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CIRCUMFERENTIAL VARIATION IN HEARTWOOD IN STANDS OF BLACK LOCUST (*ROBINIA PSEUDOACACIA* L.)

Within the framework of work on the anatomical structure and durability features of wood, as well as analyses of radial growth, a preliminary analysis was carried out in regard to variation in the heartwood within Black locust trees. The research was carried out in three stands of straight-stemmed trees in western Poland. The variation displayed by the heartwood around its circumference and the eccentricity of the trunks was characterised with reference to: the heartwood radial index (HRI), the cross-sectional shape factor for heartwood (CSsf) and the pith eccentricity index (PEcc). The results confirmed a relationship between the degree of variation around the circumference of the heartwood and the mean age of the stands, while at the same time making clear the high level of differentiation in radial variation at the level of the individual tree. The findings suggest that the fertility of the habitat does not exert much of an influence on the generation of heartwood in Black locust trees. No statistically significant relationship was obtained when the circumferential variation of the heartwood was set against the total height or diameter at breast-height. Only in the case of crown length, and then only at the Wołów site, was there a moderate negative correlation with the coefficients of circumferential variation.

Keywords: heartwood, sapwood, black locust, heartwood eccentricity

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Introduction

Black locust was the first alien species of tree brought back from North America to Europe, some 400 years ago now [Stringer, Olson 1987]. The selection of this particular species for rapid return to the homeland reflected its advantages from the ecological, technological and economic points of view [Pollet et al. 2012]. Both the density of its wood and its resistance to atmospheric factors are determined by the high proportion of heartwood [Latorraca et al. 2011]. The high level of resistance manifested is in turn associated with the presence of two flavonoids: dihydroflavonol and dihydrorobinetin, both of which curb the development of fungi in the wood [Magel et al. 1994]. In this species, the generation of heartwood begins at the ages of 4–6 years [Magel et al. 1991]. The process most probably links up with the ageing of living cells in the sapwood [Ziegler 1968]. Indeed, work by Magel et al. [1991] points to the key role played by the enzymes PAL and CHS, which are active in different periods of the year. While the former is a precursor of the process by which lignin is produced, the latter is responsible for the production of flavonoids. Both enzymes are present at high concentrations in the transitional zone between the heartwood and the sapwood, thus making it clear in which place the process of heartwood formation is initiated. The generation of heartwood is in fact understood as a process by which the sizes of vascular cells are regulated [Bamber 1976]. The size of the sapwood zone is in turn accounted for by using the Pipe Model Theory [Shinozaki et al. 1964a,b]. This theory indicates the way in which the development of a stem along the radial and axial gradient is dependent on the physiological functions of the crown: the vertical distribution of biomass, the proportion between crown and stem, the ratio of the dry mass of the assimilatory apparatus to trunk cross-section, and hence the conductive capacity of the xylem. Long et al. [1981] point to the existence of a linear relationship between the cross-sectional area of the sapwood part of a stem on the one hand and the weight of the assimilatory apparatus on the other. The regularities indicate that there is a relationship between the variation manifested by heartwood around its circumference and the dynamic of the growth of trees determined by habitat conditions. One of the reasons for undertaking the work under discussion concerning circumferential variation in heartwood was to verify the influence of selected stand characteristics, as well as the environment, on the process through which the zone of heartwood is shaped.

Materials and methods

The first stage in the process of selecting stands with straight-stemmed trees and a prevalence of Black locusts in the first storey was an analysis of archival data

from the Information System of the State Forests – a register of assessments and valuations of forest stands. This allowed for the identification of 50 stands which were then the subject of field work leading to the choice of just 7 target objects for research [Wojda et al. 2013]. Finally, three of these sites – in the Forest Districts of Krosno, Wołów and Mieszkowice – were designated for further study involving the properties of the wood, the anatomical structure of the cambium and xylem and the radial profiles [Klisz et al. 2014]. One of the stages to the research on the radial profiles was in turn an analysis of the circumferential variation characterising heartwood. The stands in question were found to differ in age, but also to occupy forest habitats optimal and suboptimal for the black locust, fresh mixed/broadleaved forest and fresh mixed/coniferous forest, respectively (table 1).

