ANATOMICAL RESPONSES OF *CEDRUS LIBANI* (LEBANON CEDAR) WOOD TO MECHANICAL STRESS

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ABSTRACT

Wood (secondary xylem) is a source of information about events that occurred during their lifespan. The aim of our research was to provide the pattern of modification of Lebanon cedar wood under the influence of mechanical stress, as a result of binding its trunk with string or wire. The wood samples were taken from a young *Cedrus libani* (14 years old - evaluated based on the number of growth rings) growing in the Agdaci campus of Faculty of Forestry, Bartin University. They were taken from three different levels of the trunk including the strangulation point, and above and below this point. Using standard protocols, cross-sections of the taken wood were prepared. Then, the morpho-anatomical features of wood were examined: (i) tracheid radial diameter (TRD), (ii) cell wall thickness of tracheid (CWT), (iii) tracheid radial diameter divided by cell wall thickness (TRD/CWT), (iv) tracheid number per mm^2 (TN), (v) tracheid length (TL), (vi) ray number per mm (RN), (vii) ray density per mm^2 (RD), (viii) ray height (RH), (ix) parenchyma cell number in rays per mm^2 (PCN), (x) percent of uniseriate rays (PUR), and (xi) percent of biseriate rays (PBR). Among the analyzed biometric features, those concerning the rays and parenchyma cells differed significantly between the wood samples taken from different trunk levels at $p < 0.01$. Both axial and radial traumatic resin ducts were observed. There was no significant difference in TRD, CWT and TRD/CWT between levels. We postulate that increased the amount of parenchyma in wound secondary xylem by producing both uni- and biseriate rays as well as traumatic resin ducts facilitates compartmentalization and wound closure and reflect the phenotypic plasticity and structural adaptations of the cedar wood to respond to injury and physiological needs.

KEYWORDS: Lebanon cedar, parenchyma cells, phytohormones, mechanical injury, tracheids, traumatic resin ducts.

INTRODUCTION

Secondary growth usually generates wood (secondary xylem), periderm and rhytidome (Esau 1965). These secondary tissues allow plants to resist environmental hazards such as winds and heavy snowfall, while also allowing water to be transported from the roots and assimilates from the above-ground tissues to the sinking tissues in the stem and roots. They also maintain a defense system.

Wood, like a whole tree considered as modular organism, appears to be a highly ordered, compartmentalized tissue (Shigo 1984). In coniferous tree, it has relatively simple structure and consists primarily of tracheids and minor amount of parenchyma cells (Słupianek et al. 2021). One of them is made of water-conducting dead tracheids, the other of parenchyma cells with long-lived protoplasm, which are mainly involved in the storage of the energy reserves. Among coniferous, there are also genera (e.g., Pinus, Picea, Larix, Pseudotsuga and Keteleeria) with resin ducts as a constitutive element of their wood (Bannan 1936; Lev-Yadun and Aloni 1995; Mercado et al. 2023) and forming as a response to insect attack, fungal invasion, and mechanical wounding (Nagy et al. 2000; McKay et al. 2003; Martin-Rodrigues et al. 2013). Other genera such as e.g., Abies, Tsuga, Cedrus or Pseudolarix, are only able to produce traumatic resin ducts in response of cambium injury (Bannan 1936; Wu and Hu 1997; Arbellay et al. 2014) whilst for example Cupressus and Juniperus are considered not to produce any resin ducts (Evert 2006). Bannan (1936) proposed a classification based on the anatomy of the cellular structures involved in resin synthesis and accumulation. In Abies, Cedrus, Tsuga, and Pseudolarix, the resin-producing cells form blisters, which are a sack-like structure lined with epithelial cells. These cells are short-lived, and their cell walls are lignified during the development program. More complex structures such as tube-like resin ducts were found in Pinus, Picea, Larix and Pseudotsuga wood. In these genera, thick-walled (except pine) and long-lived secretory epithelial cells synthesize resin (Nagy et al. 2000). The defensive effects of coniferous resin are attributed to its toxic and sticky characteristics, to massive flow of resin that can flush out or repel invading insects, and to inhibitory impact on pathogenetic fungi (Shrimpton & Whitney 1968, Gijzen et al. 1993). It is assumed that the largest number of resin ducts is formed when the cambium of an injured organ is intensively active (Fahn 1990), and auxin is a signal which is involved in the formation of the traumatic resin ducts (Hudgins et al. 2006). However, jasmonate, more specifically, methyl jasmonate, appears to be the primary and specific factor which induces traumatic resin ducts formation in conifers and this jasmonate-induced defense results may be driven by ethylene (Hudgins and Franceschi 2004; López-Villamor et al. 2021). When a tree organ is injured, the cambium responds by forming a thin layer of unique cells called the barrier zone, which separates the healthy tissue formed before the injury from the tissues formed after the injury, which is a one of the parts of compartmentalization. In conifers, barrier zone often contains traumatic resin ducts (Nagy et al. 2000; Morris et al. 2020).

