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Links between tree phenology and wood traits in sessile oak (*Quercus petraea* (Matt.) Liebl.)

Ioana Maria Gafenco (Pleșca)[1,2], Florin Dinulică[1], Bogdan Ionuț Pleșca[1,2]✉, Neculae Șofletea[1]

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Abstract Tree phenology and wood traits are considered of foremost importance in understanding species' responses to the influence of climate change, thus the existence of a link between tree phenology and wood traits has become increasingly appealing in forestry research. The aim of this study was to explore the relationship between leaf flushing and wood traits (basic wood density, tree ring width, tree ring phenology, sapwood width and number of sapwood rings) in sessile oak (*Quercus petraea* (Matt.) Liebl.). We investigated trees with distinctive phenological behaviour (early flushing and late flushing) from three peripheral populations, one non-peripheral population and one sessile oak comparative trial close to the species eastern distribution range in the Eastern Carpathians. Covariance analysis, partial correlations, nonparametric statistics, and Principal Component Analysis were used to investigate the link between tree phenology, wood density, and some structural metrics. It was statistically confirmed that, at comparable ages and radial growth, the sessile oak trees exhibiting late leaf flushing had lighter basic wood density and greater density differences between sapwood and heartwood than early flushing trees. Independent of age, trees with intermediate flushing have wider rings, the formation of which is much earlier than in early flushing trees. At the same age, late trees from geographically peripheral populations have a higher number of sapwood rings. Also, the results revealed that peripheral populations had lower basic wood density, while this was not the case for peripheral provenances tested in the comparative trail established in an ecologically optimal area. These findings help us enlarge our understanding of the relationship between leaf flushing and wood traits, which could be useful for improving sessile oak management strategies near the eastern limit of the sessile oak natural range, which is becoming more and more critical in the context of the current climate changes.

Keywords: tree phenological category, wood traits, sessile oak, peripheral populations, comparative trial, basic wood density, tree ring width, tree ring formation, sapwood width.

Addresses: [1]Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Brașov, Romania | [2]National Institute for Research and Development in Forestry (INCDS) 'Marin Drăcea', Voluntari, Romania.

✉ **Corresponding Author:** Bogdan Ionuț Pleșca (bogdan.plesca@icas.ro).

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Introduction

Tree phenology and wood anatomy are expected to provide major insights into species' responses and adaptation to future climate change effects (Denny et al. 2014, Anderegg & Meinzer 2015).

In temperate forests, spring bud burst occurrence has a substantial impact on various ecosystem processes (Polgar & Primack 2011, Panchen et al. 2014), as well as on tree functioning (Delpierre et al. 2017, 2019). Several studies have shown that individual trees within the same population can exhibit considerable differences in bud burst phenology (Richardson et al. 2013, Lechowicz 2016, Cole & Sheldon 2017, Delpierre et al. 2017, Marchand et al. 2020). In addition, significant differences in the timing of bud burst were found among individuals from different geographic locations when tested in common garden experiments (Jensen & Hansen 2008, Vitasse et al. 2009).

Phenological studies also indicate that individual trees can be classified based on their phenological rank into distinct phenological categories: early, intermediate, and late flushing trees (Chesnoiu et al. 2009, Delpierre et al. 2017, Denéchère et al. 2021). Lechowicz (1984) examined various factors influencing the timing of bud burst in temperate deciduous species, highlighting how physiological traits, including aspects of wood anatomy, contribute to differences in leaf flushing among cohabiting trees. More recently, other studies provided evidence that wood anatomy influences species differences in leaf-out phenology (Panchen et al. 2014, Savage et al. 2022). As such, in temperate species, differences in flushing time may be associated with different anatomical structures, which would be reflected in different wood properties (Popescu & Dinulica 2020).

Moreover, combined studies using wood anatomical traits and phenological data are potentially useful for explaining the environmental signals registered at the tree level during different wood formation phases (Pérez-de-Lis et al. 2016). Typically, the timings of leaf and cambium phenology do not occur concurrently and may be influenced differently by environmental cues (Delpierre et al. 2016). At the same time, it is known that the relationship between leaf and cambial phenology is species-specific and depends to a large extent on wood porosity (Takahashi et al. 2013, Gričar et al. 2020). For example, in *Quercus petraea*, which is a ring-porous species, radial growth usually precedes bud-burst (Bréda & Granier 1996, Bergès et al. 2008, Michelot et al. 2012), likely because of the winter embolism of the large xylem vessels (Rybníček et al. 2015). Importantly, for *Q. petraea* the wood growth (which is controlled by leaf phenology) was reported to have a much greater influence on the wood formation process compared to the growth rate (Pérez-de-Lis et al. 2016, 2017). Together, the growth rate and the growth duration of wood formation determine the annual tree-ring width (Stridbeck et al. 2022).

The relationship between leaf phenology and wood properties has been reported for several deciduous species, such as *Q. robu*r L. (Pérez-de-Lis et al. 2016, Guada et al. 2019), *Q. pyrenaica* Willd. (Pérez-de-Lis et al. 2016), *Q. pubescens* Willd., *Fraxinus ornus* L., *Ostrya carpinifolia* Scop. (Gričar et al. 2020) and *Fagus sylvatica* L. (Čufar et al. 2008, Prislan et al. 2013. Popescu & Dinulica 2020, Arnič et al. 2021), and - to a lesser extent - in conifers like *Picea abies* Karst., *Larix decidua* Mill. or *Pinus cembra* L. (Rossi et al. 2009). In *Q. robur*, Pérez-de-Lis et al. (2016) demonstrated that bud burst coincides with the onset of wood formation, while the onset of earlywood vessel formation influences hydraulic properties, particularly vessel size.

