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Aldona Paulina Miodek, Adam Miodek, Paweł Kojs*

Interaction between xylem rays and vessel elements

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Abstract: Increasing attention has recently been given to the connections between the two systems of secondary vascular tissues. Due to the dependencies described thus far between developing vessel elements and xylem rays, it was decided to analyze the influence of ray proximity on the tangential dimension of developing vessel element, as well as the effect of vessel element development on the width of neighboring ray. We hypothesized that rays act as obstacles to the tangential enlargement of vessel elements, thereby influencing their final tangential dimension, and that the enlargement of vessel elements is associated with localized changes in the width of the rays they encounter during growth. Two anatomical techniques were used to obtain tangential and transverse sections of the secondary xylem of Norway maple and pedunculate oak. In maple wood, the tangential dimension of vessels in contact with rays was measured, while in oak wood, the width of rays in contact with fully developed vessels was recorded. The anatomical and statistical analyses revealed a reduction in the tangential dimension of vessel that contacts ray, and showed that the tangential growth of vessel element is associated with a local decrease in the width of the ray it encounters. These findings indicate that rays generally act as obstacles to vessel element growth, independent of whether growth is intrusive or symplastic. Considering their biomechanical properties, we propose that rays may play a buffering role within the secondary xylem differentiation zone – limiting not only the tangential intrusive growth of vessel elements but also affecting their overall tangential enlargement. In addition, three theoretical explanations were introduced to account for the observed reduction in the average width of rays.

Keywords: wood anatomy, *Acer platanoides*, *Quercus robur*, light microscopy, morphometry

Addresses: A. P. Miodek, A. Miodek, P. Kojs, Polish Academy of Sciences Botanical Garden –
Centre for Biological Diversity Conservation in Powsin, Prawdziwka 2, 02-973 Warsaw, Poland;
APM https://orcid.org/0000-0002-4204-9596, e-mail: aldona.miodek@ob.pan.pl;
AM https://orcid.org/0000-0003-0941-3939, e-mail: adam.miodek@ob.pan.pl;
PK https://orcid.org/0000-0002-2906-4214, e-mail: pawel.kojs@ob.pan.pl
A. Miodek, P. Kojs, Silesian Botanical Garden, Sosnowa 5, 43-190 Mikołów, Poland
* corresponding author

Introduction

Angiosperm wood consists of two interconnected systems: axial (vertical) and radial (horizontal), both of which are essential for the proper functioning of vascular tissues (Evert, 2006). These systems are produced by two types of bifacial cambial cells (often referred to as stem cells in molecular studies) – fusiform and ray initials (Tonn & Greb, 2017; Shi et al., 2019; Smetana et al., 2019). The axial system, derived from fusiform initials, is characterized by a high diversity of cell types, including vessel elements (VEs) (Hejnowicz, 2012). A defining feature of this system is that the long axes of the cells are generally aligned with the longitudinal axis of the stem. However, the orientation of the long cell axes may be also oblique relative to the organ longitudinal axis due to the formation of wood grain other than straight (Włoch et al., 1993; Kojs et al., 2002). The second system (radial) consists predominantly of parenchyma cells (ray cells), which undergo substantial elongation in the radial direction during differentiation (Wilczek-Ponce et al., 2021). Consequently, in mature wood, the long axes of cells in the axial and radial systems are oriented perpendicular to each other (Evert, 2006).

Our previous study, conducted on five angiosperm species differing in porosity type (Gizińska et al., 2021), revealed meaningful differences in the susceptibility of cell walls to separation between the axial and radial systems adjacent to developing VEs. This finding represented an important advance, as the developmental processes of axial and radial system cells are typically considered separately. We concluded that the maintenance of continuity of rays near large VEs – in contrast to axial system cells, where complete separation of tangential walls was observed – indicates that rays hamper intrusive growth of VEs, and may suggest a specific role for rays in regulating elastic and plastic deformation within the secondary xylem cell differentiation zone (Gizińska et al., 2021). Intrusive growth represents one of the two components of transverse enlargement of VEs during differentiation phase, as observed in histological analyses (Hejnowicz, 2012; Gizińska et al., 2021). This type of growth is accompanied by the separation of cell walls in the vicinity of the intrusively growing cell, resulting in changes in cell contacts (Miodek et al., 2022). The second component of VE transverse enlargement is symplastic growth, which involves synchronous growth of cells without altering their contacts (Gizińska et al., 2021; Miodek et al., 2021).

The findings regarding the hampering role of rays on the intrusive growth of VEs (Gizińska et al., 2021) prompted us to undertake further research on the specific interaction between xylem rays and VEs developing in their vicinity. This approach allowed us to broaden our focus to include the analysis of mutual interactions among different structures and cell types. In the present study, building upon our previous findings, we first aimed to analyze the potential influence of rays adjacency on the tangential dimensions of developing VEs, which increase their transverse dimensions during differentiation. Second, we investigated the effect of VE development on the width of neighboring ray. As rays in direct contact with large, mature vessels preserve their radial continuity (Gizińska et al., 2021), the present study tested two hypotheses: (1) rays act as a physical constraint on the tangential enlargement of VEs – regardless of growth type (intrusive/symplastic) – thereby influencing their final tangential dimensions; and (2) VEs enlargement is associated with local changes in the width of the rays encountered during tangential growth.

