



Wood fiber bodies of *Robinia pseudoacacia* increase their transverse surface area without cell wall expansion

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Abstract

Fibers are a key component of wood, providing mechanical support to woody plants. Understanding their development is crucial for both tree function and industrial use. We investigated how the transverse surface area of wood fiber bodies increases in *Robinia pseudoacacia* L. Samples of vascular cambium and differentiating secondary xylem were collected and sectioned using a Tesla ultramicrotome. Zones containing cambium and wood fibers at different stages of differentiation were analyzed for cell transverse surface area, cell wall perimeter, cell width, and thickness. The shapes of fiber bodies were also examined and the obtained data were compared with mathematical considerations regarding the shape of geometric objects and the impact of shape changes on transverse surface area. Our findings show that wood fiber development involves a gradual shape change from rectangular to round, accompanied by increasing thickness and decreasing width. The increase in transverse surface area results from shape changes rather than cell wall growth in the transverse plane. This is supported by the nearly constant cell wall perimeter across the differentiation zones. Obtained results have important consequences for the analysis of xylogenesis in angiosperms, as they stay in sharp contrast to the common understanding of events occurring within differentiating xylem.

Introduction

Wood fibers are one of the cell types found in the secondary xylem of angiosperm trees. They originate from fusiform initials of the vascular cambium (the secondary meristem responsible for stem growth in girth), and are characterized by extensive

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axial growth, which makes them distinctly longer than cambial initials (Wilczek et al. 2018; Majda et al. 2021; Miodek et al. 2023). It is worth noting that evolutionarily younger (often described as more advanced) dicotyledonous angiosperm trees have developed new types of wood cells not found in evolutionarily older conifers—specifically wood fibers and vessel elements (Evert 2006; Esteban et al. 2024). As a result, substantial differences exist in the anatomical structure of tissues produced by the vascular cambium of coniferous versus angiosperms. Considering the evolutionary hormonal regulation of xylem differentiation, it has been proposed that in higher (angiosperm) plants, a differentiation occurred in the cellular response to inducing signals: auxin induces the formation of vessel elements, while gibberellin—in combination with auxin—stimulates the development of wood fibers. This contrasts with the induction of tracheids in more primitive plants, where a combined action of auxin and gibberellin triggers their formation (it is thought that both angiosperm cell types evolved from tracheids) (Aloni 2015, 2021). With the emergence of these two distinct cell types, the functions previously performed by tracheids diverged. In angiosperm wood, vessels are responsible for the conduction of water and minerals, whereas fibers (particularly libriform fibers) provide mechanical support (Kim et al. 2014; Spicer 2016; Ziemińska 2023). A typical libriform fiber of secondary xylem (wood) has a thick, lignified secondary cell wall and consists of distinctly elongated tips, and a fiber body (see: Fig. 1a, b). The fiber body can be understood as the main, central part of the fiber, directly derived from a cambial cell, and distinctly wider than axially elongating tips (Wilczek et al. 2018; Miodek et al. 2023). Protrusions (lateral expansions) may be found on these tips. A study conducted on tissues and macerates of *Lonchocarpus sericeus* (Poir.) Kunth ex DC. which has a double-storied cambium structure, showed that the mean distance between observed protrusions corresponds to the mean height of tiers of axial system cells (Jura-Morawiec et al. 2008). In this type of cambium, both axial system cells and rays are arranged in characteristic, regular tiers when observed in tangential sections (Schmitt et al. 2016). In the case of storied vascular cambium, only the cells of the axial system form regular tiers (see Fig. 1c, showing storied cambium of *Robinia pseudoacacia* L.), whereas in non-storied vascular cambium, both rays and axial system cells are unevenly distributed (Wilczek-Ponce et al. 2021). In studies concerning the growth and differentiation of wood fibers, research on species with storied or double-storied cambia is particularly valuable, as these types of cambia deposit axial system derivative cells arranged in tiers. When a cross-section is cut through the middle part (or near the middle) of a fusiform initial tier, it becomes possible to distinguish between the fiber bodies deposited by the fusiform initials visible in the cross-section and the axially elongated tips of other fibers deposited by initials in tiers located above or below the examined tier. In the case of derivatives formed by non-storied cambia, making such a distinction can be more challenging. When considering the growth mechanism of individual cambial derivatives, it is important to note that in evolutionarily younger angiosperm trees, significant changes in the arrangement of radial cell files occur in the xylem differentiation zone (Fig. 1d). This is caused by the strong lateral expansion of vessel elements and the intensive axial growth of wood fiber tips (Wilczek et al. 2018; Gizińska et al. 2021; Miodek et al. 2021a, 2025; Esteban et al. 2024). In contrast, coniferous wood consists mainly of tracheids, the arrangement of which—

