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Variation in wood density between mature sessile oak and English oak trees growing in different vegetation zones

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Abstract: Wood density is a fundamental functional trait influencing ecological adaptation, hydraulic safety, and timber utilisation in temperate hardwoods. This study investigated variation in wood density (12% moisture) across mature stands of two economically and ecologically vital European oak species, sessile oak [*Quercus petraea* (Matt.) Liebl.] and English oak (*Quercus robur* L.), growing in their characteristic vegetation zones in the Czech Republic. We assessed wood density at two heights (at 1.3 m and at the crown base) across six trees per plot and examined its relationship with tree-ring width and height. Results demonstrated statistically significant interspecific differences, with *Q. petraea* consistently exhibiting higher wood density (721 $kg \cdot m^{-3}$) than *Q. robur* (662 $kg \cdot m^{-3}$) at 1.3 m. *Q. petraea* showed a statistically nonsignificant higher density of 710 $kg \cdot m^{-3}$ at the crown base and an overall average of 717 $kg \cdot m^{-3}$, while *Q. robur* had densities of 701 $kg \cdot m^{-3}$ and 669 $kg \cdot m^{-3}$, respectively. Radial density profiles revealed species-specific patterns, with *Q. robur* showing a more uniform density distribution than the pronounced pith-to-bark gradients observed in *Q. petraea*. Regression analysis indicated that tree-ring width explained only 12–13% of the variance in density, so other anatomical factors, such as latewood proportion and tree-ring structure (number and cell size), should be examined as anatomical drivers of wood-density variation.

Keywords: Czech Republic; *Quercus petraea* (Matt.) Liebl.; *Quercus robur* L.; radial variation; wood properties

European oak ecosystems are integral to temperate forests, providing essential ecosystem services and high-quality timber resources (Leuschner, Ellenberg 2017; Mölder et al. 2019). The formation of oak wood, and therefore the quality of oak timber, is fundamentally influenced by the interactive effects of soil moisture availability, soil nutrient status, altitude, and climatic conditions experienced during the tree's growth periods, collectively resulting in significant variation in wood characteristics across different ecological sites (Móricz et al. 2025). Recent dendroecological studies across central Europe show water balance, especially summer precipitation and soil moisture, is the main

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climatic factor limiting oak growth. Water availability has become increasingly important since the warming after 1980 (Friedrichs et al. 2009; Stojanović et al. 2017, 2025; Kasper et al. 2022; Móricz et al. 2025). Compared with beech and linden, Kasper et al. (2022) indicated that oaks have a superior capacity to sustain differential growth responses and are more resilient to climatic stress than the other temperate forest species.

In Central Europe, sessile oak [*Quercus petraea* (Matt.) Liebl] and English oak (*Quercus robur* L.) are the most economically significant hardwood species, prized for their durability, mechanical strength, and aesthetic qualities (Úradníček, Chmelař 1998; Eaton et al. 2016), while according to Stimm et al. (2021), *Q. petraea* and *Q. robur* are crucial for enhancing the resilience of central European forests to severe drought. Although the two species are closely related and anatomically similar ring-porous species (Schweingruber 1990), they exhibit distinct ecological niches. *Q. petraea* typically occupies well-drained, upland sites with lower water availability, demonstrating increased physiological resilience to xerophytic conditions typical of elevated, well-drained upland areas, whereas *Q. robur* thrives in nutrient-rich, mesic floodplain environments with higher soil moisture availability (Stimm et al. 2021). These contrasting growing conditions impose different hydraulic and mechanical constraints that may drive divergence in wood anatomical adjustments and resulting wood density profiles (vessel size, cell-wall thickness, and latewood proportion) (Fonti et al. 2009; Galle et al. 2010; Sousa et al. 2021).

Wood density is widely recognised as a key functional trait that links ecosystem functions like tree biomechanics, hydraulic safety, and carbon storage (Zobel, Van Buijtenen 1989; Bergès et al. 2008; Chave et al. 2009; Zanne et al. 2009; Mölder et al. 2019). It is a primary indicator of timber quality, strongly associated with mechanical properties such as strength, stiffness, rupture, elasticity and pulp yield (Downes, Drew 2008; van Leeuwen et al. 2011; Pretzsch et al. 2018). Wood density is influenced by factors such as tree-ring width, proportion of latewood, and environmental site conditions, which are correlated with various physical and mechanical properties (Vavrčík, Gryc 2012; Zeidler, Borůvka 2016; Bergès et al. 2008; Pretzsch et al. 2018). These influences are contingent on the genus, site type, the tree's social status within the stand, silvicultural treatments during growth, the specific position on the trunk (considering radius and height), and positional variation within the stem encompassing both radial (pith-to-bark) and vertical (base-to-crown) dimensions (Guilley 2000; Vavrčík, Gryc 2012; Bergès et al. 2008).