Several wood traits have been quantified as wood quality characteristics, particularly wood density, ring width, ring count, as well as the presence and extent of different wood tissues

(Punches 2004). Wood density, apart from being a metric extensively used in ecological studies related to forest biomass and carbon stock estimation (Devi et al. 2013, Chave et al. 2014, Bastin et al. 2015, Araújo et al. 2022), is recognised as a key element for evaluating wood quality (Guilley et al. 2004, Longuetaud et al. 2009, Kurz-Besson et al. 2016, Lachowicz et al. 2019, Sousa et al. 2021) due to its effect on wood mechanical proprieties (Vavrčík & Gryc 2012, Machado et al. 2014, Longuetaud et al. 2016, Dias et al. 2019).

Wood density is influenced by several factors, including wood species, moisture content, the position of the analysed wood within the tree, the effects of ecological, and silvicultural factors (Pásztory et al. 2014), as well as the proportion of latewood (Vavrčík & Gryc 2012), because of its densely layered, thick-walled cells and smaller lumen dimensions compared to earlywood. Other factors that have the capacity to influence wood density are altitude and the phenological category (i.e., timing of tree developmental stages such as early, intermediate, or late flushing), as previously reported by Popescu and Dinulica (2020).

Recent studies suggest that functional characteristics, including wood density, may be associated with the timing and development of tree species phenophases (Galvão et al. 2021, Wang et al. 2021). Leaf phenology and wood density are plant functional traits that are useful in assessing species responses to climate change and estimating biomass production. Therefore, a considerable number of studies have described the relationship between phenological observations and wood density, especially in tropical forests (Shrestha et al. 2006, de Lima & Rodal 2010, Shimamoto et al. 2016, Tarelkin et al. 2019, de Lima et al. 2021, da Silva E Teodoro et al. 2022). These studies highlight that tree species with earlier leaf phenology generally exhibit higher wood density, and that tree phenology significantly influences stem growth rhythms and wood anatomy variability across different ecological contexts, shaping adaptive strategies and ecological dynamics in response to changing environmental conditions. In contrast, few studies have concurrently documented leaf phenology and wood density in temperate regions (Adams et al. 2021); consequently, information on this subject is still deficient. In addition, the association between leaf phenology and other wood traits has been little explored (Takahashi et al. 2014, Kolář et al. 2016, Chen et al. 2022).

Given the common genetic control observed for bud burst and bud set, along with their association with structural traits (Vaganov et al. 2006) and growth features (Lagercrantz 2009, Karlgren et al. 2013), it is reasonable to suggest that the timing difference between early and late-flushing trees (phenological gap) may impact the development of certain structural traits.

In this regard, peripheral populations, and especially those at the lower limits of the natural distribution range are particularly interesting in assessing the relationship between leaf phenology and wood traits, since they are considered among the most vulnerable to the impacts of climate change (Fady et al. 2016, Popescu & Șofletea 2020).

Within the European forests, sessile oak (*Q. petraea* (Matt.) Liebl.) is a species recognised for its significant ecological importance, as well as for its considerable cultural and economic value (Eaton et al. 2016, Mölder et al. 2019). In addition, the importance of sessile oak is more accentuated as it is expected to show an increased potential to adapt to the predicted climate changes (Maleki et al. 2018, Kohler et al. 2020), due to its relative tolerance for future warmer and drier climates (Nölte et al. 2020).

In Romania, sessile oak is one of the most important forest components, being the most abundant oak species, and accounting for 8.3% of the forested surface (NFI 2019).

Hence, the present study concerns peripheral *Q. petraea* populations, the study of which can provide valuable information on adaptability under climatic stress conditions (Mátyás 2010, Borovics & Mátyás 2013) and which are becoming increasingly useful in the context of current climate change (Fady et al. 2016).

This study aimed to investigate how the tree phenological category was related to the basic wood density, ring width, sapwood traits and tree ring phenology in sessile oak growing at three peripheral populations, one reference population, and in one comparative trial. To this end, we compared individuals with contrasting phenological behaviour (early flushing versus late flushing) indicated by the onset of leaf flushing. We aimed to explore the potential of multivariate statistical methods such as principal component analysis and cluster analysis in distinguishing distinct phenological groups based on wood traits. Additionally, we investigated how belonging to specific phenological groups influences various wood traits. This analysis aims to enhance our understanding of the relationships between these features, potentially informing more effective management strategies for sessile oak in the future. At the same time, the location of the studied populations towards the eastern limit of the species area can provide useful information for their response under ecological toleration limit conditions.

Materials and Methods

Study sites and tree sampling

Specifically, sessile oak (*Quercus petraea*) trees were monitored at four sites and in one comparative trial (Table 1 and Figure 1). A total number of 227 trees belonging to the dominant layer were previously subjected to phenological observations (Gafenco et al. 2022). The naturally regenerated monitored stands have similar levels of competition, indicated by the close values of stand densities (Table 1). Three sites (FUN, OLT, and SAT) were selected near the species' eastern geographical distribution limit, in low-elevation areas along a north-south transect (hereafter referred to as peripheral populations). The fourth site (HEL) was selected from the species' inner range in Romania (hereafter referred to as the non-peripheral population). In the sense of the present work, by natural populations we mean naturally regenerated stands.

For the comparative analysis, a sessile oak comparative trial (FAN) that was established under optimum environmental conditions for sessile oak in the eastern part of the country, was also included in the study. Here we selected and analysed 10 provenances, all originating from Romania; three of them fell into the category of peripheral populations from the eastern–north-eastern limit for sessile oak (Dolhasca, Sascut, and Botoșani), and the other seven were from areas with a climate considered favourable to sessile oak (Băbeni, Văleni, Beiuș, Făget, Blaj, Lechința, and Cluj).