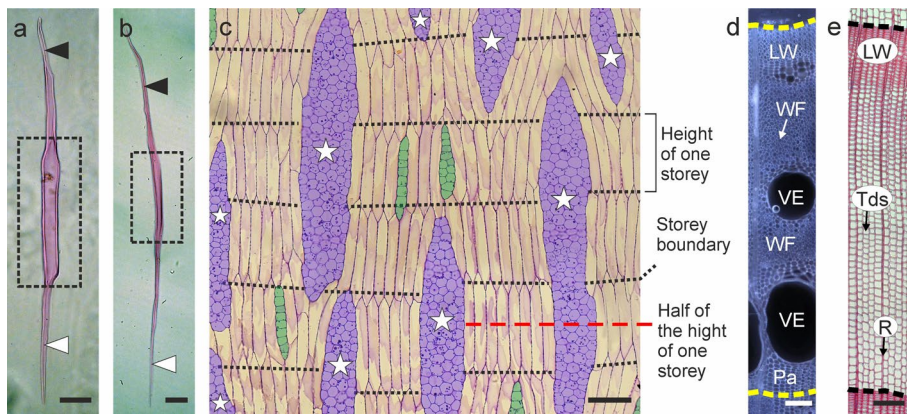


Fig. 1 General characteristics of vascular cambium and chosen cambial derivatives. **a, b** Individual wood fibers of macerated *Robinia pseudoacacia* L. secondary xylem. Wood fiber bodies are enclosed by the dashed black rectangles. Black, and white arrowheads—wood fiber apical and basal tips respectively. **c** Tangential section of storied vascular cambium of *R. pseudoacacia*. Boundaries of stories of axial system cells are indicated by black dashed lines. Large, multiseriate rays are indicated by white, five-pointed stars. Smaller, uni- to biseriate rays are without the stars. **d, e** Transverse sections of wood of *R. pseudoacacia* (**d**) and *Picea abies* (L.) H.Karst (**e**) showing fragments of annual growth rings. Growth ring boundaries are indicated by dashed lines (**d, e**). *Pa* parenchyma, *R* ray, *Tds* tracheids, *VE* vessel element, *WF* wood fiber, *LW* latewood. Staining: **a, b** safranin O; **c** PAS and toluidine blue; **d** no staining (autofluorescence of lignin); **e** safranin O and astra blue. Scale bars: **a–c** 40 μ m; **d** 50 μ m; **e** 20 μ m

assuming no disturbances in the functioning of the meristematic tissue—is highly regular and largely reflects the arrangement of cambial cells (Evert 2006; Zelenov et al. 2024; Yang et al. 2025) (Fig. 1e). The basic shape of fusiform cambial cells (note that a broad definition of vascular cambium is used in this paper, including both initial cells and mother cells; for more details see e.g. Miodek et al. 2021a) is thought to be a tetrahedron (Hejnowicz 2012). This means that in cross-section, these cells have six walls: two tangential and four radial cell walls. Because the edges separating the two radial walls on either side of the initials are often barely visible in cross-sections, these walls are typically treated as a single wall on each side (the left and right radial walls). As a result, a typical cambial cell appears as a rectangle flattened in the radial direction when viewed in cross-section. The tracheids they deposit (Fig. 1e) tend to have a similar shape—either hexagonal or rectangular. Differences in radial dimensions and cell wall thicknesses between the initial cells and their derivatives should be taken into account, as well as the exception of reaction wood tracheids, which have a distinctly rounded appearance. In contrast to typical coniferous tracheids, angiosperm fiber bodies develop a more rounded shape when viewed in transverse section during their formation (Wilczek et al. 2018). That is fiber differentiation from xylem mother cells involves a shape change from rectangular to nearly round. Therefore, it becomes necessary to consider the mathematical background (geometric formulas) related to the shape changes of the analyzed objects—differentiating wood fiber bodies—in order to uncover the rules governing their enlargement. The aim of this study was to clarify how fiber bodies increase their transverse surface area with increasing distance from the cambial initial layer during the differentiation process.

To address this question, changes in the transverse surface area (cross-sectional area) of fiber bodies were compared to their perimeters, thickness (radial dimension), and width (tangential dimension) across successive zones. Changes in the shape of fiber bodies were also analyzed. The resulting values were then compared with the geometric background associated with the considered cell shapes. This approach allowed us to determine whether the increase in the transverse surface area of the fiber bodies results from changes in cell shape itself or from the growth of the fiber body walls in the transverse plane.

Materials and methods

Plant material

Robinia pseudoacacia L., a ring-porous angiosperm tree species characterized by large-diameter earlywood vessels (Miodek et al. 2020), was selected as the study object for several reasons. First, it is representative of angiosperm tree species that produce a high proportion of wood fibers in their annual growth rings. Second, its vascular cambium exhibits a storied structure (Fig. 1c). As previously explained, the presence of a storied structure facilitates the analysis of the arrangement of cambial derivative cells after they leave the vascular cambium. Another reason for selecting *R. pseudoacacia* is its vigorous growth and strong resistance to unfavorable environmental conditions, both biotic and abiotic (Kato-Noguchi and Kato 2024; Zheng et al. 2024; Zhang et al. 2025). It is also important to note that *R. pseudoacacia* produces commercially valuable hardwood. This species is capable of forming commercial forests even under unfavorable climate change conditions, which strongly impact other forest-forming species (Vítková et al. 2017; Rebola-Lichtenberg et al. 2021).

Plant tissues—vascular cambium along with secondary xylem—were collected from the trunks of *R. pseudoacacia* trees growing in the Silesian Botanical Garden (Poland, temperate climate) during the 2013 growing season (July and August). Three trees with normally developed, single trunks were selected for analysis. They were approximately 20 cm in diameter at breast height, 12 m tall, and about 25 years old. The collected samples were fixed in a glycerol and ethanol (1:1) solution or glutaraldehyde.

Preparation of cross-sections for anatomical analysis

The collected material was dehydrated in ethanol and propylene oxide, and gradually saturated with Epon. The samples embedded in Epon were then subjected to temperatures of 35 °C, 45 °C, and 60 °C. After resin polymerization, the material was sectioned using a Tesla ultramicrotome, and thin cross-sections (approximately 3.5 µm) containing the vascular cambium and differentiating secondary xylem were obtained. These sections were then stained with PAS and toluidine blue, and mounted in Euparal (Miodek et al. 2022, 2023). Observations of stained material were performed using bright field microscopy (Olympus BX41). A detailed anatomical analysis of fiber body development was carried out, including measurements according

to the methodology described below. The high level of measurement accuracy was ensured by the quality of the preparations obtained using the Epon method (Włoch and Połap 1994).

Measurement methodology

Nine fragments of *R. pseudoacacia* tissues were selected for anatomical analysis, including precise measurements of cell transverse dimensions. To obtain reliable results, it was necessary to select fragments showing undisturbed growth of wood fibers—that is, radial files of cells in which, and in the vicinity of which, there were no: (a) developing vessel elements and/or tracheids; (b) large-scale rearrangement of cambial initial cells; (c) structural irregularities caused by external and/or internal factors.

