i.e., a positive correlation with precipitation and a negative correlation with temperature, appeared to be most decisive for the earlywood vessel size and the xylem ring width. In phloem, June precipitation was related to the increment widths, while the early phloem conduits showed no correlation with the analyzed weather conditions. In *Q. pubescens*, no statistically significant weather–xylem relationships were found except with the August conditions of the previous year. In phloem, winter temperature and March precipitation seemed to correlate positively with early phloem sieve tubes and annual increment width, respectively. In *O. carpinifolia*, statistically significant correlations were found for the xylem ring width (negatively correlated with precipitation in June) and the early phloem sieve tube (negatively correlated with temperature in April).

Discussion

Our study of xylem and phloem increment widths and conduits in earlywood and early phloem in three co-existing tree species (two ring-porous and one diffuse porous) showed different trends in terms of interannual variability and in relation to local weather conditions. Structural adjustments of xylem and phloem reflect the phenotypic plasticity of tree species, which enable them to adapt to local conditions and to overcome various stress events (Valladares et al. 2007). In this environment, natural disturbances such as droughts and fires are common and have different effects on the structure of wood and phloem (Kiorapostolou and Petit 2018, Sevanto et al. 2018, Gričar et al. 2020*a*). The contrasting response of the selected xylem and phloem traits in the individual tree species to temperature and precipitation can be explained by differences in the temporal dynamics of their formation and differences in the climate sensitivity of the two tissues. Despite great year-to-year variability in the conduits and increment widths of xylem and phloem, two consistent patterns were detected across the species and years studied: (i) wider xylem increments compared with phloem increments, and (ii) wider earlywood vessels compared with early phloem sieve tubes.

Interannual variations and climatic sensitivity of xylem and phloem

In xylem, the median values of the annual increments were largest in *F. ornus*, while earlywood vessels were largest in *Q. pubescens*. Unlike earlywood vessels, which were significantly larger in *Q. pubescens* and the narrowest in *F. ornus* in all 3 years, ring widths varied greatly across tree species and years. For example, in 2019 their median values were widest in *F. ornus* and narrowest in *Q. pubescens*. In 2020 the median values were widest in *Q. pubescens* and narrowest in *O. carpinifolia* and in 2021 they were widest in *O. carpinifolia* and narrowest in *Q. pubescens*. In the phloem, the annual increments and early phloem sieve tubes were largest in *Q. pubescens* and smallest in *F. ornus*. This pattern in the phloem remained consistent in all 3 years, while within a single species, variability in average phloem increment width and phloem conduit size was not coordinated among years. Of all the measured xylem and phloem traits, only interannual variability in ring widths was congruent in *F. ornus*, in which xylem and phloem increments were widest in 2019 and narrowest in 2021, while no such trend was found in the other two species. These observations show that the developmental patterns of xylem and phloem are species-specific, with the two tissues being controlled differently by various environmental and intrinsic factors. Indeed, the correlation analysis between xylem and phloem traits and precipitation and temperature showed differences in the response among tissues and species. In *F. ornus*, May conditions were linked with xylem development and June for phloem. In *Q. pubescens*, winter and March precipitation was related to phloem development, whereas in *O. carpinifolia*, xylem ring width was positively correlated with June precipitation and early phloem conduits were negatively influenced by April temperature. As already mentioned in the Materials and methods, the selected sub-Mediterranean site frequently experiences periods of drought, even if the plot is well-drained, but a combination of strong winds and shallow limestone soils with low water holding capacity can pose a limitation to tree radial growth (Gričar et al. 2018, Vodnik et al. 2019). Generally, reduced radial growth is one of the first and most obvious indicators of unfavorable growing conditions (Bigler et al. 2004). Drought, for example, may have a markedly negative effect on xylem