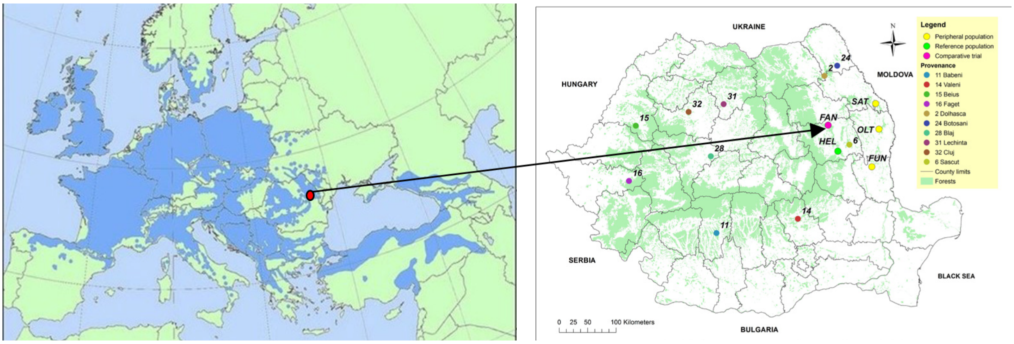
Leaf phenology and weather conditions

In each selected site the timing of spring bud

Table 1 Characteristics of the sampled sessile oak populations (Gafenco et al. 2022) and sample size.

Site plot	Stand status	Stand density (trees·ha^{-1})	Geographic location			Climatic conditions		No of trees for phenological observations	Age of trees (years)	No of sampled trees
			Latitude [N]	Longitude [E]	Altitude [m]	Mean annual temperature (°C)	Annual rainfall (mm)			
FUN	Peripheral population, natural regeneration	291	45°58′	27° 41’	210	9.6	470	34	80-95	10
OLT		283	46°34′	27° 53’	305	9.2	530	50	70-75	10
SAT		289	46°58′	27° 49’	300	9.2	535	50	75-110	10
HEL	Non-peripheral population, natural regeneration	294	46°14′	26° 55’	490	9.2	655	43	75-110	10
FAN*	Non-peripheral, ecological optimum, plantation	340	46°39′	26° 43’	260	9.6	590	50	30-40	50

Note: *Sessile oak comparative trial.



(a) (b)

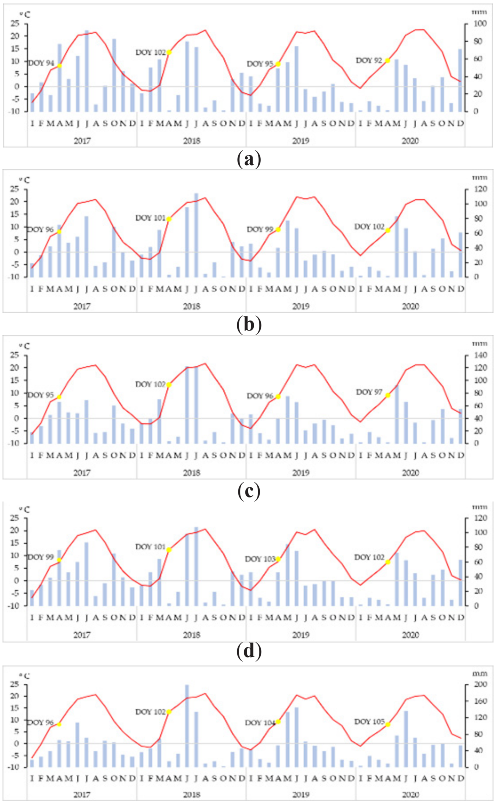
Figure 1 The natural distribution of sessile oak (Ducousso & Bordacs 2004) **(a)**, the location of the study area and the selected provenances tested in the FAN comparative trial **(b)**.

burst for sessile oak was previously recorded for four consecutive years (Gafenco et al. 2022). The bud burst date was expressed as DOY (day of the year) and was defined as the moment when more than 50% of the crown buds were swollen and had the first green leaflets visible (Figure 2). With the timeline for the onset of bud burst already established (Gafenco et al. 2022) we were able to differentiate trees based on their phenological rank. Accordingly, trees were placed into a phenological category (early flushing, intermediate flushing, or late flushing).

During the growing season of the years 2017-2020, air temperature was recorded and stored hourly with a HOBO Pro v2 data logger installed at each site. For the precipitation totals, we used data extracted from the KNMI Climate Explorer (https://climexp.knmi.nl/) (Trouet & Van Oldenborgh 2013). August is the month with the highest average temperatures, and January is the month with the lowest average temperatures (Figure 3). There are yearly fluctuations in monthly precipitation, with August typically being the driest month, while June and July are the rainiest months (Figure 3).

(a) (b)

Figure 2 Leaf flushing evaluation scores: buds fully closed (dormant stage) (**a**) and swollen buds with the first green leaflets visible (bud burst stage) (**b**).



(a) (b) (c) (d) (e)

Figure 3 Monthly average air temperature values (red lines, °C) and precipitation totals (blue bars, mm) during the growing seasons of the years 2017–2020 for the populations (**a**) FUN, (**b**) OLT, (**c**) SAT, (**d**) HEL and (**e**) the FAN comparative trial. The yellow dots indicate the average DOY bud burst values for the analyzed trees.

Wood sampling and wood trait determination

Within the peripheral populations and the non-peripheral natural regenerated population, 10 trees (five trees with early flushing and five trees with late flushing) were selected for wood analysis. On the other hand, in the comparative trial, the wood analysis included 50 trees (five trees per provenance) (trees with early, intermediate, or late flushing).

At the beginning of April 2021, trees selected for wood analysis were cored at breast height (1.3 m) with an increment borer. The samples were conditioned to a moisture content of approximately 10% by maintaining them in a temperature and humidity chamber set at 20°C and 65% relative humidity until future analysis. In the laboratory, for each core, the sapwood (SW) was delimited from the heartwood and the heartwood was divided into juvenile heartwood (JHW), which forms during the early years of the tree's life, and mature heartwood (MHW), which develops as the tree ages, depending on the dynamics of the annual ring width. The delimitation between JHW and MHW was done on the graph of variation of the width of the annual ring from pith to bark, and in parallel the variation of the proportion of latewood was examined. Juvenile wood samples included wide inner rings with large variations in width from year to year (Zobel & Sprague 2012). However, in the comparative trial, as the trees were younger, the frequency of mature wood was not long enough to separate the cores into three sections, so they were only separated into sapwood and heartwood (HW).