Cedrus libani A. Rich (Lebanon cedar) is a species of coniferous tree native to the eastern Mediterranean region. *C. libani* is now naturally distributed in Turkey, Cyprus, Syria, and Lebanon, but its distribution in other regions has been extremely narrowed except Turkey (Köse and Yılmaz 2018). In Turkey, this species is found mainly in the Taurus Mountains, and it covers the land of 402000 hectares (OGM 2021). The use of Lebanon cedar as a building material dates back to ancient times as it is resistant to fungus and insects and is a physically strong, fragrant and valuable wood (Kayacık and Aytug 1968; Aytuğ and Görcelioğlu 1987; Liphshitz 2013).

Historically, it was a highly sought-after building material for palaces, temples, and other structures in the eastern Mediterranean (Chaney and Basbous 1978; Babos and Vörös 2001). The ancient Egyptians used cedar wood to construct their temples, tombs and ships (Liphshitz and Biger 1991). There have been several studies on the anatomy of Lebanon cedar wood, which have aimed to provide a better understanding of its properties and potential uses (Erdin 1983; Cartwright 2001; Esteban et al. 2004; Fahn et al. 1986; Yaman 2007; Akkemik and Yaman 2012).

As secondary xylem is an archive of information on conditions during tree growth (Tulik 2001; Fonti et al. 2010) and results from its plasticity, hence the aim of our research is to provide the pattern of modification of *Cedrus libani* wood under the influence of mechanical stress, as a result of binding its trunk with string or wire.

MATERIAL AND METHODS

Study site and samples collection

The wood samples of the study were taken from a young Lebanon cedar tree (14 years old - evaluated based on the number of growth rings) under mechanical stress, located in the Agdaci campus of Faculty of Forestry, Bartin University (Fig. 1 A). Bartin province where the sample tree selected is under an oceanic climate, and a dry period is not present in Bartin due to the fact that the precipitation line is over the temperature line for all months based on Walter and Lieth method (Yaman and Ertuğrul 2020). This sample tree, which is 5.7 m tall, had been under mechanical stress since its early ages due to accidental strangulation where it is 43 cm above the ground on the trunk. Using an increment borer, wood samples were taken from three different levels of the trunk, including the strangulation point at 43 cm above the ground and above - below this point at 20 cm and 15 cm, respectively (Fig. 1 B). As the circumference length of the trunk at the strangulation point (LB) was 55.5 cm, it was 45.5 cm and 41 cm at the above- and below-point (LC and LA, respectively) of this strangulation level. White arrows show the points of wood sampled as Level A (LA), Level B (LB) and Level C (LC) on the trunk (Fig. 1 C).