Table 1. Locations of analysed stands and selected assessment and valuation features

Forest District	Compartment	Area [ha]	Forest site type	Age	DBH [cm]	Total height [m]	Crown length [m]	Quality class	Stand stocking	Geographical position
Krosno	90b	1.14	LMśw	31	24.7	24.8	9.21	I	0.9	N 52 5 40.2 E 14 58 13.7
Wołów	194f	2.86	BMśw	38	21.1	22.7	9.85	I	0.8	N 51 25 12.5 E 16 34 41.8
Mieszkowice	210j	1.31	LMśw	46	26.0	24.5	11.14	I	1.0	N 52 51 31.5 E 14 11 40.7

In each stand, 10 sample trees were identified, each then contributing to the research on heartwood thanks to the removal from them of discs at breast height (1.3 m above the ground). These were made subject to a standard analytic procedure on the basis of the program WinDENDRO 2009b. The extent of heartwood and sapwood in relation to the 8 main compass directions was determined by reference to the colouration of annual rings across the cross-section [Niklas 1997]. On this basis, the share of the given radius accounted for by wood of the two types was determined for each tree. A comparison of the share of heartwood in the sample trees and stands was thus achieved by reference to a one-way analysis of variance using a fixed-effects model taking the form:

$$HR_{jn} = \mu + P_j + E_{jn} \quad (1)$$

where:

HR_{jn} – is the share of heartwood for the n^{th} tree in the j^{th} population
($n = 1, \dots, 10$; $j = 1, \dots, 3$)

μ – is the overall mean,

P_j – is the j^{th} population effect,

E_{jn} – is the random error characterising the n^{th} tree in the j^{th} population.

The analysis of variance was carried out in relation to the values for the variable studied that had first been transformed using the Bliss transformation. A Levene test (with $p = 0.098$) was used to test an assumption regarding the equality of variance among the populations studied. In turn, the normality of residuals in the analysed model was tested using the Shapiro-Wilk test (with $p = 0.984$). The significance of the differences between the stands was verified using Tukey's HSD test [STATISTICA 10PL; StatSoft 2011].

The characteristics referred to in analysing the variation displayed around the circumference by the heartwood were: the heartwood radial index (HRI), the cross-sectional shape factor for heartwood (CSsf) and the index of pith eccentricity (PEcc) [Knapic et al. 2014]. The HRI is found by dividing the radius measured for the heartwood in a given compass direction by the radius noted for the northerly direction (2).

$$\text{HRI} = \text{HW radius} / \text{HW north radius} \quad (2)$$

The cross-sectional shape factor (CSsf) for heartwood is the ratio between the largest radius and the radius at right angles (3).

$$\text{CSsf} = \text{Max DiamCS} / \text{Orth DiamCS} \quad (3)$$

The pith eccentricity index (PEcc) is obtained by dividing the largest radius by the smallest (4).

$$\text{PECC} = \text{Largest radius} / \text{Smallest radius} \quad (4)$$

Pearson coefficients were then determined for the linear correlation between the cross-sectional shape factor for the heartwood or the pith eccentricity index on the one hand, and the breast-height diameters or total height of the sample trees on the other [STATISTICA 10PL; StatSoft 2011].

Results and discussion

The analysis of variance for the heartwood in the sample tree cross-sections from the three analysed sites confirmed the existence of significant differences between them (table 2). At the same time, it was possible to observe a

relationship between the percentage share of heartwood and the mean age of the sampled trees, in that the older the tree, the greater the share of heartwood at breast height. The oldest (in Mieszkowice) stand was shown to differ significantly from the youngest (in Krosno), with the two stands belonging to different homogeneous groups (fig. 1).