Prior to basic density determination, for each resulting section, we counted the number of annual rings in the section and the number of sapwood rings (NSR); we also measured the section length (L) and the proportion of sapwood (SW). Since in sessile oak annual rings are easily distinguishable due to the alternation of early wood and late wood, the number of annual rings was obtained by direct observation through a Zeiss stereomicroscope.

Moreover, for trees from the comparative trial, the stage of annual ring formation was also evaluated, microscopically, at the time of sample collection (2 April 2021). The following stages were distinguished: 1 - the 2021 ring had not formed, 2 - the 2021 ring contained only a single row of pores in the earlywood zone, 3 - the 2021 ring contained only two rows of pores in the earlywood zone and 4 - the 2021 ring contained both earlywood and part of the latewood.

Subsequently, following the maximum moisture content method (Smith 1954, Dumitriu-Tătăranu et al. 1983), all sections were saturated with water by boiling them for 12 hours in order to determine the basic wood density (BWD). During this process, the water was replaced several times in order to eliminate the content of dissolved extractives that could lead to an overestimated value of basic density (Taylor 1974, Lai et al. 1980, Zobel & Van Buijtenen 2012). In the next phase, the sections were weighed twice: (1) immediately after boiling, and (2) in the anhydrous state, after drying them at 104°C on a thermobalance until they attained a constant weight.

Finally, the basic density (in $g\cdot cm^{-3}$) of each section was calculated using Equation (1) (Smith 1954, Dumitriu-Tătăranu et al. 1983):

$$BWD = \frac{1}{\frac{m_m - m_0}{m_0} + \frac{1}{G_{so}}}, \qquad (1)$$

where BWD is basic wood density, m_m is the mass of saturated wood sections, m_0 is the mass of anhydrous wood sections and G_{so} is the average density of wood substance in the anhydrous state; a constant usually accepted as having a value of 1.53 $g\cdot cm^{-3}$, since the density of cell-wall substances is practically identical for all wood species (Usta 2003).

Additionally, the average ring width (ARW) was calculated by dividing the length of sections by the number of rings in each section which was determined through stereo-microscopy (Equation 2):

$$ARW=L/NSR \qquad (2)$$

Statistical analysis

For all data, the goodness of fit to normality was assessed using the Kolmogorov-Smirnov and Shapiro–Wilk test (Sheskin 2003) and the homogeneity of variances was assessed using Levene's test (Zar 2010). If the statistical assumptions were not satisfied (normality of observations and homogeneity of variances), we performed the Kruskal–Wallis non-parametric test.

In the case of a normally distributed random variable, variance analysis was practiced.

Because tree age and radial growth are key factors in the development of wood structure, to remove their interaction in the relationship of tree phenology with the studied wood properties, covariance analysis was used (Dytham 2011). Specifically, to assess the influence of tree phenological category on wood traits - including BWD, SW, NSR, and 2021 tree ring phenology - tree age and ARW were included as continuous covariates to control for their potential confounding effects on the dependent variables. The use of covariates ensured that the observed effects of tree phenological category were not confounded by the variability due to tree age or growth rates.

Before performing the analysis of covariance, the covariate values of tree age and radial growth were examined with analysis of variance, with wood characteristics as the dependent variables. For the analysis of variance, tree age was categorized into 10-year classes, and the ring width was categorized into four value classes based in quartile sizes.

After controlling for tree age and ring width, the partial correlation was used to estimate the relationship between wood and phenology variables.

Further, we used principal component analysis (PCA) to study the variation among wood traits and phenological categories. In addition, before performing PCA we transformed all variables (we applied a square-root transformation or $\log_{10}$ transformation) that were non-Gaussian distributed and we checked if the data set was appropriate for this type of analysis by implementing the Kaiser–Meyer–Olkin Measure of Sampling Adequacy (KMO) and Barlett's Test of Sphericity (BTS).

The data are considered adequate if the KMO value is between 0.5–1.0 and the *p*-value is less than 0.05 for BTS.

Furthermore, cluster analysis was applied to find similarities between populations or provenances by using different wood traits. For this, Ward's method and Euclidean distance were used as an amalgamation rule and distance measure, respectively.

Statistical analysis was conducted using *STATISTICA v.8.0* software and the confidence level was predefined at 95%.

Results

Basic wood density in relation to tree phenology

At the tree level, BWD was a standard Gaussian random variable (Kolmogorov-Smirnov test $d = 0.102$, Lilliefors test $p < 0.05$).

Over the entire sample, BWD decreases somewhat with tree age (Pearson's product-moment correlation coefficient = -0.272, $p = 0.01$) and increases slightly but insignificantly with mean annual ring width (Pearson $r = 0.186$, $p = 0.08$).

Analysis of covariance shows that BWD differs with respect to the phenological category of trees, independent of tree age and radial growth (Table 2).

Table 2 Analysis of covariance for the effect tree phenological category on the studied wood characteristics (*p* from *F* test).

Dependent variable	Fixed effects: tree phenological category	
	Covariates	
	Tree age	Ring width
BWD	0.01	**0.01**
SW	0.34	0.32
NSR	0.57	0.36
2021 tree ring phenology	**0.02**	**0.03**

Note: BWD – basic wood density; SW – sapwood; NSR – number of sapwood rings.

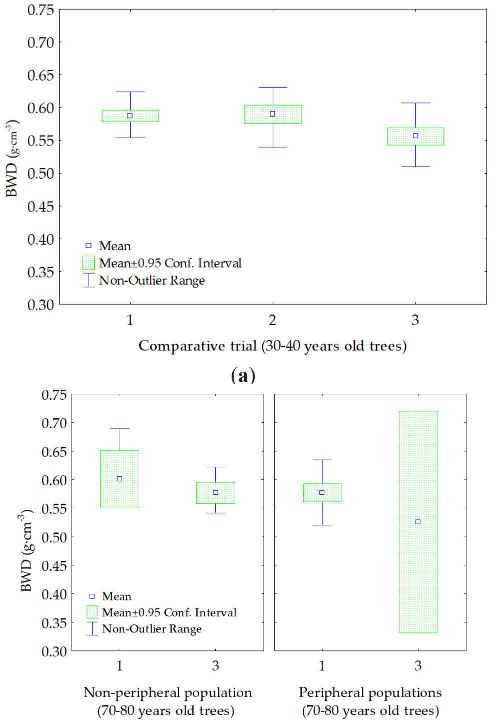
However, wood density varied with the status of the sampled tree populations (peripheral/non-peripheral, natural/plantation): F = 3.18, p = 0.04. For this reason, in Figure 4 the wood density according to the phenological category of the trees was stratified according to the type of population. It turned out that compared to the non-peripheral population, the peripheral populations had the BWD of the breast height section with 0.010 g·cm^{-3} lower.