To analyze the potential influence of neighborhood of rays on the tangential dimension of enlarging VEs, the secondary xylem of Norway maple (*Acer platanoides* L.) was selected. This species, along with similar maples such as sycamore maple (*Acer pseudoplatanus* L.), sugar maple (*A. saccharum* L.), and field maple (*A. campestre* L.), possess the following characteristics: (1) diffuse-porous wood, characterized by numerous vessels (with an average vessel density of 34–38–44 per mm^2) and relatively small vessel diameters (with an average tangential diameter of 44–65–80 μm); and (2) multiseriate rays, 1–6(–8) cells wide, occurring at a frequency of 6–9–14 per tangential mm (as described for *Acer* spp. by Richter & Dallwitz, 2000). These features made the selected species suitable for the planned analysis based on large-surface tangential sections, prepared with a core-microtome, which allowed us to preserve tissue integrity during sectioning. The wood anatomy of Norway maple in transverse, tangential, and radial views is shown in Fig. 1a–c.

To analyze the potential influence of VE development on ray width, the secondary xylem of pedunculate oak (*Quercus robur* L.) was selected. This ring-porous species is characterized by large-diameter vessels in the earlywood and small-diameter vessels in the latewood (Gizińska et al., 2021). It has numerous narrow, predominantly uniseriate (Reiterer et al., 2002), and less frequently biseriate rays (Gizińska et al., 2021), as well as a much smaller number of wide, multiseriate rays, typically 10–30 cells wide (Richter & Dallwitz, 2000; Kokociński, 2005). The reasons for selecting this species for analysis based on transverse sections of its secondary xylem include: (1) the wide range of vessel sizes; and (2) the high frequency of narrow rays (uniseriate/biseriate), which increases the likelihood of direct contact between vessels and rays – especially in the earlywood. These narrow rays exhibit varying degrees of deflection as a result of contact with vessels (Gizińska et al., 2021) and constitute the subject of the present study. Analysis of ray width was conducted separately in earlywood and latewood areas to account for anatomical differences. The wood anatomy of pedunculate oak is shown in Fig. 1d–e.