Table 2. Analysis of variance for the % of radial width accounted for by heartwood in trees from the different study sites.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	P
Stand	2	0.00383	0.00191	4.52	0.020
Error	27	0.01144	0.00042		

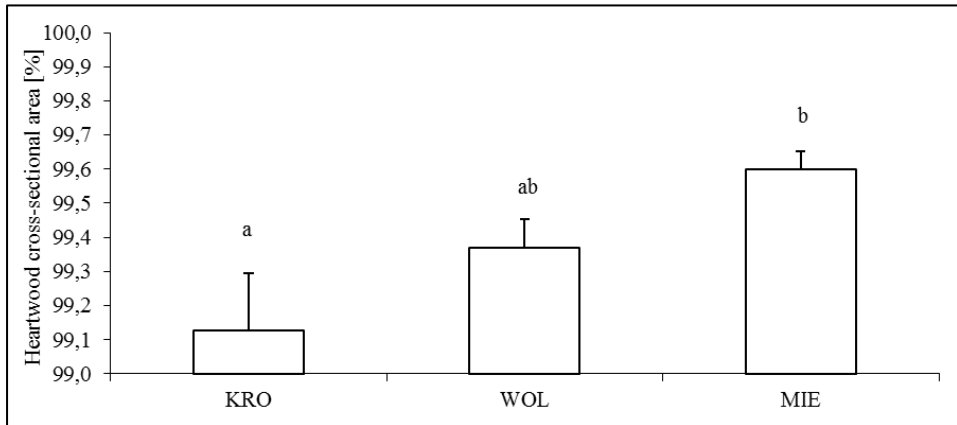


Fig. 1. Variation in the % share of cross-sectional area accounted for by heartwood – showing homogeneous groups (error bars show standard errors of the means; different letters show significant differences at $p \leq 0.05$). Study sites: KRO – Krosno, WOL – Wołów, MIE – Mieszkowice

This kind of relationship was indicated previously in work devoted to other broadleaved tree species, such as Pedunculate oak [Rybníček et al. 2006; Szymański et al. 2008, Pazdrowski et al. 2009] and Aspen [Yang, Hazenberg 1991]. Work by Szymański et al. [2008] and Pazdrowski et al. [2009] pointed to the existence of a link between the biosocial positions of trees, their age, the fertility of the habitat and the share of heartwood. The latter was found to be greater in poorer habitats and in trees from lower Kraft classes.

Work devoted to the trees in the poorest (fresh mixed/coniferous forest) habitat involved those from the Wołów site (table 1), among which values for

the shares of heartwood were intermediate. These relationships may point to the greater influence of tree age than of habitat conditions when it comes to the generation of heartwood in this species.

The analysis of the shares of heartwood present along radii in the four main compass directions confirmed circumferential variation in the generation of this kind of wood. At all sites, the heartwood zone was widest in the easterly direction (fig. 2).