Several papers discussed the effects of climate change on tree wood density (Zhang et al. 1993; Jacoby, D'Arrigo 1995; Bouriaud et al. 2004; Pretzsch et al. 2018; Arsić et al. 2021). Research specifically examining the influence of site factors on oak wood density has documented that ecological conditions exert measurable effects on wood density development independent of variation in tree-ring width. However, the magnitude of these effects remains substantially smaller than comparable influences on radial growth rates (Bergès et al. 2008). Notably, ecological factors exerted differential effects on earlywood and latewood tissue components, with latewood exhibiting substantially greater sensitivity to climatic stressors and water-related environmental variables than earlywood (Bergès et al. 2008). Furthermore, the classic relationship between tree-ring width and wood density in ring-porous hardwoods – where wider rings imply higher density due to increased latewood proportion – may vary substantially with local climatic conditions (Guilley et al. 2004). Upland environments characterised by xerophytic conditions and limited water availability impose substantial physiological constraints that fundamentally influence the development of wood composition and density (Kasper et al. 2022). Water limitations encountered at upland sites – particularly those typical of *Q. petraea* habitats – constrain cambial expansion during growth periods and foster a proportionally greater allocation to mechanical support tissues relative to growth rate (Kasper et al. 2022). Floodplain environments supporting *Q. robur* are characterised by periodic flooding cycles and alluvial soil deposition, creating nutrient-rich, moisture-abundant conditions that promote rapid cambial expansion, enhanced radial increment rates, and vigorous growth expression (Dobrovolný 2014; Móricz et al. 2025). This differential allocation of growth resources between xeric environments (favouring slower growth with increased mechanical tissue and higher density) and hydric environments (favouring rapid growth with lower wood density) represents a fundamental evolutionary adaptation strategy re-

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flecting each species' developmental history within its native environmental niche (Kasper et al. 2022). Furthermore, the radial variation in wood density within the tree reflects growth patterns common to all oak species. The highest average density values are consistently observed in the central stem regions, with density gradually decreasing toward the outer sapwood. This pattern corresponds to the formation of juvenile wood near the pith, characterised by lower density, which transitions to mature heartwood and outer sapwood, with distinct density variations (Vavrčík, Gryc 2012; Diaz-Maroto et al. 2017). Lexa et al. (1952) discovered that, given the same tree-ring widths, the wood of sessile oak exhibits a higher density value compared to that of *Q. robur*.

Contemporary climate change poses unprecedented challenges for temperate forest ecosystems, with implications for oak-dominated forest systems across Central Europe (Móricz et al. 2025). In the Czech Republic, oak stands currently occupy approximately 7.9% of the forest area, with strategic management plans projecting an increase to 12.8% to enhance forest resilience against climate change (Ministry of Agriculture 2024). Despite the economic importance of these species, comparative studies quantifying radial and vertical density variations in mature trees from their respective optimal vegetation zones remain limited in the Central European context, even though understanding these variations is essential for optimising converting and grading processes in the timber industry.

The objectives of this study were to (*i*) quantify and compare wood density profiles of mature *Q. petraea* and *Q. robur* growing in their characteristic vegetation zones (upland vs. floodplain); (*ii*) assess intra-stem density variation along radial and vertical gradients; and (*iii*) evaluate the influence of tree-ring width on wood density to determine the reliability of tree-ring width as a quality predictor for these species.

MATERIAL AND METHODS

Site description. The selection of trees was conducted across two distinct research plots. Sessile oak [*Quercus petraea* (Matt.) Liebl.] was sampled in Soběšice (385 m a.s.l., 49°15'34'N, 16°36'41'E), representing drier upland soil conditions. Conversely, English oak (*Quercus robur* L.) was harvested at the Janohrad plot (159 m a.s.l., 48°47'56'N, 16°50'35'E), which typifies a floodplain forest environment. Both research plots are classified as a warm-summer humid continental climate (Dfb) region based on the Köppen climate classification (Beck et al. 2023). Based on the Czech Forest (Site) Ecosystem Classification (Viewegh et al. 2003), the Soběšice plot belongs to the Beech-Oak vegetation zone of a typical upland with good conditions for the cultivation of sessile oak, characterised by well-drained, nutrient-rich soils and moderate water availability. The Janohrad plot is classified as the Oak vegetation zone, characterised by moisture-rich conditions, periodic inundation cycles, and alluvial soil characteristics typical of lowland forest ecosystems.