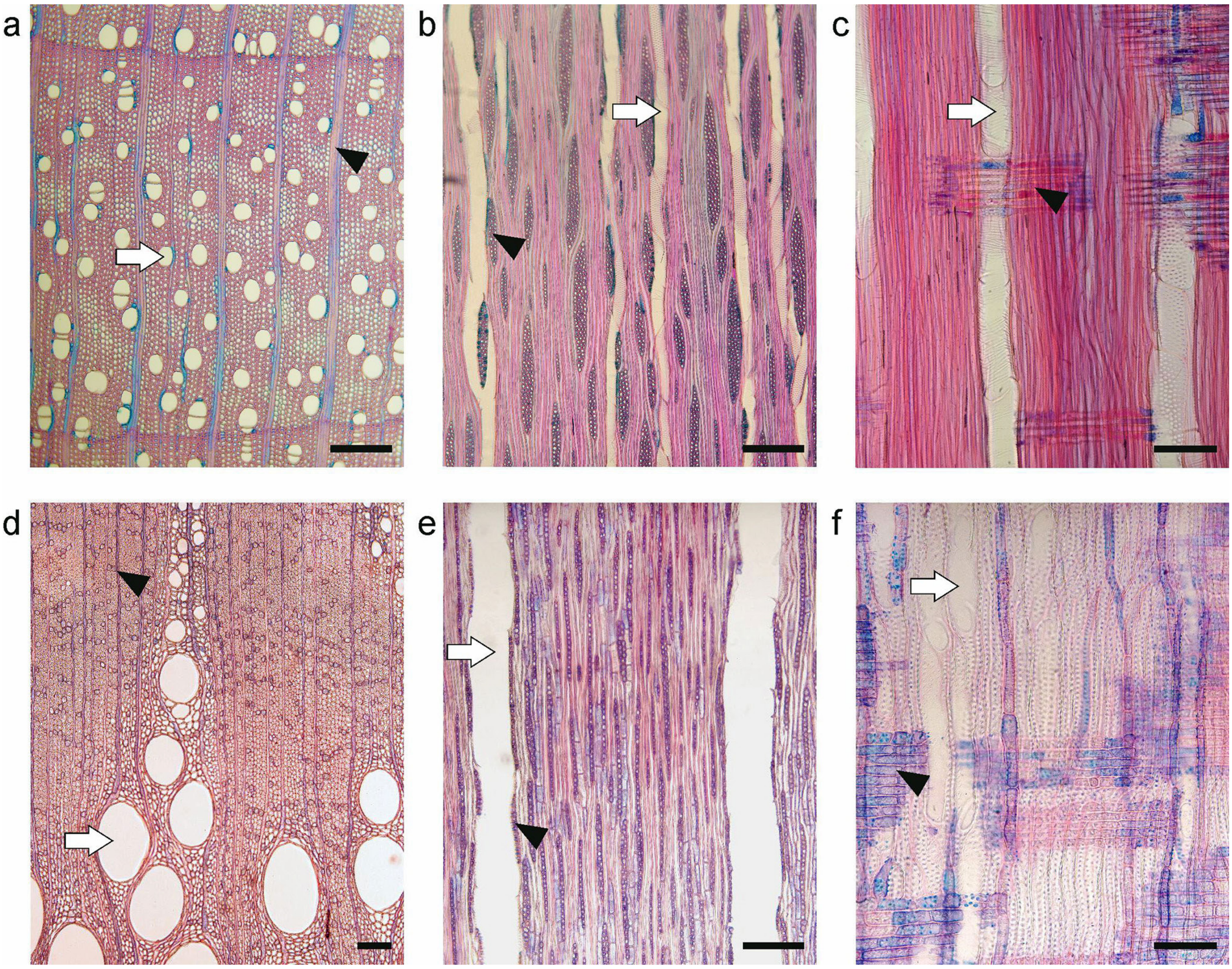

Fig. 1. Wood anatomy of Norway maple (*Acer platanoides* L.; a–c) and pedunculate oak (*Quercus robur* L.; d–f) in the three principal anatomical planes. (a, d) Cross-sections. (b, e) Tangential longitudinal sections. (c, f) Radial longitudinal sections. Black arrowheads – rays. White arrows – vessels. Scale bars: a, b, e – 200 µm; c, d, f – 100 µm

Methods

Sample collection

Samples of secondary xylem from Norway maple were collected from the trunks of three individual trees growing in the Silesian Botanical Garden, Poland (temperate zone). The diameters at breast height (DBH) of the sampled trees were approximately 48 cm, 8 cm, and 8 cm. Sample collection took place on 9 November 2018, 13 June 2025, and 25 July 2025, respectively. Samples were obtained from the breast height either using an increment borer or by cutting discs from the trunks. All samples were fixed in a 1:1 solution of ethanol and glycerol.

Samples of secondary xylem of pedunculate oak were collected from the trunks of two individual trees growing in the Silesian Botanical Garden, Poland. The first sampling was conducted during the 2016 growing season (2 March) using chisels, from a tree with a DBH of approximately 28 cm. The second sampling involved collecting vascular cambium and secondary xylem in the form of microcores (2 mm in diameter) using Trephor tool (Rossi et al., 2006) from a tree with a DBH of approximately 32 cm. These microcores were taken during the 2022 growing season, between April and June (8, 15, 29 April, 6, 13, 20 May, and 30 June). All samples were collected approximately at breast height, and fixed in a 1:1 solution of ethanol and glycerol.

Material preparation for anatomical analyses

Tangential and transverse sections were prepared from material collected from Norway maple and pedunculate oak during the 2016 growing season (2 March), respectively, using a WSL core-microtome (Gärtner & Nievergelt, 2010; Ivanova et al., 2015). Prior to sectioning, the fixed material was rinsed with distilled water (Gizińska et al., 2021). Sections approximately 20 μm thick were obtained and then stained using a 1:1 mixture of safranin O and astra blue. This was followed by rinsing the sections with distilled water and dehydration in an ethanol series (50%, 75%, and 96%) (Piermattei et al., 2015). All sections were mounted in Euparal (Roth).

Fixed samples collected from pedunculate oak during the 2022 growing season were dehydrated in graded series of ethyl alcohol and propylene oxide, embedded in an epoxy embedding medium (Sigma-Aldrich), and subjected to gradually increasing temperatures (35 °C, 45 °C, and 60 °C) to accelerate the polymerization process (Miodek et al., 2022, 2023). Using a Tesla ultramicrotome, a series of cross-sections of the vascular cambium and secondary xylem, approximately 3.5 μm thick, were obtained. The sections were stained with Schiff's reagent (PAS reaction) and toluidine blue, and mounted in Euparal (Roth) (Miodek et al., 2022, 2023). All sections were analyzed using bright-field microscopy (Olympus BX41).

Measurement methodology of vessel tangential dimension

The potential influence of ray neighborhood on the tangential dimension of developing VE was analyzed using tangential sections of Norway maple secondary xylem. Tangential longitudinal sections allowed us to assess the tangential dimension of a vessel both at the point of direct contact with a ray, and in the region above the point where the ray terminates, where it no longer interacts with the vessel. Only cases where a direct contact between a xylem ray and a developed vessel was observed were included in the analysis. The tangential dimension of the vessel was measured at two locations: (1) at the point where the adjacent ray was the widest – typically corresponding to the central portion of the ray; and (2) at a distance of 40–45 μm from the end of the same ray (Fig. 2a–b). Measurements were taken from the inner surface of one secondary cell wall to the inner surface of the opposite secondary cell wall. Cases of vessel–ray interactions were analyzed in tangential sections prepared from the most recently formed wood layers, taken at depths of approximately 2000–4000 μm into the secondary xylem tissue. In total, 420 instances of ray–vessel adjacency were analyzed, yielding 840 individual measurements. Detailed measurement data are provided in Table S1.