In each fragment, four zones were designated according to the following rules for classifying cells: (1) *Zone 1* (vascular cambium; no fiber tips): cells belonging to the vascular cambium, showing the greatest degree of radial flattening, and which have no contact with the intrusively growing tips of wood fibers. (2) *Zone 2* (low amount of wood fiber tips): derivative cells located adjacent to the intrusively growing tips of wood fibers, retaining most of the tangential and radial cell wall contacts with neighboring cells of the same story. (3) *Zone 3* (medium amount of wood fiber tips): a group of cells located farther from the initial layer of the vascular cambium, where most of the radial cell walls of fiber bodies have become separated. (4) *Zone 4* (high amount of wood fiber tips): a group of cells located even farther from the initial layer of the vascular cambium, where most of the tangential and radial cell walls of fiber bodies have become separated. Note that in the analyzed zones, the cell walls are not lignified, and secondary cell wall deposition is not visible. An example of an analyzed fragment with designated zones is shown in Fig. 2. All the studied fragments are presented in Supplementary Information Figures S1–S9. In each case, four to eight radial rows of cells were examined. In each radial file, four cells were designated in each zone for measurement, resulting in sixteen cells per radial row. In total, 832 cells were analyzed. Measurements of cambial cells and differentiating fiber bodies involved: (1) cell transverse surface area (TSA); (2) cell wall perimeter (CWP); (3) cell width (CW; tangential dimension); and (4) cell thickness (CT; radial dimension). CW and CT were measured in central part of a cell. The results of all measurements performed on *R. pseudoacacia* tissues are presented in Supplementary Information Tables S1–S18. The high quality of the digitized anatomical sections, combined with the use of the analysis extension tool in Adobe Photoshop CS6 Extended version 13.0 × 64 (<https://www.adobe.com>), enabled precise measurements during the primary wall phase (the developmental period in which only the primary cell wall is present and undergoing modifications).

For each zone, and within each *R. pseudoacacia* tissue fragment analyzed, cell circularity was calculated (based on average values obtained for these zones), in order to determine the extent to which the shapes of the observed objects approach an ideally rounded form. Cell circularity (C) was calculated using the formula: $C = 4\pi A / P^2$, where A is the area (measured as TSA) and P is perimeter (measured CWP); the more circular profile a cell has, the more the cell circularity approaches a value of 1.0

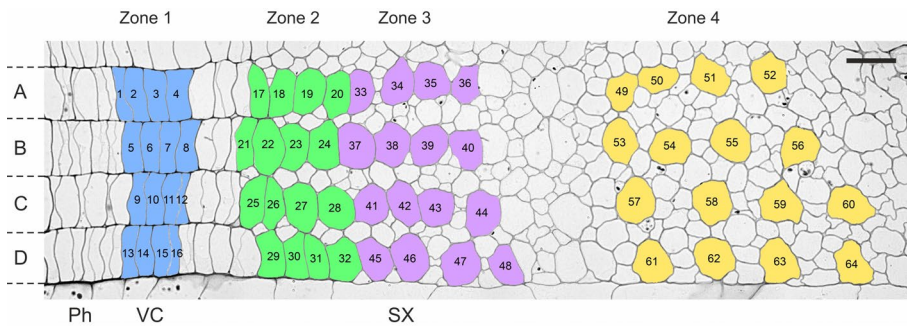


Fig. 2 Transverse section of the vascular cambium and secondary xylem of *Robinia pseudoacacia* L. with designated zones and numbered cells. In this case, four radial files **A–D** were analyzed, with a total of 64 cells examined (four zones; each containing sixteen cells). Four zones were designated for analysis: zone 1 (cells nos. 1–16); zone 2 (cells nos. 17–32); zone 3 (cells nos. 33–48), and zone 4 (cells nos. 49–64). For a detailed description of zone designation see the main text. *Ph* secondary phloem, *VC* vascular cambium, *SX* secondary xylem. Scale bar = 20 μ m

(Peh et al. 2013). Additionally, the average value of cell circularity was calculated for zones 1–4 across all samples.

Statistical analyses

Measurement results (Supplementary Information Tables S1–S18) were subjected to statistical analyses using PQStat ver. 1.8.6 software (PQStat Software Inc., Poznań/Plewiska, Poland). The Shapiro-Wilk test ($\alpha = 0.05$) (Supplementary Information Tables S19–S27), and histogram analyses were performed to determine whether the analyzed data followed a normal distribution. Some of the data did not show a normal distribution. Therefore, the Mann-Whitney *U* test (independent model; $\alpha = 0.05$) was applied to determine whether the values obtained for the considered categories—TSA, CWP, CW, and CT—differed significantly between the compared zones, taking into account the developmental sequence (i.e., zone 1 vs. 2, zone 2 vs. 3, zone 3 vs. 4, and zone 1 vs. 4).

Results

In the vascular cambium (zone 1), a regular arrangement of cells is visible. The geometric shape of the cambial cells most closely resembles a rectangle, with elongated tangential walls and shorter radial walls (as seen in cross-section). The walls of the cambial cells exhibit varying degrees of undulation (the walls are curved to different extents), thereby locally deviating from the ideal parallel alignment with the tangential surface of the stem (in the case of tangential walls) or from the ideal perpendicular alignment with the tangential surface of the stem (in the case of radial walls). Within the designated zone 1, all tangential and radial walls of cambial cells are in contact with one another, except for small, local rearrangements within the initial layer of the cambium. For example, this rearrangement is evident in the eighth ana-

lyzed fragment of *R. pseudoacacia* tissues (see Supplementary Information Fig. S8). As one moves away from the initial layer, and thus from zone 1, the contact surface between the walls of individual fiber bodies decreases. By zone 4, many of the analyzed fiber bodies no longer make contact with each other (Fig. 2). This reduction in cell contacts is accompanied by changes in the shape of the differentiating fiber bodies, which begin to take on a more rounded form (to see described changes see Supplementary Information Figs S1–S9). When analyzing cell circularity calculated for individual samples, it can be observed that circularity is lowest in zone 1 (ranging from 0.41 to 0.46), increases in zone 2 (0.54–0.69), and reaches its highest values in zones 3 (0.63–0.76) or 4 (0.65–0.77). The differences in circularity between zones 3 and 4 are minimal within individual samples (Table 1). The average cell circularity across all samples is 0.43 in zone 1, 0.60 in zone 2, and 0.71 in both zones 3 and 4.