When considering the entire sample, early-flushing trees had a BWD 0.031 g·cm^{-3} higher than late-flushing trees.

At the comparative trial level, which was installed in a non-peripheral site, the peripheral provenances (Dolhasca, Sascut and Botoșani) had slightly higher BWD than non-peripheral provenances (Băbeni, Văleni, Beiuș, Făget, Blaj, Lechința and Cluj), but the differences were not statistically significant ($F = 0.47$, $p = 0.50$).

The BWD also varied along the wood radius (Figure 5). In the comparative trial, the SW basic density was consistently lower than the HW basic density (Kruskal–Wallis test: $H = 18.95$, $p < 0.001$), but the differences were higher in late flushing trees (Figure 5a). Also, in the natural regenerated populations, BWD differences were observed between juvenile and mature heartwood, the latter being less dense (Figure 5b).

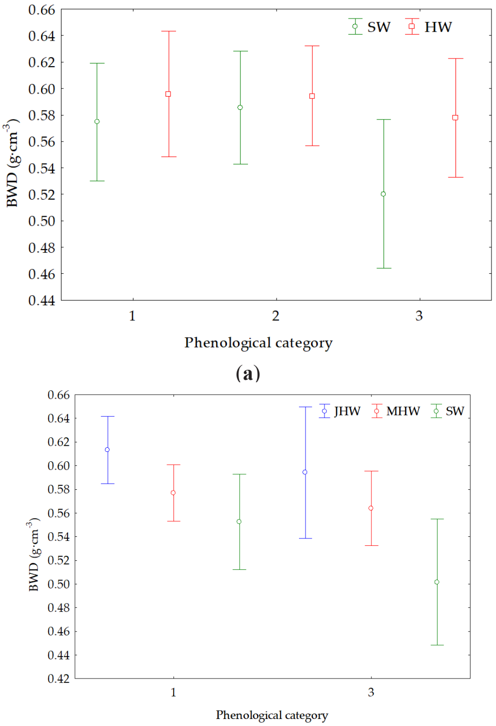
When we separated the heartwood from the sapwood, the differences between early flushing and late flushing trees regarding wood density were accentuated (Figure 5a,b). Also, after stratifying the density values according to the age of the trees and the position of the sample along the radius, it turned out that, in the comparative trial, the sapwood and



(a)

(b)

Figure 4 The variation of BWD according to the tree phenological category (1- early flushing, 2- intermediate flushing, 3- late flushing) and sampling locations (comparative trial (**a**) and natural regenerated populations (**b**))



(a)

(b)

Figure 5 Sapwood *versus* heartwood BWD (mean ± standard deviation) according to the phenological category (1 - early flushing, 3 - late flushing) in the trees from the comparative trial (**a**) and in the natural regenerated populations (**b**).

heartwood BWD of the early and intermediate flushing trees was higher than that of the late flushing trees (Figure 5a).

In the natural regenerated populations, late flushing trees had the sapwood BWD on average with 0.100 $g\cdot cm^{-3}$ lower than JHW (Figure 5b). Thus, in trees aged 70-80 years, the BWD of early flushing trees was on average 0.021 $g\cdot cm^{-3}$ higher in the sapwood, 0.026 $g\cdot cm^{-3}$ higher in the MHW, and 0.028 $g\cdot cm^{-3}$ higher in JHW than the BWD of late flushing trees.

Structural traits in relation to tree phenology

The width of annual rings was not a Gaussian variable (Shapiro-Wilk test $W = 0.943$, $p < 0.001$). Differences between plots were statistically significant ($W = 22.60$, $p = 0.04$) and it was primarily due to the age of the trees, especially those from the comparative trial ($H = 50.88$, $p < 0.001$). At the same tree age, peripheral populations had narrower rings at breast height than the non-peripheral population, as well as a greater amplitude of ARW, but the differences were not statistically significant (Kruskal Wallis multiple comparison array $p = 0.13$). To eliminate the influence of the age of the trees, in Figure 6, the variation of the ARW according to the phenological category was presented for two representative age classes.

Concerning the variation of the ARW according to the phenological category (Figure 6), we observed that the widest average annual rings were found for intermediate-flushing trees, and the narrowest for late-flushing trees, the differences being statistically significant (Kruskal–Wallis test: $H = 8.369$, $p < 0.05$) independent of the age of the trees.

Comparing different wood parts, the sapwood had narrower average rings than heartwood, and both wood parts had narrower average rings in late flushing trees (Figure 6).

There were no differences between site plots in respect to SW ($H = 19.42$, $p = 0.11$). Across the entire sample of trees, SW was not related to tree age (Pearson $r = -0.0043$, $p = 0.69$), but it increased significantly with radial growth (Pearson $r = 0.491$, $p < 0.001$).