Measurement methodology of ray width

A study on the potential influence of VE development on the width of neighboring ray was conducted using transverse sections of pedunculate oak secondary xylem. Wood preserves a record of changes occurring in the vascular cambium and the xylem differentiation zone (Hejnowicz, 2012). Consequently, transverse sections of formed wood can be used to compare ray width before vessel formation and in the immediate vicinity of a vessel. Only cases in which direct contact between a ray and a VE occurred at a specific stage of VE development (i.e., where no other cells were present between the analyzed ray and the VE) were examined. In all analyzed cases, ray width was measured at two locations: (1) near the center of the VE, typically at its widest point – where the VE in question had the largest tangential dimension; and (2) further away from the vessel, closer to the trunk pith, which developmentally corresponded to the stage prior to the formation of that VE (i.e., before its influence on the ray) (Fig. 2c–d). For earlywood, measurements at location (2) were taken 80–100 μm from a vessel. Care was taken to ensure that the course of the rays at this location was not disrupted by structures such as other developing VEs or by tissue deformations caused by other factors. In one instance, where such conditions were unavoidable, the measurement was taken at a slightly shorter distance than 80 μm but as far as possible under the circumstances. For latewood, measurements were generally taken 30–50 μm from a vessel. In a few cases where the course of the rays was noticeably disrupted by the factors mentioned above at that distance, the measurement was taken at 20–25 μm. All measurements were made from primary cell wall to primary cell wall (specifically, at the boundary between the primary wall and the middle lamella). Ray dimensions were measured perpendicular to the course of the ray at the point of measurement. The analyzed cases of vessel–ray interactions were limited to the most recent annual growth ring for material collected in 2016 and to the two most recent rings for material collected in 2022. The measurement data are presented in Table S2. It should be noted that pedunculate oak latewood vessels are characterized by a small width, with distinctly limited tangential enlargement. Therefore, considering the purpose of this part of the study (i.e., examining the effect of VE development on the width of adjacent ray), it was necessary to analyze cases in which interaction between these two wood components occurred during their development. It was assumed that the presence of at least minimal (noticeable) deflection of the ray wall adjacent to a VE indicated such an interaction, and only these cases were included in the analysis. In total, 100 instances of ray–earlywood vessel adjacency and 100 instances of ray–latewood vessel adjacency were analyzed. Considering the two measurement locations, this resulted in 400 measurements (200 + 200).