Experiment design. Six healthy specimens were randomly chosen at each location. The average number of tree rings counted at the breast height was 108 in Soběšice and 84 in Janohrad. The diameters of trees at breast height for *Q. petraea* and *Q. robur* ranged from 31.5 cm to 43.5 cm (average 38.2 cm) and from 41.0 cm to 58.0 cm (average 48.3 cm), respectively. The average tree height was 20.3 m for the Soběšice plot and 29.4 m in the Janohrad plot.

The wood samples were collected from two different positions on the stem: at a breast height of 1.3 m and at the base of the crown (crown base height). The samples were marked in the radial direction with letters in alphabetical order, starting from A from cambium to pith. The methodology used to produce the test samples is illustrated in Figure 1.

The samples designated for density determination measured 20 × 20 × 300 mm. The atypical dimensions are attributable to the subsequent detection of mechanical properties testing (not included in this paper). The samples were acclimated to a moisture content of 12%. Each specimen was measured in three anatomical directions, and its weight was recorded. The wood density of the specimens at 12% moisture content was calculated as shown in Equation (1):

$$\rho_{12} = \frac{m_{12}}{V_{12}} \tag{1}$$

where:

ρ_{12} – wood density ($kg \cdot m^{-3}$) at 12% moisture content (MC 12%);

m_{12} – weight of the sample (kg) at MC 12%;

V_{12} – volume of the sample (m^3) at MC 12%.

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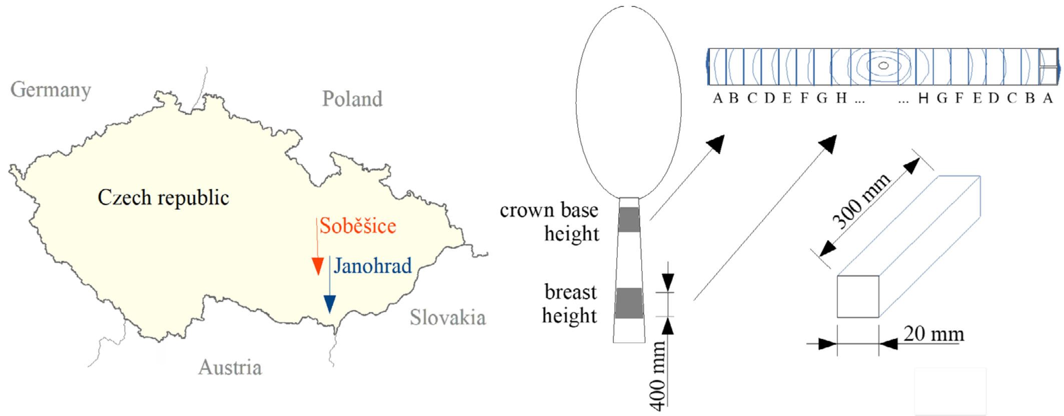

Figure 1. Map of research plot locations and sampling methodology for test material

For each test sample, a straight line (perpendicular to tree-ring boundaries) was drawn on the transversal section over all complete tree rings. The length of that line (*L*) represented the sum of all tree-ring widths. It was measured using a digital calliper (Mitutoyo, Japan) at 0.01 mm precision. All tree rings on that line were counted (*n*); The average tree-ring width (*TRW*) of the sample was calculated using Equation (2):

$$TRW = \frac{L}{n} \tag{2}$$

where:
TRW – average tree-ring width (mm);
L – length of the line (mm);
n – number of tree rings on the line.

Statistical analyses. Statistical analysis included a multifactor ANOVA to test for differences between wood sections and sites, despite moderate normality violations. If the ANOVA test rejected the null hypothesis, Scheffé's method was used for post-hoc testing. The significance level (α) value was set at 0.05 for all statistical tests. Linear regression was performed to establish relationships between tree-ring width and wood density. All statistical tests were conducted using Statistica software (Version 14.0.0.15, 2022). All graphs were created using Microsoft Excel (Version 14.0.6023.1000, 2010) spreadsheet processor and Statistica software.