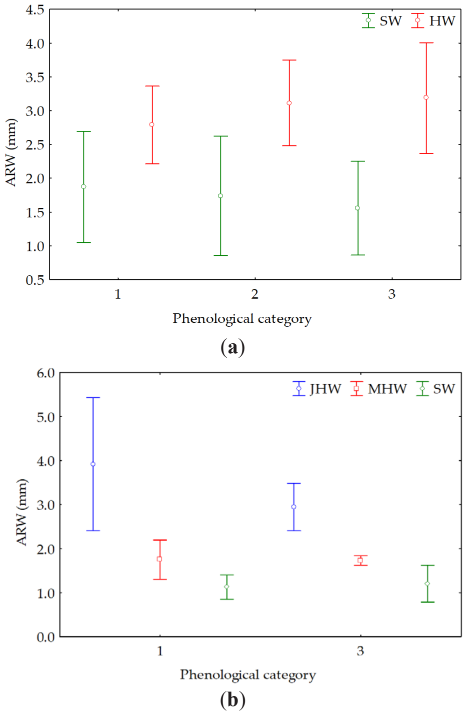


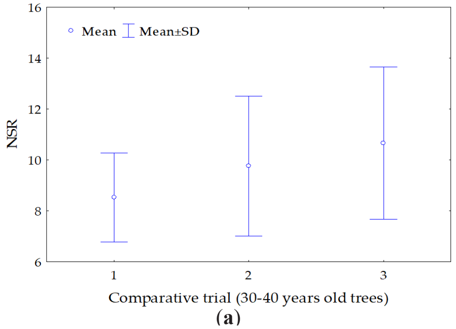
Figure 6 ARW (mean ± standard deviation) according to phenological category (1 - early flush-ing, 2 - intermediate flushing, 3 - late flushing) in trees from the comparative trial, 30-40 years old (**a**) and in natural regenerated populations, 70-80 years old trees (**b**).

Differences between sites with respect to NSR were statistically significant ($H = 42.83$, $p < 0.001$). Across the whole sample of trees, NSR increased with tree age (Pearson $r = 0.613$, $p = 0.69$, $p < 0.001$), but decreased with radial growth (Pearson $r = -0.574$, $p < 0.001$).

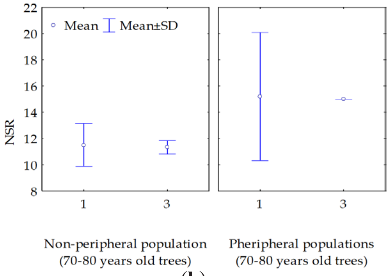
The average NSR of all trees from the comparative trial (trees 30-40 years old) was 9 ± 2.5 (Figure 7a), with a range of variation between 5 and 16 rings, and of the naturally regenerated populations (70-80 years old trees), 14 ± 4.4 (Figure 7b), ranging from 6 to 27 rings. Apparently, NSR increased with tree age (as revealed from the simple correlation), but after controlling for the ring width effect, NSR on the contrary decreased with age (partial correlation = -0.279, $p = 0.01$).

Additionally, we tested for the relationship between the NSR and the geographical coordinates of the ten provenances' origins, and we found that the NSR was significantly and negatively correlated with the longitude of the provenances' origins (Spearman rank order correlation $R = -0.230$, $p < 0.05$). Therefore, although the correlation was weak, our sessile oak provenances showed a decreasing tendency of the NSR from west to east, i.e., the peripheral provenances had fewer NSR. When we compared the naturally regenerated populations, the peripheral populations presented an obviously higher NSR compared to the non-peripheral one (Figure 7b).

The differences between early and late-flushing trees were also analysed regarding the sapwood metrics. Possible differences between trees with different phenology in relation to SW and NSR (NSR decreased from late, to intermediate, to early flushing trees, Figure 7a) were due to radial growth. For example, in the comparative trial, trees NSR decreased with ARW (Spearman Rank Order Correlations = -0.354, $p = 0.02$). However, after accounting for the contribution of radial growth to sapwood size through analysis of covariance, the phenological category no longer has a significant effect on sapwood size differences (Table 2).



(a)



(b)

Figure 7 The variation of NSR according to phenological category (1 - early flushing, 2 - intermediate flushing, 3 - late flushing) depending on the age of the trees and the status of the population

In the comparative trial (30-40 years old trees), tree phenology was also analysed in relation to the 2021 annual ring formation. The non-parametric test (Kruskal–Wallis test: $H = 13.151$, $p < 0.05$) revealed significant differences between the phenological stages of 2021 ring formation according to the trees' phenological category.

Unexpectedly, in 49% of the early-flushing trees (22% of the total number of trees from the comparative trial), a ring had not formed by 2 April 2021, while in some late-flushing trees, the ring was advanced in formation (Figure 8). Furthermore, in most intermediate flushing trees (61%, or 23% of the total number of trees from the comparative trial), the formation of the 2021 ring was advanced (Figure 8).

When we inspected provenances, surprisingly, in provenance Cluj, which had among the slowest onsets of bud burst in previous years (Gafenco et al. 2022), the formation of the 2021 ring was advanced. In contrast, the peripheral provenances (Dolhasca, Sascut, and Botoşani) were among the fastest to flush (Gafenco et al. 2022), but in most cases

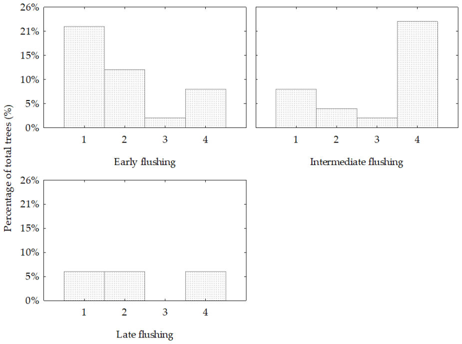


Figure 8 2021 annual ring phenology according to phenological category for trees 30-40 years old: 1 - the 2021 ring had not formed, 2 - the 2021 ring contained only a single row of pores in the earlywood zone, 3 - the 2021 ring contained only two rows of pores in the earlywood zone and 4 - the 2021 ring contained both earlywood and part of the latewood.

the 2021 ring had either not been formed or was at an initial development stage.