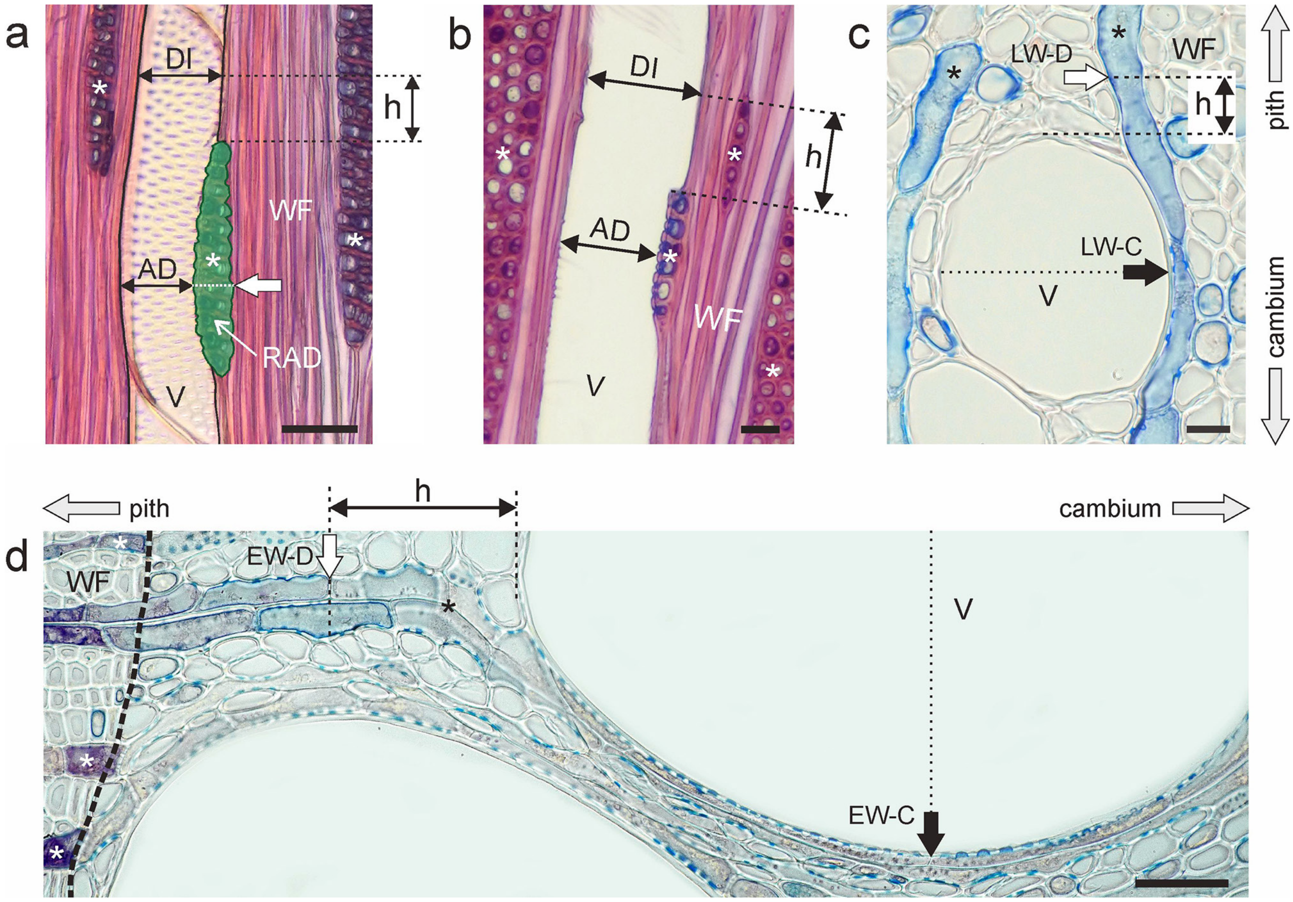

Fig. 2. Measurement methodology of the two analyses performed. (a, b) Vessel tangential dimension analysis based on tangential sections of secondary xylem of Norway maple (*Acer platanoides* L.). Two locations of vessel tangential dimension measurement are shown: (AD) at the point where the ray in direct contact with the vessel is the widest, and (DI) at a distance of 40–45 μm from the end of the same ray. White arrow in (a) indicates the widest part of the ray adjacent to vessel (RAD). (c, d) Ray width analysis within the latewood (c) and earlywood (d) based on transverse sections of secondary xylem of pedunculate oak (*Quercus robur* L.). Two locations of ray width measurement are shown: (LW-C/EW-C) near the center of the vessel, typically at its widest point – where the vessel under consideration has the largest tangential dimension (indicated by black arrow), and (LW-D/EW-D) further away from the vessel, closer to the trunk pith (usually at a distance of 80–100 μm for earlywood and 30–50 μm for latewood; indicated by white arrow). V – vessel. Asterisks – rays. WF – wood fibers. h – exemplary distance of measurements taken within the specified range for a given analysis. The thick black dashed line in (d) indicates the growth ring boundary. Note that ray width was measured perpendicular to the course of the ray at the point of measurement. Scale bars: a – 50 μm; b, c – 20 μm; d – 50 μm

Statistical analyses

Descriptive statistics (mean, minimum, maximum, and median values, as well as standard deviations and errors) were calculated for all measurement data, taking into account the measurement location (Tables S3–S5 for maple and Tables S6–S7 for oak). Statistical analyses were performed using PQStat software, version 1.8.6 (PQStat Software Inc., Poznań/Plewiska, Poland). The Shapiro–Wilk test ($\alpha = 0.01$) was used to assess normality (Tables S8–S11). Since the part of the data did not follow a normal distribution, a Wilcoxon matched-pairs test (dependent model; $\alpha = 0.01$) was conducted to determine: (1) whether the tangential dimension of the vessel adjacent to a ray (at the location of maximum ray width) differed significantly from the tangential dimension of the same vessel measured 40–45 μm away from the end of the ray in case of maple wood, and (2) whether the ray width near the center of an adjacent VE differed significantly from the ray width measured farther away from the vessel (ontologically prior to the formation of a VE) in case of oak wood. For the analysis of maple wood, statistical significance was assessed using data collected from all trees both collectively and separately, with a distinction made between older and younger trees based on diameter. For oak wood, the analysis was conducted separately for earlywood and latewood datasets.

Results

Analysis of vessel tangential dimension

Based on the analyzed cases of vessel–ray interaction within maple wood (Fig. 3), it was stated that the average vessel tangential dimension at the point where the adjacent ray is the widest was smaller by ca. 18% than at a distance of 40–45 μm from the end of the same ray (the change calculated based on the mean values obtained across all analyzed trees; Table S3). Results of the Wilcoxon matched-pairs test (α = 0.01) indicated that there were statistically significant differences in vessel tangential dimensions between the two locations (Table S12). The results of analyses accounting for tree age classes (older versus younger individuals) showed the same trend: a decrease in the average tangential dimension of vessels near the widest part of adjacent rays (Tables S4 and S5). For both locations, the differences remained statistically significant even when trees were divided into two diameter classes (Tables S13 and S14).

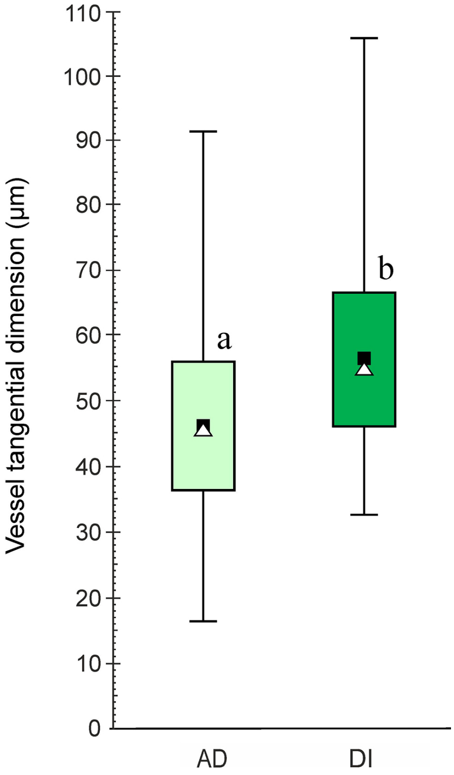

Fig. 3. Measurements of vessel tangential dimensions in the secondary xylem of Norway maple (*Acer platanoides* L.) calculated for two scenarios: (AD) vessels measured at the location corresponding to the greatest width of the adjacent rays, and (DI) the same vessels measured at a distance of 40–45 μm above the point where rays terminate. The median (white triangle), mean (black square), standard deviation (box around the mean), and minimum–maximum range (whiskers) are shown. Different letters indicate statistically significant differences between paired variables (Wilcoxon signed-rank test, $p < 0.01$)

Analysis of ray width

The measurement results indicate that in the case of pedunculate oak earlywood the average ray width measured near the center of the adjacent vessel, typically at its widest point, was smaller by ca. 58% than measured 80–100 μm away from the vessel (closer to the trunk pith) (Fig. 4a; Table S6). In the case of pedunculate oak latewood the average ray width measured near the center of the adjacent latewood vessel (typically at its widest point) was smaller by ca. 38% than at a distance of 30–50 μm from the vessel (closer to the trunk pith, and thus in an ontogenetically older region) (Fig. 4b; Table S7).