RESULTS AND DISCUSSION

Tree-ring width. Descriptive statistics of the average tree-ring width obtained from test samples are presented in Table 1. The average tree-ring width for *Q. petraea* in Soběšice was 1.5 mm at breast height and 1.6 mm at crown base height. Conversely, the tree-ring width for *Q. robur* at the Janohrad plot was greater, measuring 2.6 mm at breast height and 2.2 mm at crown base height. A broader range of tree-ring widths and maximum tree-ring widths were observed at Janohrad for *Q. robur*. Similar results regarding tree-ring width were reported previously by Vavrčík and Gryc (2012), who investigated the same oak species in comparable locations. Our findings are consistent with those of Rybníček et al. (2016), who studied the growth response of various oaks to climatic factors. Their results suggest that the average growth of *Q. robur* surpasses that of *Q. petraea*.

The average tree-ring width exhibits significant variation along the stem radius and tree heights at both monitored plots, as illustrated in Figure 2. In the case of *Q. robur*, the most substantial difference in average tree-ring width at breast height is 1.68 mm, observed between the peripheral section (section A, with a tree-ring width of 1.32 mm) and the central part of the stem (section H, with a tree-ring width of 3 mm). For *Q. petraea*, the difference between the central and peripheral regions of the trunk is 0.82 mm. Similar patterns are evident at the base of the crown. The trend of decreasing tree-ring width is generally observed not only in oaks but also across all woody-growing species (Zobel, van Buijtenen 1989; Rybníček et al. 2016). An analysis of variance (multifactor ANOVA) indicates that the average tree-ring widths from the monitored locations and sections differ significantly.

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Table 1. Descriptive statistics of average tree-ring width (mm) for *Q. robur* and *Q. petraea*

Plot	Position	Average	Q1	Median	Q3	Min.	Max.	SD	CV (%)
Q. robur	breast height	2.6	1.9	2.5	3.4	0.9	5.2	1.0	38.0
	crown base height	2.2	1.6	2.1	2.6	1.0	4.3	0.7	33.5
Q. petraea	breast height	1.5	1.2	1.4	1.7	0.7	3.4	0.5	32.6
	crown base height	1.6	1.2	1.5	1.8	0.9	3.4	0.5	33.1

SD – standard deviation; CV – coefficient of variation

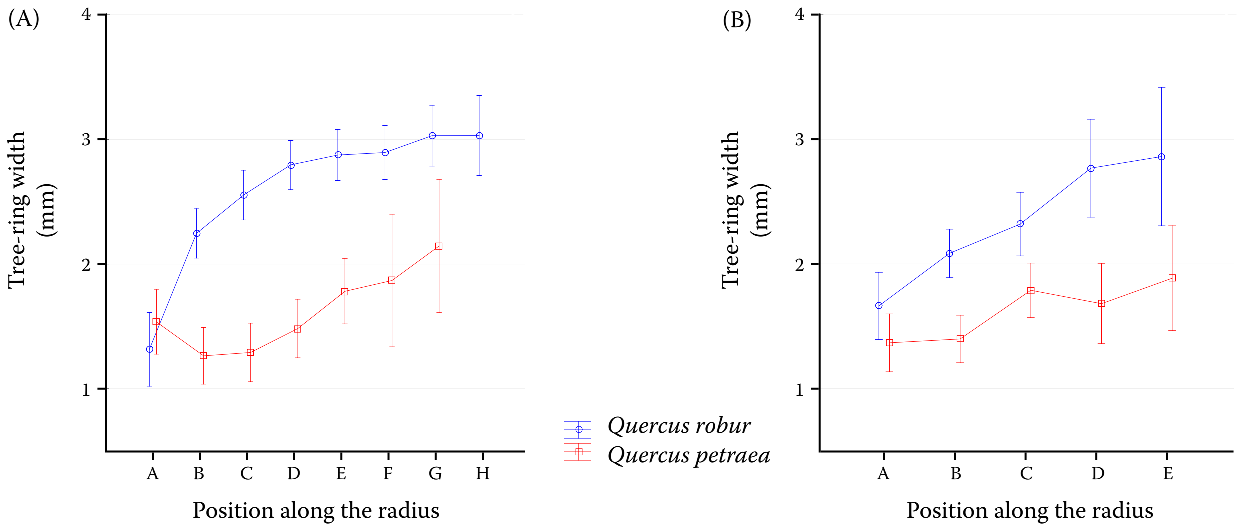

Figure 2. Tree-ring width distribution along the stem radius for both research plots and both positions on the stem: (A) breast height, (B) crown base height