Changes in TSA, CWP, CW, and CT within the designated zones are described below. The results of measurements taken from nine analyzed tissue fragments of *R. pseudoacacia*—including the average value, standard deviation, and minimum and maximum values obtained for each zone in each tissue fragment—are presented in Supplementary Information Table S28. Supplementary Information Tables S29–S37 contain the results of the Mann–Whitney *U* test ($\alpha = 0.05$) performed for comparisons of all zones considered (zone 1 vs. zone 2, zone 2 vs. zone 3, zone 3 vs. zone 4, zone 1 vs. zone 4) within all tissue fragments analyzed.

Transverse surface area of a cell

The average cell TSA (calculated from all combined analyzed tissue fragments) changes from $95.95 \mu\text{m}^2$ in zone 1 to $135.49 \mu\text{m}^2$ in zone 2, $158.78 \mu\text{m}^2$ in zone 3, and $155.59 \mu\text{m}^2$ in zone 4. This represents a 62% increase in average TSA from zone 1 to zone 4 (Fig. 3). For all *R. pseudoacacia* tissue fragments examined in the study, cell TSA showed a statistically significant increase from zone 1 to zone 4 (Table 2; Supplementary Information Tables S29–S37). It should be noted that in tissue fragments 1–5, 8, and 9, the highest average TSA was actually measured in zone 3. In six of these seven cases, the difference in average TSA between these two zones did not exceed $9.26 \mu\text{m}^2$. Notably, in three of these instances, the average cell TSAs were very similar to each other (Fig. 4; Supplementary Information Table S28).

Table 1 Obtained cell circularity value for each zone considered, i.e., zone 1—vascular cambium; zone 2—low amount of wood fiber tips; zone 3—medium amount of wood fiber tips; zone 4—high amount of wood fiber tips, in each analyzed tissue fragment (1–9) of *Robinia pseudoacacia* L.

Zone	Tissue fragment analyzed								
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
1	0.46	0.46	0.41	0.42	0.41	0.41	0.44	0.45	0.44
2	0.56	0.60	0.56	0.55	0.57	0.61	0.54	0.67	0.69
3	0.71	0.74	0.69	0.72	0.66	0.63	0.72	0.76	0.76
4	0.70	0.71	0.66	0.73	0.66	0.65	0.71	0.76	0.77

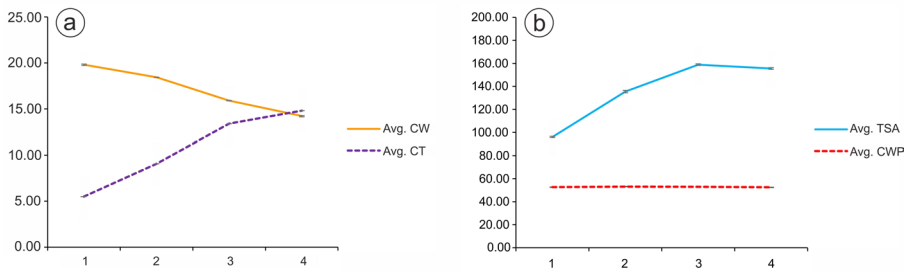


Fig. 3 Graphs showing combined data for all analyzed tissue fragments of the vascular cambium and secondary xylem of *Robinia pseudoacacia* L. The graph on the left **a** shows the combined average cell width (Avg. CW) and average cell thickness (Avg. CT) across four consecutive zones. The graph on the right **b** shows the combined average cell transverse surface area (Avg. TSA) and average cell wall perimeter (Avg. CWP) across the same four zones. In graph **a**, the values on the y-axis are in μm . In graph **b**, the values on the y-axis are in μm^2 for Avg. TSA and in μm for Avg. CWP. The consecutive zones (1–4) are indicated on the x-axis. Standard error is shown

Cell wall perimeter

The average CWP (calculated from all combined analyzed tissue fragments) changes from 52.68 μm in zone 1 to 53.15 μm in zone 2, 52.94 μm in zone 3, and 52.51 μm in zone 4, representing a 0.3% decrease from zone 1 to zone 4 (Fig. 3). For CWP, no statistically significant differences were observed between zone 1 and zone 4 in eight out of nine tissue fragments (Table 2; Supplementary Information Tables S29–S37). The average CWPs across consecutive zones showed only minor differences within each tissue fragment (Fig. 4; Supplementary Information Table S28).

Cell width

The average CW (calculated from all combined analyzed tissue fragments) changes from 19.80 μm in zone 1 to 18.44 μm in zone 2, 15.90 μm in zone 3, and 14.23 μm in zone 4, representing a 28% decrease from zone 1 to zone 4 (Fig. 3). A consistent decrease in average CW was noted in all analyzed *R. pseudoacacia* tissue fragments (Fig. 4; Supplementary Information Table S28). In all nine fragments, the change in CW between zone 1 and zone 4 was statistically significant (Table 2; Supplementary Information Tables S29–S37).