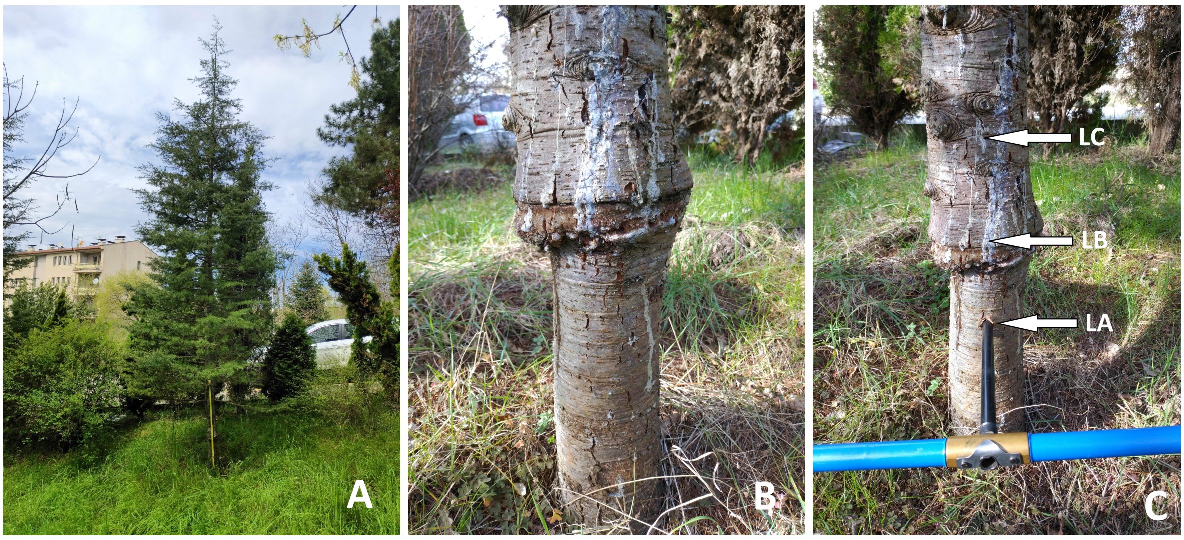

Fig. 1. Morphology of *C. libani* selected for study (A) with visible changes in trunk circumference (B) and levels at the trunk height from which the samples for testing were collected (white arrows; C).

Laboratory methods

The transversal, radial and tangential sections, all of which were 20-30 µm, were taken using a sliding microtome (GSL-1, WSL) from the last two growth rings of the increment cores. All thin wood sections were stained with astra blue-safranin mixation (Gärtner and Schweingruber 2013), and they were prepared as temporary preparations by placing them in glycerine medium between the slide and coverslip. The Ladell method was adopted to measure the length of the tracheids (Ladell 1959).

Quantitively analysis of biometrical traits of wood cells and wood anatomy

Thin sections were examined by light microscopy (Olympus CX_21) and the measurement and counting procedures were performed related to the following biometrical traits of wood anatomy: (i) tracheid radial diameter (TRD), (ii) cell wall thickness of tracheid (CWT), (iii) tracheid radial diameter divided by cell wall thickness (TRD/CWT), (iv) tracheid number per mm2 (TN), (v) tracheid length (TL), (vi) ray number per mm (RN), (vii) ray density per mm2 (RD), (viii) ray height (RH), (ix) parenchyma cell number in rays per mm2 (PCN), (x) percent of uniseriate rays (PUR), and (xi) percent of biseriate rays (PBR). For the per group, the total number of observations (measurement and counting) were decided as 120 for TRD and CWT, 30 for RN and RH, 20 for TL, RD, PCN and PBR, and 10 for TN. The terminology of wood anatomy was used based on IAWA List of Microscopic Feature for Softwood Identification (IAWA Committee 2004).

Statistical analysis

Since the selection of appropriate statistical methods is crucial in analyzing and interpreting the data obtained from the study, first, whether or not the variances are equal between each group (homogeneity test) and whether a single variable is normally distributed (normality test) were investigated using Levene test and Shapiro test, respectively. According to the results of these tests, parametric or nonparametric analysis methods were selected to determine whether the differences occurred among groups (FFisher and X2Kruskal-Wallis, respectively), and Student's t and Dunn test were used to determine which groups were different. In R environment, the 'car' package was used for Levene test and Shapiro test (Fox and Weisberg 2019), and the 'ggstatsplot' package was used for FFisher, X2Kruskal-Wallis, Student's t, and Dunn test (Patil 2021).

RESULTS AND DISCUSSION

In the examined wood increments (at every level), the arrangement of tracheids was changed, which resulted from the appearance of traumatic resin ducts (Figs. 2A, B and 3A). On the cross-sections of wood, the axial traumatic resin ducts (ATRD) usually formed a continuous tangentially arranged line (Fig. 2). Close to the resin ducts, the tracheids did not form radial rows. We observed a temporary duplication of rows or their elimination (Fig. 2 A). Both uniseriate and biseriate rays were found (Fig. 3).