Vertical lines indicate 0.95 confidence intervals

Wood density. A total of 754 samples were analysed for experimental determination of wood density, 311 samples for *Q. petraea* and 443 for *Q. robur*. It was found that the average wood density was 721 kg·m^{-3} for *Q. petraea* at the Soběšice plot and 662 kg·m^{-3} for *Q. robur* at the Janohrad plot, as measured at breast height (Table 2; Figure 3). Previous research conducted by Vavrčík and Gryc (2012) reached the same conclusions that *Q. petraea* wood from upland plots has a higher density than *Q. robur* wood from floodplain conditions. The oak wood density ranges from 448 kg·m^{-3} to 920 kg·m^{-3} for both analysed species. A similar density range, i.e. a minimum of 430 kg·m^{-3} and a maximum of 960 kg·m^{-3}, is reported for both oak species by Wagenführ (2000), with an average wood density of 690 kg·m^{-3}.

A larger difference between the minimum and maximum wood density was observed for *Q. petraea*. The coefficient of variation for wood density was between 6% and 11%, with lower values observed for *Q. robur*.

The pattern of wood density along the stem radius was notable. It was determined that the wood density in the outer regions of the trunk (section A), i.e. nearest to the cambium, is the lowest. As one moves towards the centre of the trunk, the wood density increases, a variation that is more pronounced at breast height. In *Q. petraea*, a decrease in wood density near the pith (sections G, H) was observed. Multifactor ANOVA indicated statistically significant differences in wood density between research plots and among most of the monitored sections at breast height. At the crown base height, no difference in wood density was observed between the monitored plots; only the peripheral parts of the stem exhibited differing densities from the rest. This discrepancy can be attributed to the smaller trunk diameter, greater variability in wood density, and an increased presence of reaction tension wood. The trend of wood density variation along the stem radius aligns with previously published findings by Mamoňová (2013), Zobel and

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Table 2. Descriptive statistics of wood density (kg·m^{-3}) at MC 12 % for *Q. robur* and *Q. petraea*

Locality	Position	Average	Q1	Median	Q3	Min.	Max.	SD	CV (%)
Q. robur	breast height	662	644	664	686	448	755	41	6.3
	crown base	701	669	700	736	600	821	49	7.1
Q. petraea	breast height	721	675	723	768	461	906	75	10.5
	crown base	710	657	711	759	501	920	79	11.3