Cell thickness

The average CT (calculated from all combined analyzed tissue fragments) shows a pronounced increase (approximately threefold) from zone 1 to zone 4, with progressively higher values in each subsequent zone (Fig. 3). In zone 1, the average CT is 5.49 μm , in zone 2–9.06 μm , in zone 3–13.41 μm , and in zone 4–14.80 μm . This represents a 170% increase in average CT from zone 1 to zone 4. A consistent increase in average CT was observed in all analyzed tissue fragments (Fig. 4; Supplementary Information Table S28). In all nine fragments, the change in CT between zone 1

Table 2 Obtained P values of Mann-Whitney U test ($\alpha = 0.05$) of all analyzed tissue fragments (1–9) of *Robinia pseudoacacia* L. These values relate to comparison between zone 1 and zone 4 within indicated tissue fragments

Zone 1 vs. 4	Tissue fragment analyzed								
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
TSA	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100
CWP	0.361643	0.163626	0.738964	1.000000	0.754354	0.800301	0.159609	0.388950	0.002922
CW	0.000100	0.000100	0.00010	0.00010	0.00010	0.00010	0.00010	0.00010	0.00010
CT	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100	0.000100
TSA cell transverse surface area, CWP cell wall perimeter, CW cell width, CT cell thickness									

and zone 4 was statistically significant (Table 2; Supplementary Information Tables S29–S37).

Discussion

Theoretical framework for cell geometry

Observations indicate that the differentiation of cambial cells into fiber bodies is associated with a change in cell shape as they exit the vascular cambium. As the distance from the vascular cambium (designated as zone 1) increases, fiber bodies begin to take a more rounded form. This aligns with observations of the shape of mature wood fibers, which have thick secondary cell walls, in *R. pseudoacacia* wood (Wilczek et al. 2018). Since a gradual transition from a rectangular to a more rounded shape occurs between zones 1 and 4, the necessary mathematical concepts related to the geometry of these structures are introduced below.

To assess the impact of shape transformation on surface area while maintaining a constant perimeter, consider a hypothetical case where a rectangle is transformed into a circle without altering its perimeter. The question arises: does the surface area of the resulting shape change, even though the perimeter remains unchanged? The answer is affirmative—the surface area does change. This can be demonstrated through a comparison of the geometric properties of a rectangle and a circle. Let the rectangle have side lengths a and b . Its perimeter is given by: $P_{\text{rectangle}} = 2a + 2b$. The surface area of the rectangle is $A_{\text{rectangle}} = a \times b$. Assuming that the rectangle is transformed into a circle while preserving its perimeter, the circumference of the resulting circle can be expressed as: $P = 2\pi r$. Solving for the radius r , we obtain $r = P/2\pi$. The surface area of the circle is then given by: $A_{\text{circle}} = \pi r^2 = \pi \times (P/2\pi)^2 = \pi \times P^2/4\pi^2 = P^2/4\pi$. For comparison, the surface area of the original rectangle is: $A_{\text{rectangle}} = a \times b$ and the surface area of the transformed circle is: $A_{\text{circle}} = P^2/4\pi$. To compare these surface areas in a biologically relevant context, consider a rectangle representing a cambial derivative cell at the point of exit from the vascular cambium. This analysis is based on transverse sections of cells typical of *R. pseudoacacia*, excluding cells at the onset of vessel element differentiation. Prior studies have shown that in angiosperm tissues, cells destined to become vessel elements initiate significant lateral expansion at the boundary between the vascular cambium and the differentiation zone (Miodek et al. 2021a). For this example, let the dimensions of the rectangular cell be: $a = 10 \mu\text{m}$, and $b = 20 \mu\text{m}$ (Miodek et al. 2021b; Wilczek-Ponce et al. 2021). Using the previously defined dimensions, the perimeter of the rectangle is calculated as follows: $P_{\text{rectangle}} = 2 \times 10 \mu\text{m} + 2 \times 20 \mu\text{m} = 60 \mu\text{m}$. The surface area of this rectangle is: $A_{\text{rectangle}} = 10 \mu\text{m} \times 20 \mu\text{m} = 200 \mu\text{m}^2$. As established earlier, the comparison is based on maintaining an equivalent perimeter during the transformation from a rectangle to a circle. Thus, the perimeter of the corresponding circle is also: $P_{\text{circle}} = 60 \mu\text{m}$. The surface area of a circle with this perimeter is calculated using the formula: $A_{\text{circle}} = P^2/4\pi = (60 \mu\text{m})^2/4 \times 3.14 = 3600 \mu\text{m}^2/12.56 = 286.62 \mu\text{m}^2$. This comparison demonstrates that, for a given perimeter P , the surface area of a circle—expressed as $P^2/4\pi$ —is always greater than the surface area of a rectangle with the same perimeter. This phenom-

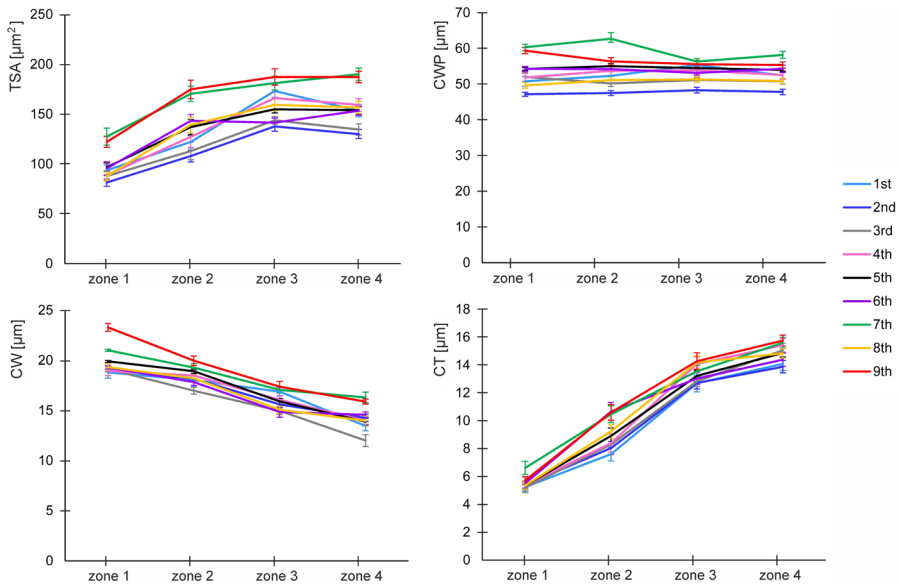


Fig. 4 Average cell transverse surface area (TSA), cell wall perimeter (CWP), cell width (CW), and cell thickness (CT) across four consecutive zones in nine tissue fragments of *Robinia pseudoacacia* L. Analyzed fragments are indicated on the right (1st to 9th). Standard error is shown