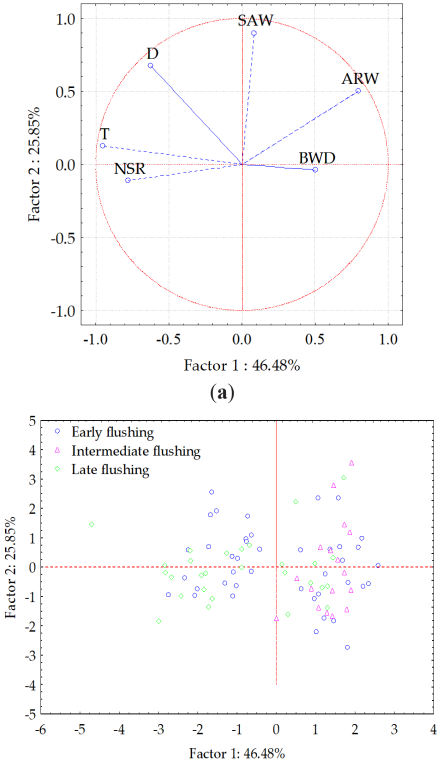
Principal component analysis and cluster analysis

We confirmed the adequacy of the data for PCA (*KMO* = 0.517, and BTS returned a significance value lower than 0.001). The PCA results showed that the first two factors described 72% of the total variance, i.e. 46% and 26%, respectively (Figure 9a,b).

The first axis was mainly influenced by tree age and NSR, while the second axis was highly correlated with SW. Among traits, the BWD had the lowest variance contribution and was notably correlated with tree age. Furthermore, the NSR varied in tandem with the age of the trees. PCA did not highlight obvious differences between phenological categories, except the intermediate-flushing trees, which had positive values on Factor 1. Therefore, among the phenological categories, intermediate flushing trees were better associated with the studied properties of wood (Figure 9b).

From the hierarchical cluster analysis, we could distinguish two groups based on the five wood traits selected (BWD, tree age, ARW, SW, and NSR) (Figure 10): one represented by the comparative trial and one by the natural populations. Furthermore, their differences were highlighted by the long Euclidean distance.

The dendrogram separated the natural regenerated populations from the comparative trial, and within the comparative trial/ plantation were differentiated two large groups of provenances, which, however, were not associated according to their geographical position within the Romanian area of sessile oak (Figure 10). For instance, the Sascut peripheral provenance fell into a separate subcluster along with the non-peripheral provenance Lechința. Furthermore, in the natural populations, there were some similarities between the peripheral populations and the non-peripheral population: these similarities stemmed from the trees' age.



(a)

(b)

Figure 9 Principal component analysis (a) and scatter plot of PCA scores (b). Notes: BWD – basic wood density, T – tree age; D – tree diameter at breast height; SW – sapwood; ARW – average ring width; NSR – number of sapwood rings.

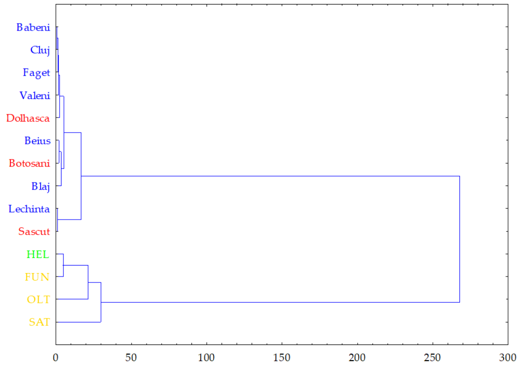


Figure 10 Cluster dendrogram based on four wood traits (BWD, tree age, ARW, SW, NSR). The horizontal axis represents the Euclidean distance; the vertical axis represents the comparative trial provenances and the four natural regenerated populations (the non-peripheral provenances are represented with blue; the peripheral provenances are represented with red; the non-peripheral natural population with green and the peripheral natural populations with orange).

Discussion

All the studied characteristics of the wood were growth-related and partly age-related. This raised difficulties in interpreting tree phenology relationships with wood, which is why we used covariance analysis and partial correlations. Although the dispersion of the values was not impressive, the wood density differentiated between the trees' phenological categories (Figure 4), especially at the sapwood and heartwood scales (Figure 5).

The wood density in the comparative trial, where the trees were younger, seemed to exceed the density in the older stands (Figure 4). The result could be explained by the higher growth rate of young trees, translated into wider rings, which are associated with heavier wood, due to the high latewood content (Zhang 1997, Bergès et al. 2000, 2008, Vavrčík et al. 2010, Vavrčík & Gryc 2012, Pretzsch et al. 2018).

Although it has generally been stated that density gradually increases from pith to juvenile heartwood, and then to mature heartwood (Knapic et al. 2007), we attained greater values for BWD in the JHW section. The higher density in the juvenile wood of the oaks is the consequence of the higher proportion of latewood in the annual rings (Figure 5). Furthermore, in support of our findings, Pásztory et al. (2014), as well as (Diaz-Maroto & Tahir (2018), observed a higher oven-dry density in the juvenile heartwood of sessile oak.

The difference in BWD between early flushing and late flushing trees (Figure 4, Figure 5) is in fact the result of differences in growth and wood structure: a faster start of radial growth is assumed in early flushes and, implicitly, a longer duration of growth, leading to wider rings, which will have a higher density (Wang et al. 2021).

Tree phenology was associated with wood density in beech (Popescu & Dinulica 2020), spruce (Lacaze & Polge 1970) and in tropical dry forests species (Kaewthongrach et al. 2019), the effects compared to sessile oak being understood to be different, due to the different wood anatomy and the different climatic context.

Geographical variations of basic density are highlighted both in the natural stands sampled and by the provenances from the comparative trial (Figure 4). Although the differences were not substantial, peripheral populations had the lowest average values for BWD, which confirms that wood density in ring-porous hardwoods is higher under optimal ecological conditions (Bergès et al. 2008).

Unlike the BWD, sapwood width does not reflect phenological gaps between trees. However, in the comparative trial where trees experience homogeneous environmental conditions, the NSR indicates a delay in the transition to heartwood formation in late-flushing trees by an average of two years compared to early-flushing trees (Figure 7). The average NSR value obtained for the natural populations was identical to that reported by Nechita et al. (2018) for sessile oak found in the northwestern part of the country. Furthermore, the same author indicated a very similar range of variation (i.e., between 8 and 32 rings).