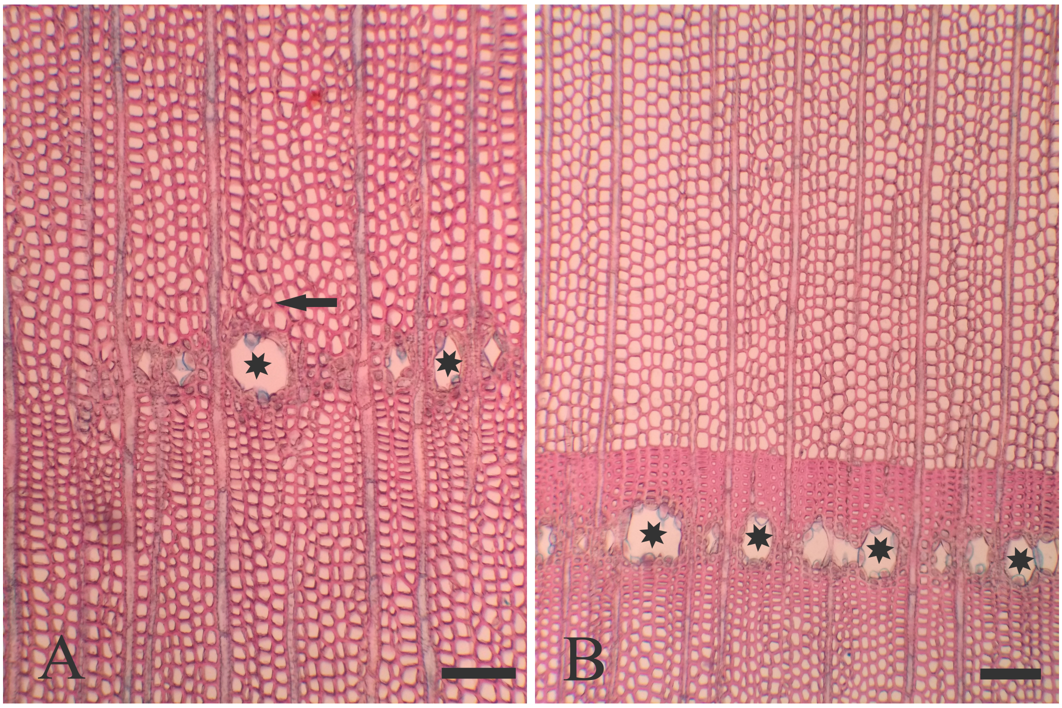

Fig. 2. Cross sections *via* studied wood increments in *C. libani* trunk at level C (LC). Axial traumatic resin ducts highlited with asteriks and temporary duplication of tracheids row by an arrow. Scales: 80 µm for 2A and 2B.

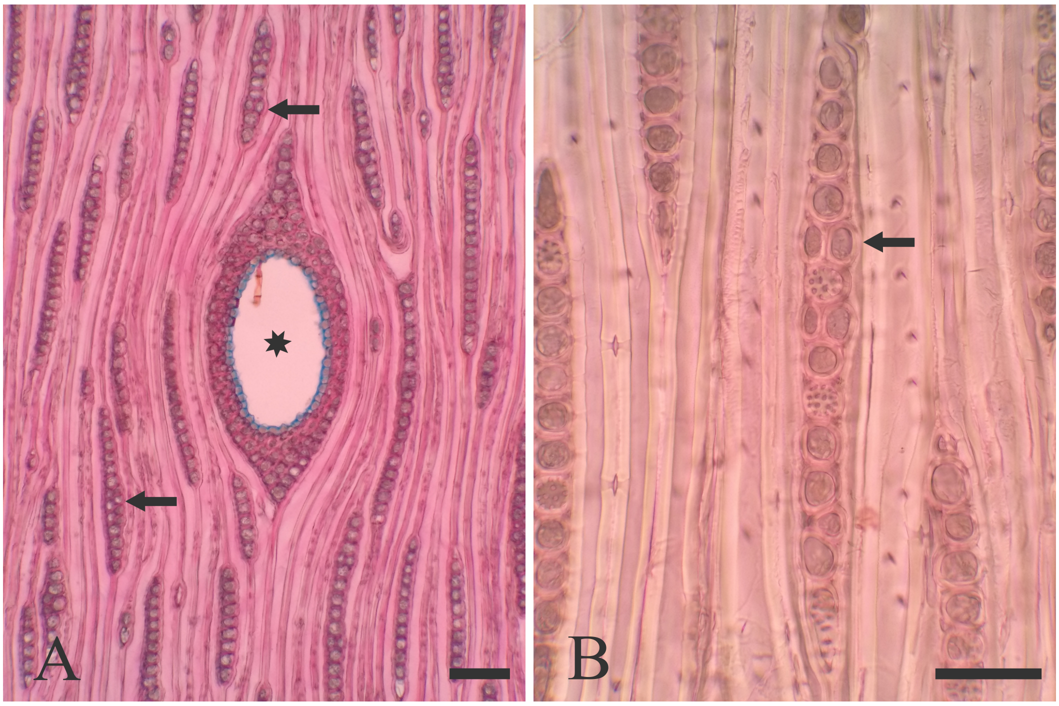

Fig. 3. Tangential sections *via* studied wood increments in *C. libani* trunk at Level C. Radial resin duct highlited with an asterik [(A) and biseriate rays by arrows (A and B)]. Scales: 150 µm for 3A and 100 µm for 3B.