Ray–width characteristics at both measurement locations – one closer to the trunk pith, away from the vessel, and the other near the center of the adjacent vessel, typically at its widest point – are presented for all analyzed cases, without distinguishing between earlywood and latewood vessel types, in Fig. 4c.

Results of Wilcoxon matched-pairs test (α = 0.01) indicate that, for both earlywood and latewood of pedunculate oak, there are statistically significant differences in ray width between analyzed locations – at some distance from the vessel (toward the trunk pith) and near the center of the adjacent vessel (Table S15).

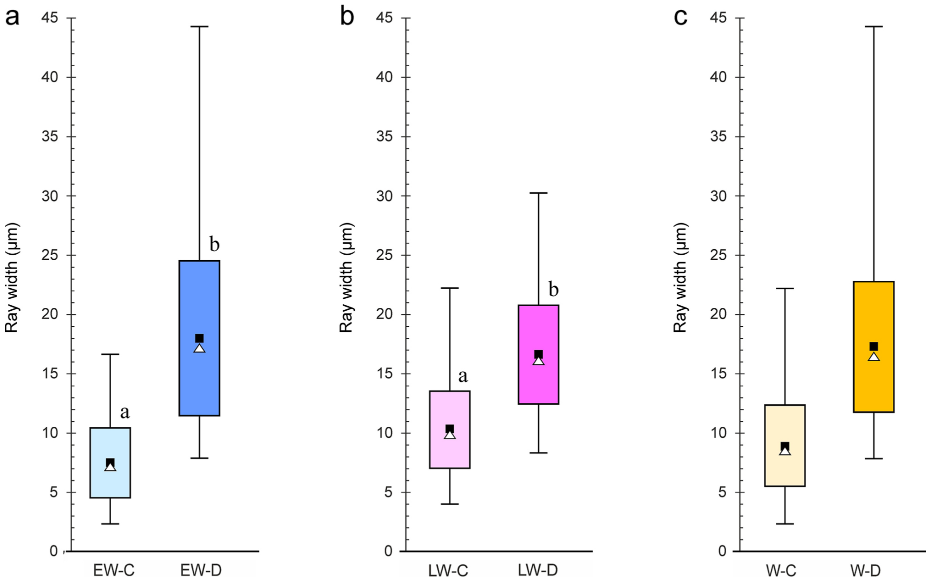

Fig. 4. Measurements of ray width in the secondary xylem of pedunculate oak (*Quercus robur* L.), calculated for six scenarios: (EW-C) rays measured near the center of an adjacent earlywood vessel; (EW-D) rays measured at a distance of 80–100 µm from the earlywood vessel toward the trunk pith; (LW-C) rays measured near the center of an adjacent latewood vessel; (LW-D) rays measured at a distance of 30–50 µm from the latewood vessel toward the trunk pith; (W-C) rays measured near the center of an adjacent vessel (whole wood, i.e., earlywood and latewood); (W-D) rays measured at a distance from the vessel toward the trunk pith (whole wood, i.e., earlywood and latewood). In a few cases, measurements were taken at slightly different distances (see the Methods section for details). The median (white triangle), mean (black square), standard deviation (box around the mean), and minimum–maximum range (whiskers) are shown. Different letters within a panel indicate statistically significant differences between paired variables (Wilcoxon signed-rank test, $p < 0.01$). Statistical tests were performed separately for each panel

Discussion

Rays, composed of horizontally arranged parenchymatous cells, and vessels, formed by functionally connected VEs, represent components of two distinct secondary xylem systems – the radial and axial systems (Gizińska et al., 2021). Both of them are essential for the proper functioning of this vascular tissue. These cell types exhibit significant structural and functional differences (Crang et al., 2018; Słupianek et al., 2021). Their hormonal regulation also differs: while VEs are primarily regulated by auxins and cytokinins, rays are controlled by the gaseous phytohormone ethylene, synthesized in the sapwood by maturing tracheary elements (Sorce et al., 2013; Aloni, 2013, 2021).

Previous studies have shown that specific relationships exist between the two components of the axial and radial systems. In 2011, Wilczek et al. examined anatomical sections of three angiosperm species – ivory terminalia (*Terminalia ivorensis* A. Chev.), Japanese wisteria (*Wisteria floribunda* (Willd.) DC.), and *Millettia laurentii* De Wild. – and observed that rays may act as obstacles to VE growth, causing growth anisotropy (i.e., VE growth may be stronger in the opposite direction relative to the ray) and, as a result, tangential vessel deflection. However, as noted by Miodek et al. (2021), not all local tangential deflections of vessels can be explained solely by this phenomenon. Analysis of the secondary xylem of angiosperm trees differing in porosity type (Gizińska et al., 2021) indicated that the vicinity of rays restricts the intrusive growth of VEs and that VE located in direct vicinity of a ray may grow symplastically in tangential direction. The previously mentioned qualitative analysis of VE growth anisotropy (Wilczek et al., 2011) and the stated decrease in the contribution of VE intrusive growth near rays (Gizińska et al., 2021) led to a new question: does interaction with neighboring ray generally reduce VE growth in the tangential direction (i.e., is there a reduction in tangential growth of VE regardless of the growth type – intrusive or symplastic – and without considering growth anisotropy)? Quantitative anatomical and statistical analyses of the secondary xylem of Norway maple confirmed the expected relationship: the direct proximity of rays results in a decrease in the mean tangential dimension of vessels in both older and younger trees (Fig. 3), supporting the first hypothesis of the present study – that rays act as a physical constraint on the tangential enlargement of VEs. Tangential dimensions of vessels measured near the widest part of adjacent rays and at a distance from ends of rays differ significantly. This indicates that vessels are considerably broader at a distance of 40–45 µm from ends of rays (Tables S3–S5, and