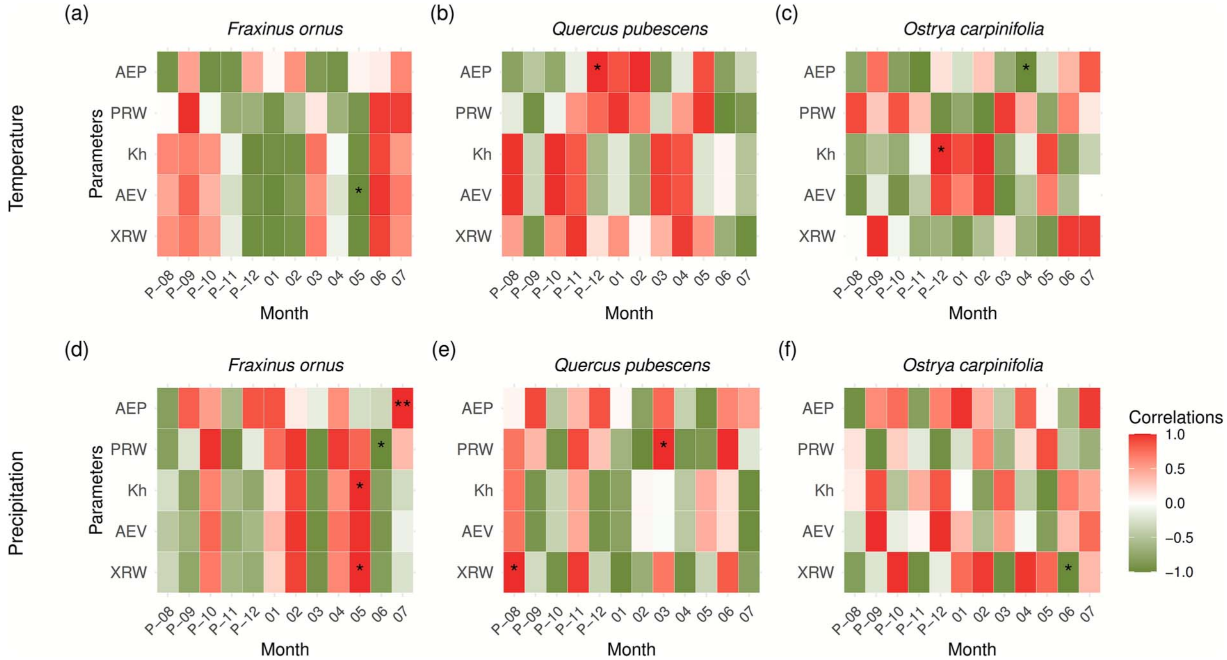

Figure 9. Pearson correlations between monthly temperature (a–c) and precipitation (d–f) (for the period from August of the previous year to July of the current year) and selected xylem and phloem anatomical parameters in *Fraxinus ornus*, *Quercus pubescens* and *Ostrya carpinifolia*. Significant correlations are marked with asterisks ($P \leq 0.05$). Red colors indicate positive and green colors display negative correlations. The y-axis shows the parameters analyzed: Xylem ring width (XRW), earlywood vessel area (AEV), theoretical hydraulic conductivity (Kh), phloem ring width (PRW) and early phloem sieve tube area (AEP). P—previous year.

increment, which can even be locally absent (e.g., Novak et al. 2016). This may also affect the ratio between xylem and phloem increments in favor of phloem (Gričar et al. 2014). The ratio between wood and phloem growth was in favor of wood in all cases, indicating that the trees were not under such severe stress as to jeopardize their long-term functioning in the years studied. Furthermore, our findings indicate that drought periods, which can occur in different months at this site, have an unequal impact on the radial growth of these three (sub-)Mediterranean deciduous trees (Figure 2). For example, the dry spring of 2020 did not uniformly reduce the measured xylem and phloem parameters compared with other years. Nevertheless, in this year, the lowest values were reached in most cases (7 out of 12 measured parameters), although they were not always statistically significant. Only in one case was the highest mean value recorded, i.e., the width of the xylem ring in *Q. pubescens*. An only 3-year data record does not permit strong weather-xylem/phloem anatomy analyses but merely a simple comparison of the response of xylem and phloem structural adjustments of the co-existing tree species to changes to identical weather conditions.

The high plasticity of wood anatomy (e.g., vessel characteristics, ring width) to site conditions has already been reported in several tree species (e.g., Campelo et al. 2010, Fonti et al. 2010, Stojnic et al. 2013, Arnič et al. 2021), while phloem anatomy is less studied in this respect, in particular in sub-Mediterranean tree species (Kiorapostolou and Petit 2018, Gričar et al. 2020*a*, 2022, Balzano et al. 2021). Although cambial cell production in temperate tree species occurs simultaneously on the xylem and phloem sides, the temporal dynamics of their development differ, which explain different climatic influences on the studied traits (Gričar et al. 2015, 2022). The temporal dynamics of phloem and xylem formation were not the subject of the present study but the data from 2019 on the same tree species showed that cambial activity starts in March and ends in the period mid-July and mid-August at this location, depending on the weather conditions in the current growing season (Gričar et al. 2020*b*, 2022). Consequently, weather conditions in the late summer months with a high probability of drought or fire do not have a significant impact on xylem and phloem ring widths, because cambial cell production is normally finished at this time. Such timing of cambial phenology could indicate an adaptation of sub-Mediterranean deciduous tree species to local environmental conditions to accomplish the majority of radial growth before the appearance of potentially stressful conditions and is a good prerequisite for successful growth in drought-prone environments (Zweifel et al. 2006, Gričar et al. 2022). It must be emphasized that species- and tissue-specific sensitivity to temperature and precipitation should not be generalized to a single tree species. Namely, a recent study on *P. abies* and *F. sylvatica* showed that the response of xylem and phloem traits to weather conditions in the same tree species is variable and may not be uniform in different environments, especially when some sites are optimal for tree growth and others are more restrictive, e.g., due to drought (Gričar et al. 2024). The observed growth patterns thus cannot be considered to be a general rule until comparative studies are conducted across contrasting sites over a longer time period.