Among the analyzed biometric features, those concerning the rays and parenchyma cells differed significantly at $P < 0.01$ between the wood samples (Table 1). The highest RN was found at level C, reached 8.6 mm^{-1} and was significantly different from the RN of the wood sampled from level A. A significant difference in RN was also observed between wood from levels B and A (Table 1). A similarly significant difference was found in the case of RD. The highest RD was found in wood from level B, which had an average value of 33.15 mm^{-2} and differed significantly between levels C and A. There was also a statistical difference in RD between levels A and C (Table 1). The highest rays were found at level C with an average value of 456.67 μm and a significant difference from level A, where RH was significantly lower (261.67 μm) compared to wood from level B of the trunk (Table 1). The comparison of the PCN values between the wood samples showed no significant difference, 494.40 mm^{-2} for level A, 490.40 mm^{-2} for level B and 503.20 mm^{-2} for level C. The opposite was shown for PUR and PBR. A significant difference in the mean values of these features was found in the wood from the B-A and B-C levels (Table 1).

There was no significant difference in TRD, CWT and TRD/CWT between levels (Table 1). The highest TRD was recorded in wood at level B with an average value of 17.83 μm, the lowest at level C, which reached 16.73 μm. In turn, tracheids in wood from level A had a thicker cell wall than tracheids from levels B and C (Table 1). The TRD to CWT ratio was the highest in wood sampled from the level C compared to the other levels, but the differences were not significant.

We measured the thickness of the secondary protective tissues as well. The thickest rhytidome was found in the sample from level B with a value of 1.05 cm, 0.8 cm in a sample from level C and 0.7 cm from level A (data not shown in Table 1).

Table 1. Mean biometrical traits of tracheids and radial parenchyma cells in studied wood increments in the trunk of *C. libani*.

	Level A	Level B	Level C	P < 0.01
TRD	17.08 ± 8.36	17.83 ± 9.18	16.73 ± 12.09	NS
CWT	4.02 ± 1.41	3.70 ± 1.20	3.98 ± 1.72	NS
TRD/CWT	5.48 ± 4.0	5.99 ± 4.12	6.00 ± 5.28	NS
TN	1561 ± 432.8	2251.5 ± 845.8	1568.5 ± 91.56	S (B-A, B-C)
TL	1.80 ± 0.69	2.08 ± 0.63	1.98 ± 0.53	NS
RN	7.1 ± 1.03	8.4 ± 1.13	8.6 ± 1.22	S (B-A and C-A)
RD	27.25 ± 1.94	33.15 ± 1.73	23.50 ± 1.93	S (B-A, B-C, C-A)
RH	261.67 ± 96.28	445.33 ± 227.86	456.67 ± 241.54	S (B-A, C-A)
PCN	494.40 ± 81.40	490.40 ± 67.34	503.20 ± 73.68	NS
PUR	95.34 ± 6.56	54.34 ± 15.83	94.77 ± 6.65	S (B-A, B-C)
PBR	4.66 ± 6.56	5.66 ± 15.83	5.23 ± 6.65	S (B-A, B-C)

TRD: tracheid radial diameter (μm), CWT: cell wall thickness of tracheid (μm), TRD/CWT: tracheid radial diameter divided by cell wall thickness , TN: tracheid number per mm^2, TL: tracheid length (mm), RN: ray number per mm, RD: ray density per mm^2, RH: ray height (μm), PCN: parenchyma cell number in rays per mm^2, PUR: percent of uniseriate rays, PBR: percent of biseriate rays, NS: Non-significant, S: Significant