S12–S14). Therefore, it can be stated that: (1) rays act as obstacles to VE growth – in general, regardless of growth type, i.e. intrusive/symplastic; and (2) the proximity of rays does not completely inhibit the overall tangential growth of VEs, but it limits it to some extent. Growth of VEs also occurs toward the rays, which is associated with the formation of characteristic deflections of rays visible in transverse sections, which is particularly pronounced in the earlywood of ring-porous species (Gizińska et al., 2021). Not only are narrow (uniseriate/biseriate) rays deflected by neighboring vessels, but, as shown in this study, their mean width also decreases in the immediate vicinity of enlarged VEs (Fig. 4), supporting the second hypothesis – that VEs enlargement is associated with local changes in the width of the rays they encounter during tangential growth. As presented in Fig. 4 and Table S15, the width of oak rays near the centers of vessels is significantly smaller than the width of rays located at some distance from vessels (prior to VE formation from a developmental perspective). In the analysis of ray width, a distinction between earlywood and latewood was made. This division was applied because of the pronounced differences in vessel size between earlywood and latewood of ring-porous species (Richter & Dallwitz, 2000). It is well established that the size and distribution of vessels within annual growth rings play a crucial role in a plant's functioning and its adaptation to environmental conditions (Gizińska et al., 2015). For example, wider vessels tend to exhibit higher hydraulic conductivity, but also greater vulnerability to freezing-induced embolism (Davis et al., 1999; Utsumi et al., 1999; Hacke et al., 2017). In this study, a decrease in the average width of rays was observed in both wood types (earlywood and latewood). However, a greater reduction in average ray width was found in rays adjacent to wider earlywood vessels. The average difference between ray width prior to VE formation and measured near the center of the VE was 10.49 μm for earlywood and 6.29 μm for latewood. This may indicate that the larger the transverse size of the formed vessel, the greater its impact on ray width.

The analyses conducted in this study, together with previous findings on interactions between developing VEs and rays, suggest that rays may function as a mechanical buffering system for growing VEs. Specifically, VE growth occurs between the tangential walls of axial system cells (Hejnowicz, 2012; Miodek et al., 2021), which are more prone to separation than the tangential walls of radial system cells (Gizińska et al., 2021). Considering the assumptions of the tensile stress hypothesis (Kojs et al., 2023), which posits the presence of radial tensile stress in the cambium – demonstrated in ring-porous species through incisions of their cambial tissue (Hejnowicz, 1980) – one might expect that the degree of separation of the tangential walls of cells in the axial system is somehow regulated to prevent large tangential fractures within the zone of secondary xylem differentiation (particularly in the case of very wide VEs). This may be of particular importance, as tangential enlargement is often associated with the intrusive growth of a developing VE between numerous surrounding cells, leading to the separation of their tangential cell walls. As mentioned, in previous studies (Wilczek et al., 2011; Gizińska et al., 2021) the preservation of ray continuity in the vicinity of developed vessels was observed, which, on one hand, directly indicates differences in the susceptibility of axial and radial system cell walls to separation, but, on the other hand, may indirectly suggest a potential role of rays in controlling and preventing the formation of large fractures. This is particularly significant given the growing attention in recent years to the numerous functions performed by the parenchymatous cells of wood (including rays). The role of xylem parenchyma – comprising ray cells and parenchymatous cells of the axial system – is highly diverse. These cells connect the xylem and phloem; perform storage functions (e.g., of water and carbon, particularly in the form of starch, glucose, sucrose, and fructose); contribute to defense mechanisms within trees; provide mechanical support (e.g., by maintaining turgor pressure and rigidity); and participate in the regulation of xylem hydraulic conductivity and embolism repair (as discussed in Słupianek et al., 2021). Furthermore, rays may influence neighboring cells of the axial system. For example, Xue et al. (2018) investigated the effect of rays on wood shrinkage during drying and found that wood fibers in the immediate vicinity of rays exhibit less shrinkage than those located farther away. Among the many described properties and functions of rays, their mechanical role within wood is particularly noteworthy. Burgert et al. (1999), for instance, analyzed the mechanical function of rays in European beech (*Fagus sylvatica* L.) and demonstrated that rays act as mechanically functional and adaptive tissue when considered in the transverse plane. They also emphasized the importance of relative ray volume, orientation, and distribution, demonstrating that these parameters play a key role in the mechanical adaptation of the tree (Burgert et al., 1999). The role of rays in tree biomechanics is particularly prominent, as studies have shown that they contribute to the radial strength of wood. In an investigation of European beech with isolated rays, Burgert and Eckstein (2001) found that rays possess distinctly high radial tensile strength, which is significantly greater than that of the axial tissue. These findings may suggest that rays play a crucial role in modulating excessive radial tensile stress resulting from the swelling of living cells, primarily those of the secondary phloem (Kojs et al., 2023). The high radial tensile strength of rays (Burgert & Eckstein, 2001) appears to support the hypothesis that rays play controlling role in the differentiation of secondary xylem (Gizińska et al., 2021) in two ways, particularly regarding ray–vessel interactions: (1) by preventing the formation of large fractures caused by the separation of numerous tangential walls of axial system cells; and (2) by moderately limiting the overall tangential growth of VEs, regardless of growth type.