The phenology of each organ/tissue is inter-connected, species-specific and regulated by a combination of different environmental and internal factors, which is reflected in great differences in the ability of tree species to adjust to environmental changes (Delpierre et al. 2016). Differences among these deciduous tree species in response to weather conditions can be partly ascribed to the timing of leaf development, in connection with wood porosity, with *F. ornus* and *Q. pubescens* having a ring-porous wood structure and *O. carpinifolia* a diffuse-porous wood structure, which affects tree phenology and physiology (e.g., seasonal variations in photosynthesis and transpiration in leaves), as well as the distribution of non-structural carbohydrates, their dynamics and availability (Barbaroux et al. 2003). Since cambial activity and cell development are costly processes, they are influenced by the carbon budget of the tree and consequently depend on the yearly carbon gain of a tree, which is reflected in diminished tree radial growth in the case of unfavorable growing conditions, such as drought. Tree carbon status in terms of seasonal fluctuation and accumulation thus indirectly influences tree performance also during and after stress events (Trifilò et al. 2017). In ring-porous species, cambium growth resumes before budbreak, while in diffuse-porous species, budbreak occurs before or at the onset of stem radial growth (Savage and Chuine 2021). Consequently, the large proportion of earlywood and early phloem in ring-porous species relies on non-structural carbohydrates produced in previous years and stored in the parenchyma cells, while in diffuse-porous species, the great majority of xylem and phloem tissues are formed after leaf expansion, so their formation largely depends on recent carbohydrates derived directly from photosynthesis (Barbaroux et al. 2003). A positive effect of weather conditions in the previous autumn/winter (precipitation in June and temperature in December) on xylem ring width was found only in *Q. pubescens* but not in *F. ornus*. It is interesting that *F. ornus* and *Q. pubescens*, which are both ring-porous species, respond differently to identical weather conditions, although the main milestones of leaf, xylem and phloem development in 2019 were similar. These 1-year data cannot be generalized to all years and all conditions, but they clearly show that growth-weather relationships depend on numerous other factors and that structural and/or physiological adjustments, which contribute to functional balance among different tissues and organs, are species-specific (Bréda et al. 2006, Valladares et al. 2007, Galmés et al. 2012).

Although adapted to grow in drought-prone environments, different tree species are not equally capable of surviving severe drought events in terms of radial growth. Recently, dendrochronological analyses of xylem-ring widths of *F. ornus*, *Q. pubescens* and *Pinus nigra* from eight different sites in Slovenia and Italy revealed that *F. ornus* appears to be the least sensitive to drought stress (Krajnc et al. 2025). It had the shortest post-drought recovery periods, with the minimum number of permanently affected trees. However, the study also showed that even within the same species at the same location, noticeable differences in radial growth response to drought existed; while most of the trees were affected by drought stress, some trees remained unaffected (Krajnc et al. 2025). To assess fully the response of individual trees of the same species to (stressful) environmental conditions, other parameters, such as soil properties or genetic differences, should also be considered. Namely, in karst areas, where only little soil water can be stored within the soil profile and crevices, information on the soil depth and type at the micro location of individual trees is important, since it has been suggested that bedrock can store considerable amounts of available water that the trees can use to survive drought conditions (Nardini et al. 2024).