CONCLUSIONS

The evolutionary success of trees as long-lived organisms can be partly attributed to their ability to resist a hostile environment. It is known that trees in the course of evolution have developed sophisticated stress response mechanisms that occur both in directly damaged tissues (local response) and in an undamaged site (systemic response) (León et al. 2001; Savatin et al. 2014). It also seems that mechanical injury triggers defense mechanisms comparable to those induced by herbivores and insects, e.g. through phytohormones, such as jasmonic acid, ethylene, salicylic acid (Schmidt et al. 2011). The reaction to injury observed at the morpho-anatomical level of the analyzed cedar wood was mainly the formation of traumatic resin ducts, present not only in the axial but also in the radial system, forming a highly complex, interconnected three-dimensional network ensuring continuity of resin production. Our observation is consistent with literature data providing information that cedar creates both axial and radial TRDs as part of an inducible defense (Fahn et al. 1979; Esteban et al. 2021). The formation of functional TRDs with secretory activity in response to wounding or pathogen attack is a characteristic defense mechanism in the xylem of many conifers (Hudgins et al. 2004) and is thought to be quite rapid. In cedar branches wounded during the growing season, TRDs formed after a month as a system of longitudinally oriented ducts that reached a greater length above the treated area (Fahn et al. 1979). Similar results were presented by Nagy et al. (2000), who showed that Norway spruce forms a functional TRD in two to four weeks.

TRD formation occurs through reprogramming of derived cambial cells that would normally develop into tracheids (Werker and Fahn 1969; Nagy et al. 2000; Krekling et al. 2004), but the mechanisms controlling this process are still poorly understood. As among intrinsic factors, auxin and its cross-interaction with other hormones initiate the transcriptional program of secondary xylem differentiation (Immanen et al. 2016; Hartmann et al. 2021), and biomechanical signals appear to be important for division, growth and differentiation (Yeoman and Brown 1971; Louveaux et al. 2016), hence we hypothesize that the rapid formation of TRDs in cedar wood influenced the formation of tracheids, resulting in their dislocations (lack of arrangement in radial files) seen in close proximity to TRDs.

The tracheids formation, which are the main elements of wood in conifers, involves successively phase of cambial cell division, radial expansion of its derivative cell, deposition of its secondary wall layers with lignification, and programmed genetic cell death described as a type of autophagic death (van Doorn and Woltering 2005; van Doorn *et al.* 2011). Parenchyma cell formation also consists of the same phases as tracheid; however, the time and space of secondary cell walls deposition, lignification and cell death are separated (Nakaba et al. 2006; Arakawa et al. 2018; Bieniasz and Tulik 2022). Every step of xylem element formation is controlled by various environmental (Frittts et al. 1991; Eilmann et al. 2011) and intrinsic factors (Uggla et al. 1996; Samuels et al. 2006). We did not observe any significant differences in the biomechanical features of tracheids between the tested levels of the trunk except for the number of tracheids with the highest value at B level (the widest point at the height of the trunk). Wound secondary xylem showed narrower tracheids in *Pinus halepensis*, *Larix decidua* and *Pinus pinaster* (Fahn and Zamski 1970; Stoffel and Hitz 2008; Ballesteros *et al.* 2010), however the values of TRD obtained by us were within the range typical for cedar wood (Yaman 2007). Nonsignificant differences in TRD between studied levels seems to be related to the dual function of these cells: safe water transport and support as usually mechanical support constrain the hydraulic efficiency of the xylem (Pittermann *et al.* 2006; Sperry *et al.* 2006). The appropriate diameter of the tracheids guarantees the supply of water to every cell and ultimately the survival of the organism.

Significant discrepancies were mainly observed in parenchyma cell features, but RD was the only feature differentiating the wood collected from different heights of the trunk. It is known that in *Psudotsuga menziesii* and *Larix occidentalis*, changes in the density of rays were also most pronounced in the immediate vicinity of the fire scar, while changes in the size of the rays were more evenly distributed with increasing distance from the wound edge (Arbellay et al. 2014). Increasing the amount of parenchyma in wound secondary xylem (mainly at levels B and C) by producing both uni- and biseriate rays as well as traumatic resin ducts facilitates compartmentalization and wound closure. This reflects the phenotypic plasticity and structural adaptations of cedar wood in response to injury and physiological needs. Moreover, our results provide data on the spatio-temporal response of cedar wood to local damage seen at heights of its trunk.

Author contributions

BY proposed the subject of research. BY, MT, EP participated in field and laboratory work. MT, BY wrote the manuscript with the assistance of EP. All authors participated in the editorial work and approved the submitted version of the manuscript.

Conflict of interest

The authors declare that the study was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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