MC – moisture content; SD – standard deviation; CV – coefficient of variation

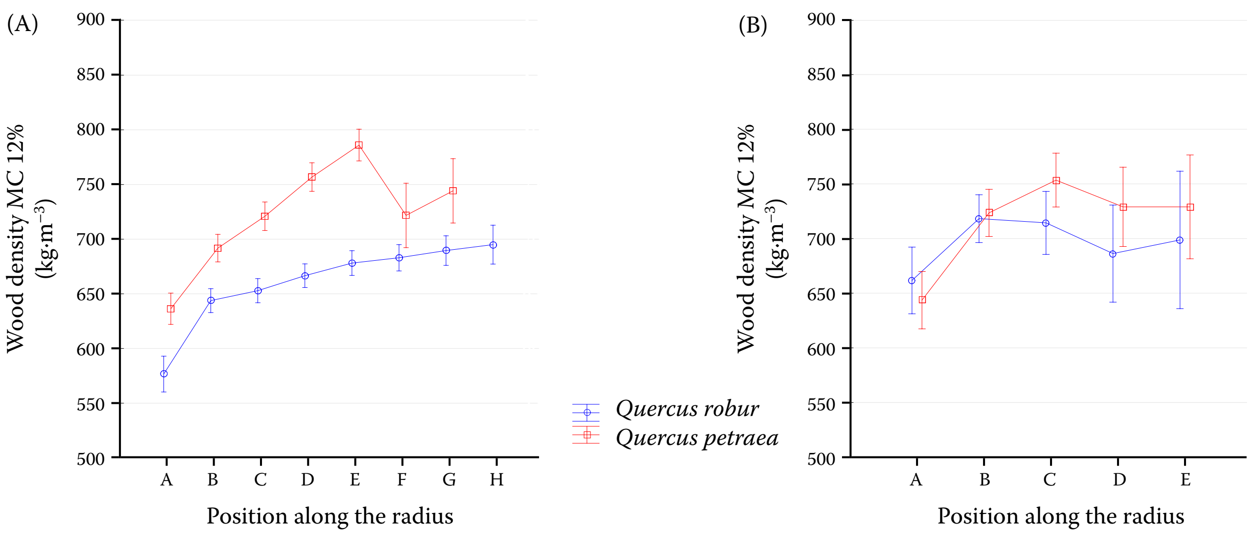

Figure 3. Wood density at MC 12% distribution along the stem radius for both research plots and both positions on the stem: (A) breast height, (B) crown base height

MC – moisture content; vertical lines indicate 0.95 confidence intervals

van Buijtenen (1989), Vavrčík and Gryc (2012), and Jakubowski and Dobroczyński (2021).

ANOVA indicated a statistically significant variation in wood density among the monitored trees within the research plots (Figure 4). The Soběšice plot exhibited greater variability in wood density for *Q. petraea*, which can be attributed to differences in site conditions and forest management practices. The Soběšice location features a mixed-age, diverse forest type, whereas Janohrad (*Q. robur*) represents a typical even-aged floodplain forest predominantly composed of two species: oak and ash.

Linear regression analysis (Figure 5), which examines the dependence of wood density on tree-ring width, confirmed a relationship between these parameters at breast height; however, such a correlation was not observed at the crown base height in *Q. robur*. The R^2 value for *Q. robur* at breast height was 0.13, and for *Q. petraea*, it was 0.12. This indicates that only 12% and 13%, respectively, of the total variance in wood density can be attributed to the width of the tree ring.

The results emphasise the critical importance of local edaphic and climatic site conditions, alongside species-specific physiological and anatomical adaptations, as primary factors influencing wood quality characteristics and wood structure (Zanne et al. 2010). These findings hold significant implications for evidence-based forest management decision-making and species-site matching strategies, as well as for the optimisation of timber utilisation protocols within Central European temperate forest ecosystems. The observed differences in density illustrate fundamental trade-offs between hydraulic efficiency and mechanical support, reflecting the evolutionary divergence between these closely related oak species under varying environmental selection pressures (Pratt, Jacobsen 2017). Contemporary research employing advanced analytical methods has established that wood density responds sub-

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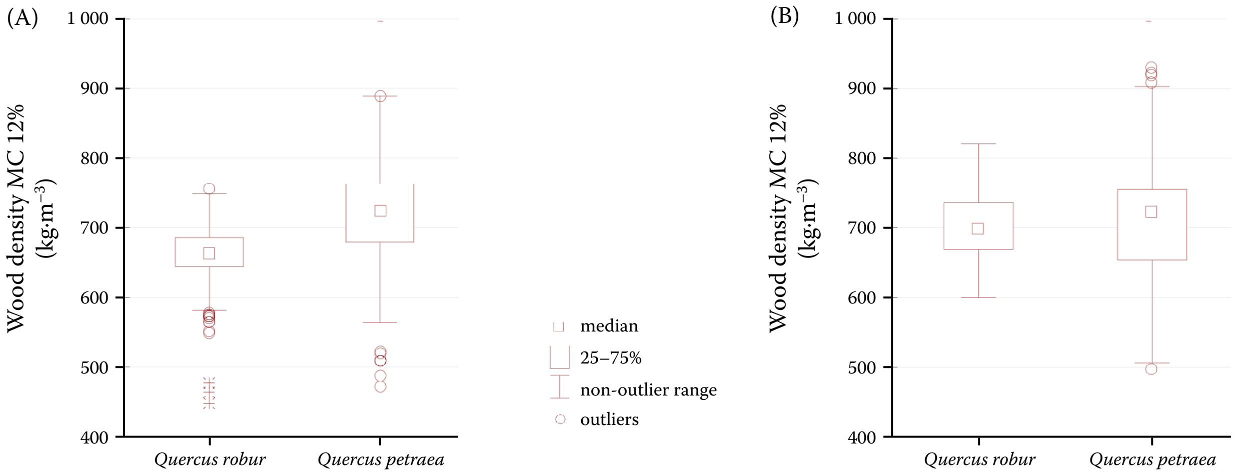

Figure 4. Wood density distribution at MC 12% among the analysed trees for both research plots and both positions on the stem: (A) breast height, (B) crown base height