Conduit characteristics

The conduit size is generally related to turgor pressure in the expanding cells, which is controlled by water potential, osmoregulation and hormonal signals (Jyske and Hölttä 2015). Precipitation is thus expected positively to influence the conduit size, but this relation was found only in the case of earlywood vessels in *F. ornus*. In addition, only in this species did we find the smallest xylem and phloem conduits in 2020, when the conditions in spring were dry. Earlywood vessels were considerably larger in *Q. pubescens* than in the other two species, indicating great differences in the efficiency of the xylem conducting system among tree species (Figure 2). The most efficient water transport is provided in *Q. pubescens* and the least in *O. carpinifolia*. Even though *Q. pubescens* and *F. ornus* are ring-porous species, the former had almost 70% larger earlywood vessels than the latter, which is in line with previous findings (Italiano et al. 2023). This is reflected in distinguished differences in calculated hydraulic conductivity among species, which increases proportionally to the fourth power of its radius, according to the Hagen-Poiseuille law (Hacke et al. 2022). Thus, in *Q. pubescens*, earlywood vessels were 10.4-times and 114-times more effective than in *F. ornus* and *O. carpinifolia*, respectively. At the same time, the risk of breakage of the water column due to embolism under drought stress is higher in the wider conduits in *Q. pubescens* than in the other two species and may jeopardize the viability of the trees (Cochard and Tyree 1990, McElrone et al. 2013). However, water transport in ring-porous species mainly relies on the vessels in the youngest xylem increments, because of the dysfunction of wide earlywood vessels due to tylose formation, which occurs within 1–2 years of their formation (Kitin and Funada 2016). In one of our previous studies on *Quercus pubescens*, we confirmed that tyloses may appear in earlywood vessels formed in the current year as early as the end of the growing season (i.e., in August) (Figure 3), which affects the hydraulic integrity of earlywood vessels (Gričar et al. 2020*a*). In contrast, the small-diameter latewood vessels usually remain functional for many years. Despite their much lower conducting capacity, the more cavitation-resistant latewood vessels in ring-porous species are important for water conduction and serve as a high-safety, low-efficiency backup system during stressful events, potentially preventing complete transport failure (Taneda and Sperry 2008). Unlike ring-porous species, earlywood vessels in diffuse-porous species remain functional for many years (Gasson 1985), which needs to be taken into account when comparing total water-transport capacity among tree species.

Our previous data from 2019 on the same tree species also revealed that initial sieve tubes in early phloem started to expand around the time of cambial reactivation in all species and reached their final size at the time of swollen buds in *Q. pubescens* and *F. ornus*. In *O. carpinifolia*, the initial sieve tube expansion was completed 2 weeks after the emergence of the first leaves (Gričar et al. 2020*b*). The final size of initial sieve tubes in all three species occurred much earlier than the complete maturation of initial earlywood vessels, i.e., 1 month earlier in *Q. pubescens* and *F. ornus*, and 2 months earlier in *O. carpinifolia* (Gričar et al. 2020*b*). Although year-to-year variability in the timing of leaf and cambial phenology in the case of *Q. pubescens* was found, their chronological sequence was fairly fixed (Gričar et al. 2022). This suggests that any changes in autumn/winter and spring climatic conditions for this area could affect the timings of leaf and cambial phenology in the coming years, which would affect xylem and phloem structure and, consequently, tree functioning in the sub-Mediterranean. This type of research is also important for studying the resilience of forests to climate change. The divergent response of co-existing tree species to identical environmental variables positively contributes to forest resilience in drought-prone environments (Krajnc et al. 2025).

Conclusions

Three years of data on xylem and phloem traits from three co-existing deciduous tree species allow a more detailed comparison of their ability to modify stem vascular structure in response to local conditions. Our data showed high interannual variability in the selected xylem and phloem traits, which can be explained by differences in the temporal dynamics of their formation and different climatic controls. Longer data sets spanning many years and multiple plots would be needed to increase the reliability of analyses of the climate impact on xylem and phloem formation patterns in the selected tree species across contrasting environments; however, our findings are particularly relevant for the phloem, as such data are critically lacking. Of the selected tree species, the radial growth patterns and anatomy of *F. ornus* and *O. carpinifolia* are generally poorly known due to their current low economic importance. Nevertheless, given climate change scenarios, their relevance is likely to increase, since Mediterranean forest types are projected to expand in Central Europe (Buras and Menzel 2019). Therefore, new information on the plasticity of vascular tissues to local conditions is one of the first steps toward a more holistic understanding of their performance and adaptation abilities to environmental changes, which is a key aspect of their life strategies for surviving in a variety of habitats, including diverse and even extreme environmental conditions.

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Author contributions

J.G., K.E., P.H. and P.P. conceived and designed the work; P.H. collected the samples; S.O. prepared, checked and selected the cross-sections for the analyses and prepared the images; D.C., S.K. and M.T. carried out the anatomical analyses; P.P. and K.E. performed the statistical analyses; P.P. prepared the final figures and tables; J.G. wrote the manuscript; all authors critically revised the manuscript; all authors approved the final version of the manuscript to be published.

Conflict of interest

The authors declare that they have no conflicts of interest.

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Data availability

The data underlying this article are available in DiRROS repository at (https://doi.org/10.20315/Data.0012).

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