enon arises from the geometric principle that the circle represents the most efficient shape for maximizing surface area under a fixed perimeter constraint (Howards et al. 1999). In the specific example analyzed here, transforming a rectangular object into a circular one (while maintaining the same perimeter) results in an increase in surface area from $200 \mu\text{m}^2$ to $286.62 \mu\text{m}^2$, corresponding to an increase of about 43%.

Theoretical considerations vs. obtained results

To contextualize the above mathematical considerations within the framework of cell growth, consider a hypothetical scenario in which a cell alters its shape from a rectangular to a circular form, as viewed in cross-section. In such a case, the primary cell wall may not require expansion to achieve an increase in transverse surface area (TSA). That is, an enlargement of the TSA can occur without actual growth of the cell wall in either the tangential or radial direction. With this understanding, attention can now be directed to the developmental changes that occur during the differentiation of cambial derivatives on the secondary xylem side. From an anatomical perspective, distinct stages can be identified in the development of secondary xylem cells originating from the initial cells of the vascular cambium. Mitotic divisions of these initial cells give rise to what are termed xylem mother cells. It is important to acknowledge that the terminology associated with the vascular cambium varies across the classical developmental and anatomical literature (Wilson et al. 1966; Larson 1994; Lachaud et al. 1999; Hejnowicz 2012; Miodek et al. 2021a; Groover 2023). For the sake of clarity and consistency, the present study adopts a broad definition of the vascu-

lar cambium, encompassing not only the cambial initials but also the mother cells of both secondary xylem and secondary phloem (Hejnowicz 2012; Miodek et al. 2021a). These two cell types are frequently considered components of the cambial zone, as described in several recent studies (da Silva et al. 2023; Moshchenskaya et al. 2023; Pace et al. 2023; Tiyyasa et al. 2024; Zhao et al. 2024; Miodek et al. 2025). After leaving the vascular cambium and cessation of cell divisions, cells deposited on the xylem side are thought to undergo the substantial radial enlargement, subsequently entering the maturation phase, which involves, among other processes, the deposition of secondary cell walls (Wilson et al. 1966). Radial expansion also occurs within the vascular cambium itself, as cambial initials divide and subsequently grow to their pre-division size within the secondary meristem (Miodek et al. 2021b). However, cells that enter the radial expansion zone typically exhibit more pronounced enlargement in the radial direction (Eckes-Shephard et al. 2022), which is accompanied by an increase in their transverse surface area (TSA). As demonstrated in the present study, the transverse shape of wood fibers—when compared to the vascular cambial cells from which they originate—undergoes a notable transformation. Specifically, the shape shifts from a predominantly rectangular form to a more circular or rounded profile. This transformation in cell shape is accompanied by a substantial increase in average CT, with a 170% rise observed between zone 1 and zone 4, as well as a 28% reduction in CW across the same zones. A more rounded cell profile is particularly evident in mature wood fibers characterized by thick secondary cell walls (Beck 2010; Wilczek et al. 2018). It may be hypothesized that, during development into fiber bodies, mother cells increase their perimeter through transverse expansion of the cell walls. However, the present analysis demonstrates that the average cell perimeter remains relatively constant throughout the developmental zones examined, with a mean value of approximately 53 μm across all tissue fragments. Furthermore, changes in the CWP between zone 1 and zone 4 were not statistically significant, with the exception of a single tissue fragment. This is consistent with the mathematical reasoning presented earlier, wherein alterations in cell shape may lead to an increase in total surface area (TSA) without a corresponding increase in cell wall perimeter (CWP). Notably, in zone 3 and zone 4, the morphology of the cells observed in cross-section approximates a more circular form. Given that the average CWP does not exhibit substantial variation and that the average cell TSA increases significantly from zone 1 to zone 4, it can be inferred that, in the case of developing wood fiber bodies, the increase in average TSA is more likely attributable to changes in cell shape rather than to the expansion of the primary cell wall—at least within the developmental stages analyzed. These findings suggest that wood fiber bodies may not conform to the commonly held assumption that cambial derivatives, as they exit vascular cambium to become secondary xylem, undergo marked radial enlargement (growth). Specifically, although an increase in average cell thickness (CT) is observed, there appears to be no substantial evidence of actual cell wall growth in the fiber bodies. This contrasts notably with at least some vessel elements, which exhibit pronounced enlargement in both radial and tangential directions, particularly in earlywood vessels of ring-porous species (Gizińska et al. 2021). The intensive growth of such vessels typically initiates near the boundary between the vascular cambium and the zone of xylem differentiation (Miodek et al. 2021a). Although the increase

in average TSA of wood fiber bodies within the xylem differentiation zone—at least in the regions analyzed in this study—appears to result primarily from changes in cell shape rather than from growth of the primary cell walls per se, it is important to note that the tips of wood fibers exhibit distinct growth in axial, tangential, and radial directions (Miodek et al. 2023). This suggests that, in the species examined, the observed mechanism of TSA increase may facilitate the occupation of additional space with relatively minimal, or no, changes in the perimeters of cambial cells as they differentiate into wood fiber bodies. At this stage of wood fiber development, structural carbon—the primary building material—appears to be predominantly allocated to the formation of fiber tips, supporting both their axial elongation and transverse expansion, which necessitates an increase in tip perimeter. This process contributes substantially to the mechanical reinforcement of the developing wood structure.