In the context of the observed mutual influence between VEs and rays on their tangential dimension/width, another important aspect is the difference in the timing and extent of lignification of these two wood components. Ray cells are typically living cells within the active xylem; their walls may be lignified, but they are relatively thin compared to the dead vessels, which usually have thick, strongly lignified walls (Evert, 2006; Słupianek et al., 2021). Observations of cell walls during the growing season using fluorescence technique revealed temporal differences in the lignification of axial and radial system cells (Miodek et al., 2025a). Ray sectors exhibit delayed lignification compared to axial system sectors. For example, in tissues of black locust (*Robinia pseudoacacia* L.), unlignified portions of rays are visible within the developing annual growth ring, and their lignification is clearly delayed relative to neighboring axial system cells (see Fig. 6 in Miodek et al., 2025a). Interestingly, a previous study examining the relationship between axial and radial system cells within the vascular cambium and developing secondary xylem showed that these systems dynamically interact by adjusting their tangential dimensions. This coordination enables the harmonious growth of both tissue types in a circularly symmetrical manner. Specifically, it was demonstrated that the growth of wood fibers within axial system sectors does not disrupt the circular symmetry of the tree trunk, owing to compensatory changes in ray characteristics (ray tangential dimension) within the vascular cambium and the xylem differentiation zone (Miodek et al., 2025a). Taking into account all the information presented, the reduction in average width of narrow oak rays observed in this study may hypothetically be associated with three mechanisms. The first is strong stretching in the radial direction; according to the tensile stress hypothesis (Kojs et al., 2023), high radial tensile stress occurs in areas of future VE formation. In this scenario, the influence of vessel development on the width of neighboring rays would not be direct, as both events – VE development and ray narrowing – would result from the local occurrence of strong radial tensile stress. A second possible mechanism is the direct compression of a ray by a tangentially enlarging VE, driven by turgor pressure. The third explanation is the direct compression of a non-lignified ray by the newly formed, highly stiffened structure of an already lignified VE in its immediate vicinity. It should be noted that none of these theoretical explanations necessarily exclude the others.

It is also worth emphasizing that, in mature oak wood, in addition to the analyzed, frequently occurring uniseriate and biseriate rays – often deflected by neighboring vessels – very wide rays occasionally occur (Richter & Dallwitz, 2000). Although these rays were not the focus of the present study, the literature indicates that multiseriate oak rays (10-30-cells wide) tend to follow a rectilinear course (Kokociński, 2005). Consequently, these wide rays do not exhibit the pronounced deflections observed in narrower rays that contact vessels. Investigating the interactions between vessels and wide, multiseriate rays could provide a valuable next step in understanding vessel–ray relationships. The question remains whether interactions between such wide rays – which likely exhibit substantially higher radial tensile strength – and vessels forming nearby would be detectable at all. It is possible that the wide, multiseriate rays of pedunculate oak act as such a robust barrier that any influence of vessel development is entirely imperceptible.

From the above considerations, a picture emerges of the mutual dependencies among the developing components of secondary xylem. Given the established role of rays in the biomechanics of the tree stem (Burgert et al., 1999; Burgert & Eckstein, 2001; Reiterer et al., 2002), as well as the mechanism of VE growth – specifically, growth between the tangential walls of neighboring axial system cells (Gizińska et al., 2021; Miodek et al., 2021) – it appears that establishing the mechanical basis of the processes occurring in the vascular cambium and differentiating secondary xylem remains an intriguing subject for future investigation. It is known that many processes and events within these and other plant tissues depend on the mechanical stress pattern (Hamant et al., 2008; Heisler et al., 2010; Nakayama et al., 2012). For example, the orientation of the division plane may be related to mechanical stress (Lintilhac & Vesecky, 1984; Zhou et al., 2006; Robinson, 2021). Unraveling the mechanical background would be of great interest for advancing our understanding of the relationships between developing VEs and rays. Interestingly, if the growth of VEs occurs under conditions of radial tensile stress, as postulated in the literature (Hejnowicz, 1980; Kojs et al., 2023), one might expect that VE growth and differentiation induce local changes in the mechanical stress pattern (Miodek et al., 2021, 2025b), presumably also influencing their immediate surroundings. This could explain the interplay between xylem rays and tangential enlargement of VEs.

Conclusions

The present study provides further evidence of the complex relationship between the two wood systems – axial and radial – by examining how developing vessel elements interact with the rays they encounter. During development, vessel elements increase in tangential dimension, however our results show that rays restrict this tangential growth irrespective of growth type (intrusive or symplastic), as evidenced by a reduction in the mean tangential dimension of vessels at points of contact with rays. Vessel development, in turn, is associated with a local reduction in the width of the contacted ray, accompanied by tangential deflection of the ray. Thus, both hypotheses tested in this study were confirmed. Our findings provide new insights into the interplay between developing vessel elements and rays, contributing to a deeper understanding of the axial and radial components of secondary xylem. Given the pronounced structural differences of these systems – observable in transverse, radial, and tangential planes – and their derivation from two distinct types of cambial initials, the observed interactions suggest that, beyond their well-established roles in vascular tissues, additional functional relationships exist between the axial and radial systems.

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