Besides the geographical location of the sampling sites, the different NSR values observed between the natural populations and the comparative trial are related to tree age, with younger trees having fewer sapwood rings (Rybníček et al. 2006, Jevšenak et al. 2019). As with tree phenology, a delay in the transition to heartwood can be assumed in peripheral populations, which had a consistently higher NSR than in non-peripheral populations (Figure 7b).

The structure of the annual rings is a complex of growth-related variables, which make the properties of the wood dependent on the width of the annual rings (Rao et al. 1997, Gričar et al. 2013, Sousa et al. 2021). In *Q. petraea*, as a ring-porous heartwood species, ring width is positively correlated with the proportion of latewood (Zhang et al. 1993, Bergès et al. 2000, Guilley et al. 2004), in the sense that, along with an increase of the annual ring width, there is also an increase of the proportion of latewood, and implicitly of wood density (Vavrčík & Gryc 2012).

Moreover, Hroš and Vavrčík (2014) assessed the differences between *Q. petraea* and *Q. robur* growing at the same site and found that the number of earlywood vessel rows manifests a dependence on the tree-ring width. On the opposite, Feuillat et al. (1997) reported that the number of earlywood vessel rows was independent of total ring width, but manifested a strong dependence on earlywood width.

In addition, a positive correlation between ring width and wood density has been reported in sessile oak (Delpierre et al. 2016), indicating that wider annual ring widths are related to an earlier start of wood formation (Marchand et al. 2021). In ring-porous species, the cambial phenology starts several weeks before bud burst (Savage & Chuine 2021). Thus, bud burst was not essential for the earlywood vessel formation in ring-porous hardwoods (Kudo et al. 2015).

The analysis of the 2021 annual ring phenology (Figure 8) showed, however, that only a small part of the early flushing trees was also early in the formation of the annual ring. In this respect, further research is needed.

The link between tree phenology and 2021 annual ring formation was unanticipated (Figure 8), since it was expected that an earlier start of wood formation would result in early bud flushing. It is important to note that several studies have highlighted that different definitions of bud burst - such as the initial swelling of buds compared to the emergence of visible leaf tips - can result in variations of several days in the observed onset of cambial activity (Basler & Körner 2014). This variability significantly impacts the interpretation of phenological data, as the critical temperatures necessary for initiating wood formation may be met at different times depending on the specific bud burst definition employed (Antonucci et al. 2015).

The observation that wood formation in intermediate-flushing trees often precedes wood formation in early-flushing trees seems to occur independently of other related phenological events. A plausible explanation for this pattern is that the timing of leaf phenology - whether early or late - may be more strongly linked to processes such as anthesis and flower formation rather than the timing of annual ring formation. Another possible explanation is related to the provenance origins of the trees with intermediate flushing trees. As shown in a previous study, the bud burst was negatively correlated with the longitude of the provenances and positively with the provenance altitude origins (Gafenco et al. 2022). Thus, as observed in other provenance studies (Chmura & Rozkowski 2002), the effect of longitude on bud burst may be considered a possible mechanism for adapting to local conditions which allows provenances to avoid exposing leaves to late frosts.

Employing the same leaf phenological methodology, Chesnoiu (2017) investigated the relationship between wood formation and leaf phenology in various native *Quercus* species during the 2016 growing season. The results revealed that the previously held assumption that trees with early flushing exhibit early wood formation has been rejected, with wood formation starting independently of the trees' phenological category. As shown for *Q. petraea* (Chesnoiu 2017), the first earlywood vessels started to form only in the second stage of leaf phenology (i.e., more than 50% of the crown buds have grown leaflets without a distinguishable petiole or base shape), an aspect also observed in most *Q. pedunculifora* trees.

In a previous study on pedunculate oak, Puchałka et al. (2017) did not find a correlation between the phenology of leaf flushing and earlywood-vessel formation. Others studies (Gričar et al. 2022) support the findings that the two events are not associated. However, some studies report that leaf phenology is likely to be connected to wood formation (Sass-Klaassen et al. 2011, Michelot et al. 2012, Guada et al. 2019).

However, since it is only one year (2021), the results regarding the phenology of the annual ring cannot be extrapolated and require further investigation. Since we did not monitor leaf phenology in 2021, we cannot know if there were provenance-level changes regarding the onset of leaf flushing. However, the variability of xylem formation in oaks is largely climatic shaped (Gričar et al. 2013), especially at the peripheral range (Roibu et al. 2020) and deserves a dendrochronological study in relation to tree phenology.

Regarding the PCA (Figure 9) we could see that among the identified phenological categories, intermediates flushing had a more reliable association with wood traits. Also, the cluster analysis allowed us to separate the naturally regenerated populations from the comparative trial when considering all investigated wood traits. The lack of a clear separation between provenances inside the comparative trial might be related to the limited traits included in the analysis (Bessa et al. 2022).

Conclusions

The present study aimed to investigate the influence of leaf flushing on different wood traits in sessile oak found close to its eastern distribution range.

All analysed characteristics of wood from breast height (BWD, tree age, ARW, SW, NSR) are growth-related and they required controlling for the effect of the ring width and tree age.

Wood traits polarized according to the phenological category of the trees (early, intermediate, late) were: basic density, the average tree ring width and tree ring phenology.

We found that early-flushing trees had denser wood compared to late-flushing trees. Density differences between sapwood and heartwood are considerably greater in late than in early flushing trees. At a certain age, late-flushing trees have narrower rings, and the intermediate ones, the widest rings.

PCA revealed the association of intermediate trees with high values of wood density and ring width. Surprisingly, in early flushing trees, annual ring formation in 2021 was far behind intermediate trees. At the same age, late-flushing trees have more rings in the sapwood, which suggests a delay in heartwood formation. Besides, the leaf phenology and sapwood width were not linked.

The study also followed the behaviour of sessile oak tree populations according to the geographical position of the sample plots and the origins of the comparative trial. Basic density was superior in non-peripheral stands due to wider rings. Peripheral populations have a higher number of rings in the sapwood, suggesting a delay in the transition to heartwood formation.

Further work is needed to explore and interpret these results in relation to wood anatomical features, wood quality, and tree physiology.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

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