Interestingly, during the progressive morphological transformation of the observed cells in the transverse plane, a decrease in their average tangential dimension (CW) is observed across successive zones, while their average radial dimension (CT) increases markedly. It is plausible that the reduction in average tangential dimension may result from, or be associated with, concurrent axial elongation of wood fiber tips whose main bodies are situated above or below the analyzed tissue sections. As fiber tips undergo axial elongation, they also exhibit an increase in both thickness and width, corresponding to radial and tangential dimensions observed in the transverse plane (Miodek et al. 2023). These tips grow between the tangential and radial cell walls of adjacent fiber bodies (Rao et al. 2011; Miodek et al. 2023), ultimately occupying a substantial portion of the cross-sectional area in the developing secondary xylem, which is particularly evident in zone 4 of all analyzed tissue fragments (see Supplementary Information Figs S1–S9).

Considering the previously described developmental stages of secondary xylem cell formation described in the literature (Wilson et al. 1966; Hejnowicz 2012), it is essential to compare the present findings on wood fiber body development with those pertaining to cells that do not exhibit comparable changes in shape—specifically, those in which no pronounced rounding is observed in the transverse plane. As noted in the Introduction, in the secondary xylem of coniferous trees, developing tracheids may retain characteristic hexagonal, rectangular, or square shape inherited from their mother cells. Morphological consistency is typically accompanied by a concurrent increase in radial cell dimension, as seen in transverse sections. Example of such tracheids is shown in Fig. 5. Performed analysis of a transverse section of *Picea abies* (L.) H.Karst (Fig. 5), conducted using a methodology analogous to that applied in the study of *R. pseudoacacia*, enabled the characterization of secondary xylem tracheid development from cambial cells. Between the cambial cell zone (Zone I) and the final analyzed zone containing tracheids at the most advanced stage of development (Zone IV), the average TSA of cells increased by 313.6%, the average CWP increased by 42.58%, the average CW decreased slightly by 0.7%, and the average CT increased by 307.8%. Further details are provided in Supplementary Information Tables S38 and S39. A comparative analysis of developmental changes in studied wood fiber bodies and tracheids reveals that both analyzed cell types exhibit an increase in average CT, and TSA. However, in developing cells that retain more angular morphology—such

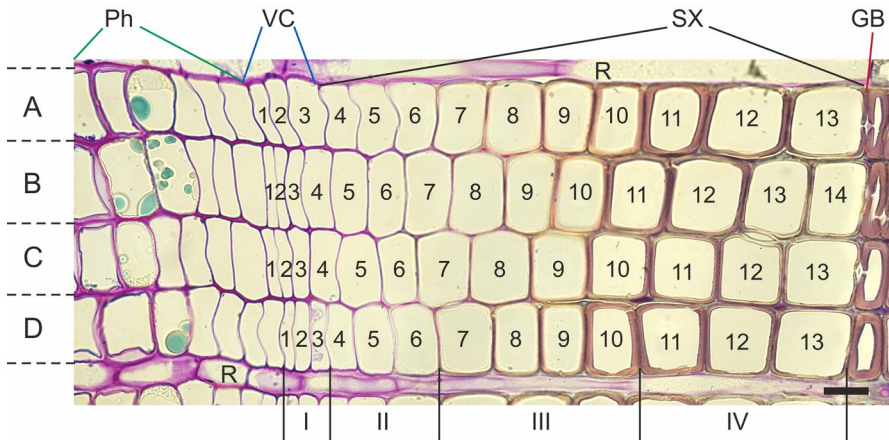


Fig. 5 Transverse section of the vascular cambium and secondary xylem of *Picea abies* (L.) H.Karst. Four radial cell files (labeled A–D), located between two uniseriate rays (denoted R), were analyzed. Cells within each file are numbered sequentially, beginning with the cambial initial cells and extending to the oldest derivatives on the secondary xylem side of the most recent annual growth ring. Cambial activity is still ongoing. A portion of the secondary phloem is visible on the left. *Ph* secondary phloem, *VC* vascular cambium, *SX* secondary xylem, *GB* growth ring boundary, *I–IV* four designated and examined zones. Scale bar = 20 μ m

as the hexagonal, rectangular, or square shapes characteristic of tracheids—the average CW remains relatively stable across developmental zones. Moreover, an increase in average TSA in tracheids is accompanied by a corresponding increase in average CWP, as shown in Supplementary Information Table S39. This pattern contrasts with that observed in the studied angiosperm species where TSA increase appears to result primarily from changes in cell shape rather than wall expansion. Consequently, it may be inferred that in studied tracheid development, the observed increase in average cell TSA is likely attributable to the expansion (actual growth) of cell wall. In support of this, the 42.58% increase in average CWP from zone I to zone IV in the indicated conifer species likely reflects a substantial investment of structural carbon in the expansion of the cell wall. A schematic representation illustrating two distinct developmental pathways of cambial derivative cells—wood fiber bodies in the angiosperm *R. pseudoacacia* and tracheids in the conifer *P. abies*—as observed in the transverse plane, is presented in Fig. 6. Analyzed cases of angiosperm wood fiber bodies and coniferous tracheids, which differ in shape during their development, indicate the need for further research, particularly in the latter case. The example shown was selected to compare two groups of cells with strikingly different shapes: cells that begin to round during their development versus cells that acquire more hexagonal, rectangular, or square shapes. It is worth to note that measurements, for both wood fiber cells and tracheids, were taken at the positions of their primary cell walls. Therefore, even though the cells located closer to the growth ring boundary in the examined coniferous tissue fragment are in the maturation phase (with secondary cell wall deposition), the comparison between cross-sections of angiosperm wood fiber cells and conifer tracheids can still be considered valid to some extent. However, it is important to remember that: (1) the four zones analyzed are not completely