MC – moisture content

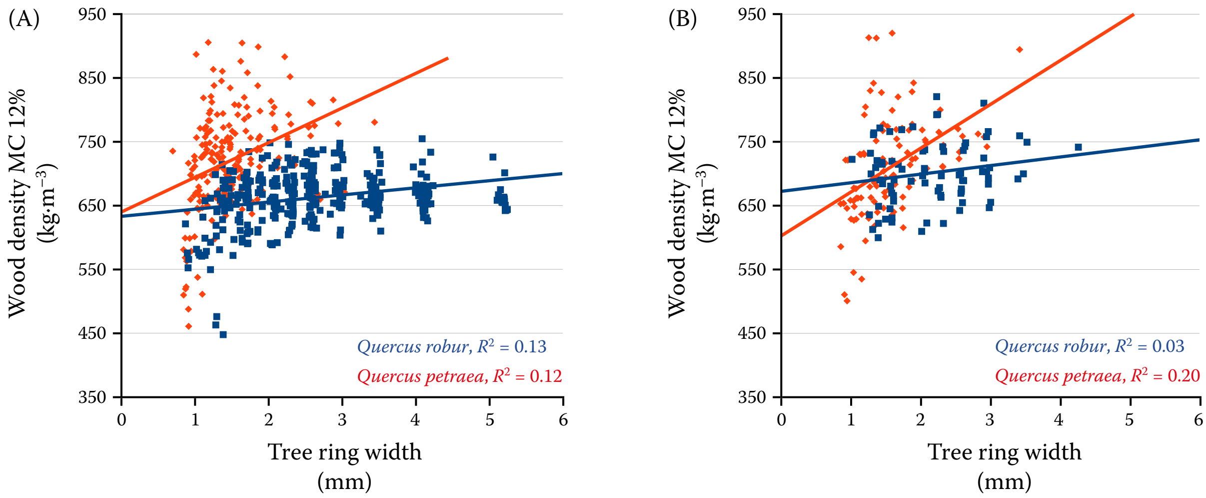

Figure 5. Regression analysis of wood density at MC12 % and tree-ring width for both analysed species and positions in the stem: (A) breast height, (B) crown base height

MC – moisture content

stantially and measurably to environmental site conditions, water availability, and climate-related stressors, with these responses frequently mediated through modifications in the proportional allocation of earlywood and latewood tissue within tree rings (Bergès et al. 2008). Under optimal soil moisture and nutrient availability, trees preferentially allocate growth resources to the formation of large-diameter earlywood vessels. These vessels facilitate efficient water transport but also increase susceptibility to hydraulic failure via cavitation-induced embolism during subsequent water stress episodes (Pérez-de-Lis et al. 2018). Conversely, under water-limiting conditions imposed by low soil moisture availability or drought stress, trees exhibit adaptive anatomical responses including the formation of smaller-diameter vessels coupled with proportionally greater allocation to latewood tissue characterised by thicker cell walls and elevated wood density, representing a developmental strategy that simultaneously enhances mechanical support capacity and xylem hydraulic safety at the metabolic cost of reduced water transport efficiency (Pérez-de-Lis et al. 2018; Fontes et al. 2022).

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CONCLUSION

Oak wood density can vary significantly across different species, locations, individual tree characteristics, trunk position, and wood structure (sapwood and heartwood zones). It has been demonstrated that: (*i*) the wood density of *Q. petraea* is considerably higher than that of *Q. robur* in the research plots; (*ii*) the variability of wood density across the radius is lower in *Q. robur* compared to *Q. petraea* at breast height; and (*iii*) tree-ring width accounts for 12–13% of the variability in wood density at breast height in both oak species. These results indicate that a deeper understanding of wood density necessitates examining the wood's structure in greater detail. The research on oak wood density at 12% moisture content demonstrates that both *Q. petraea* and *Q. robur* exhibit complex patterns of density variation influenced by multiple interconnected factors. *Q. petraea* generally exhibits higher mean density values than *Q. robur*, particularly when both species are grown in their optimal ecological niches. The radial distribution of density, relationships with annual ring structure, and the influence of ecological factors all contribute to within-species variation that exceeds differences between species in many circumstances.

Future studies should concentrate on parameters such as the shape and distribution of vessels, libriform fibres and tracheids. Overall, these findings underscore the importance of species-specific density profiles for informing adaptive forest management and enhancing timber utilisation strategies in the context of a changing climate.

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