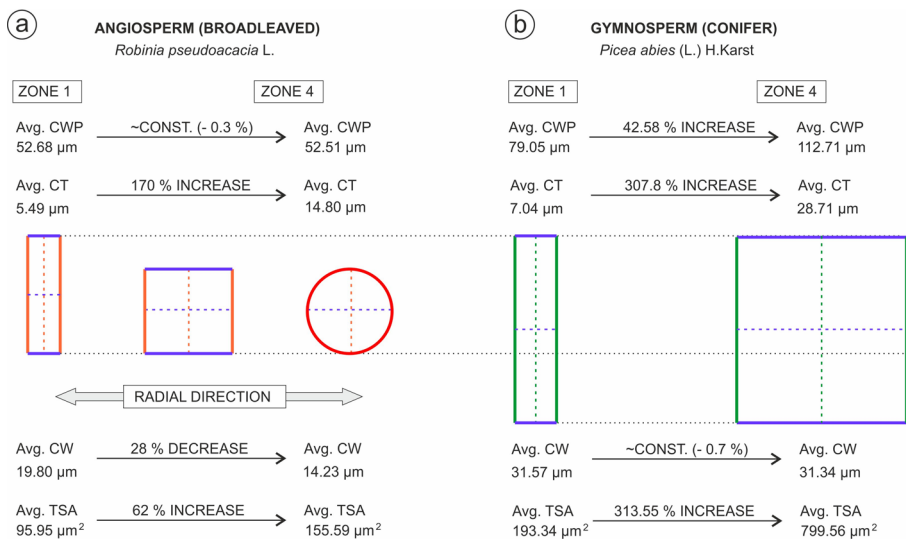


Fig. 6 Schematic representation of two different ways of development of analyzed cambial derivative cells as observed in the transverse plane depending on their shape change. Panel **a** illustrates the development of a wood fiber body in angiosperm species *Robinia pseudoacacia* L., while panel **b** depicts the development of a tracheid in the gymnosperm species *Picea abies* (L.) H.Karst. The numerical values, apart from the percentage changes indicated above the arrows, represent the average measurements obtained. The dimensions of the geometric figures were determined based on these mean values. Note that this comparison applies specifically to the values obtained for analyzed groups of cells in this study (limitations of the presented comparison are indicated in the main text)

equivalent to each other in both cases (in zone III, tracheid maturation begins, while fiber bodies are at an earlier developmental stage); (2) analysis of conifer tracheids was conducted on a relatively small sample size; (3) different tracheid shapes may be observed in coniferous wood, as is the case with reaction wood (Purusatama and Kim 2024); and (4) seasonal gradients in cell geometry should also be considered in future research. Moreover, when performing similar anatomical analyses (regardless of the cell or wood type), it should be kept in mind that it is not possible to track the development of the same cell (such as developing secondary xylem fiber body within the tree trunks of *R. pseudoacacia* individuals or tracheids in coniferous species) through all phases of cell development. To the best of our knowledge, there is currently no available method that allows for tracking the development of the same cell across sequential phases, particularly when working with anatomical sections of the examined tissue. Therefore, it is necessary to compare the characteristics of cells located in different zones, each representing distinct developmental stages. While this approach provides valuable insights, it also introduces a general limitation that should be acknowledged when interpreting the results. It should be noted that the observations regarding the growth pattern of wood fibers were based on 832 cells of *R. pseudoacacia*. Given the importance of the obtained results, further research in the indicated area is crucial. These studies should focus on, among others, examining other tree and shrub species, particularly those with high wood fiber content and storied cambial structure (though they should not be limited to these), in order to deter-

mine whether a similar relationship between CWP, and changes in cell TSA exists in other species as the cambial initial layer moves further away from the developing xylem cells. More generally, it is also recommended to analyze the growth pattern of other xylem cell types (such as tracheids of angiosperms and axial parenchyma) and compare the obtained relationships between CW, CT, cell TSA, and CWP to the commonly acknowledged description of the secondary xylem cell enlargement during differentiation process. Consideration of the effects of seasonal gradients in cell properties (e.g., dimensions) would also be interesting in future studies. Since the present study was conducted in July and August, analyzing the potential influence of seasonal gradients on observed patterns of wood fiber development would require multiple sampling points throughout the growing season, starting from the early stages of earlywood formation. We encourage the consideration of using the cell circularity formula in future studies. In our opinion, the described approach will enable a better understanding of the xylogenesis process.

Conclusion

Based on the results obtained in this study, the following conclusions can be drawn regarding the development of wood fiber bodies of *R. pseudoacacia* in the transverse plane:

(1) The development of the wood fiber body from the cambial cell is related to a gradual change in cell shape, from approximately rectangular to more round, which is accompanied by an increase in the average radial dimension (thickness) and a decrease in the average tangential dimension (width);

(2) The change in the shape of wood fiber bodies observed in the transverse plane is accompanied by the growth of tips of other fibers, the bodies of which are located below or above the analyzed cross-section. With increasing distance from the vascular cambium, the number of wood fiber bodies not in contact with each other increases, and fiber bodies become completely or almost completely surrounded by axially elongating and transversally enlarging wood fiber tips;

(3) During the development of wood fiber bodies, in the zones identified and analyzed in this study, the average cell TSA increases from zone 1 (vascular cambium) to zone 4 (fiber bodies at the greatest distance from vascular cambium). The increase in average cell TSA appears to result primarily from changes in cell shape rather than from the transverse growth of the fiber body cell wall per se, since the average CWP showed only slight change (a decrease) from zone 1 to zone 4. This contrasts with the analyzed example of coniferous wood, where the increase in the cross-sectional area of tracheids primarily results from the expansion of cell walls;

(4) Changes in the shape of wood fiber bodies may represent an adaptive mechanism for the efficient use of plant structural resources during the wood formation process. The increase in average cell TSA, with relatively minor changes in average CWP, suggests an optimization of structural carbon use, favoring the elongation of wood fiber tips. This may contribute to the mechanical stability of the wood and its resistance to environmental factors.

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Declarations

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