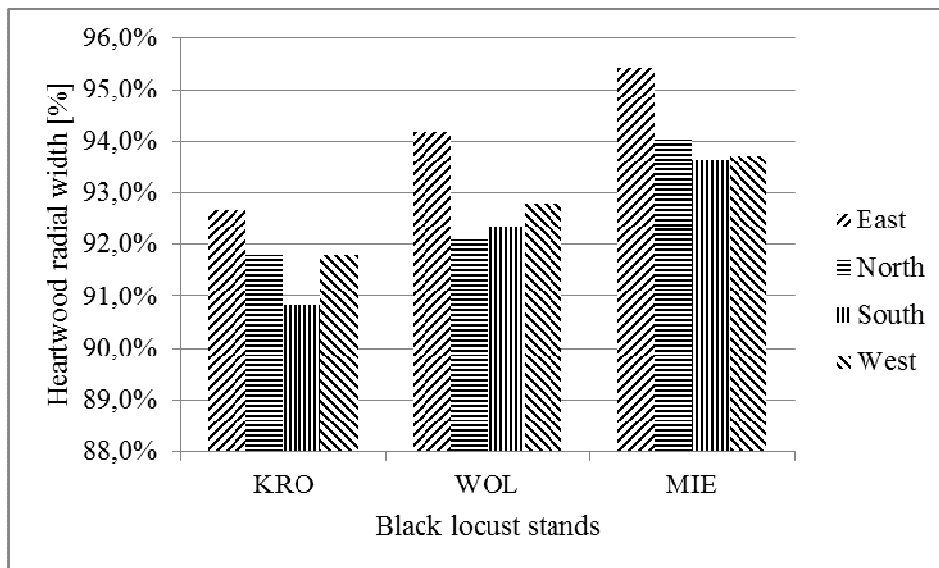


Fig. 2. Share of radial widths in the 4 main compass directions accounted for by heartwood. Study sites: KRO – Krosno, WOL – Wołów, MIE – Mieszkowice.

Such irregularity to the radial formation of heartwood was observed previously in conifers such as the Maritime pine [Berthier et al. 2001; Knapic et al. 2014; Stokes, Berthier 2000], the Lodgepole pine [Yang, Murchison 1992] and the Scots pine [Jelonek et al. 2006]. In relation to conditions for growth and the forms of trunks and crowns in the trees studied, causes identified for irregularities around the circumference of the heartwood have been: prevailing wind direction [Berthier et al. 2001], a high level of insolation on west-facing slopes [Yang and Murchison 1992], growth conditions on former farmland [Jelonek et al. 2006], irregularity of crown structure [Knapic et al. 2014] and eccentricity of trunk shape [Stokes, Berthier 2000].

Circumferential variation in the heartwood in the sample trees from each of the three sites was described with reference to diagrams for the heartwood radial index (fig. 3). In the case of the youngest stand (in Krosno), it proved impossible

to distinguish a dominant direction in which the heartwood is developing, while in the older stands (in Wołów and Mieszkowice) there is a marked difference between the southerly and south-easterly directions and the remaining directions where the heartwood radial index is concerned (fig. 4). An increase in cross-sectional diameter is thus associated with greater eccentricity to the trunk cross-section (fig. 5).

Studies concerning radial differentiation in the generation of heartwood lack information on differences around the circumference, the works in question having focused on durability aspects, or the content of different extractives [Stringer, Olson 1987; Pollet et al. 2008]. However, work on the share of heartwood in conifer species does supply certain interesting observations on the conditioning of variation around the circumference. The results of measurements of the widths and numbers of discs relating to sapwood in Jack pine and American larch, as carried out by Yang et al. [1985], point to the width of the sapwood zone (and indirectly also that containing heartwood) being dependent on the ages and rates of the growth of the trees. At the same time, these authors indicate a wider zone of sapwood on the south-facing side of a trunk – which is not in accordance with our findings for Black locust. Barthier et al. [2001] gave as their reason for circumferential variation in heartwood the non-symmetrical development characterising crowns, this translating into differences from one part of a crown to another in the size of the photosynthetically active surface, with this in turn directly determining the development of sapwood [Jelonek et al. 2010]. At the same time, the area of sapwood through the profile is associated with the conductive capacity of the trunk, with this volume in turn deriving from the stem water-storage capacity of a given tree [Sellin 1994]. Asymmetrical crown-development may in turn be determined by greater insolation on one part of the crown, with this in turn being influenced by land relief [Yang, Murchison 1992]. Commencing with cambial activity before the assimilatory apparatus develops each year, the Black locust is a species affected by increasing trunk temperature on the sunny side. Thus, in the early phases of the growing season, it is possible to anticipate the same effect as is observable in hybrid poplars (*Populus sieboldii* × *P. grandidentata*), whereby differences in the trunk temperature between the sunny and shady sides are capable of giving rise to differences in the time of onset of cambial activity, and therefore indirectly to differences in radial growth within a given tree [Begum et al. 2007].

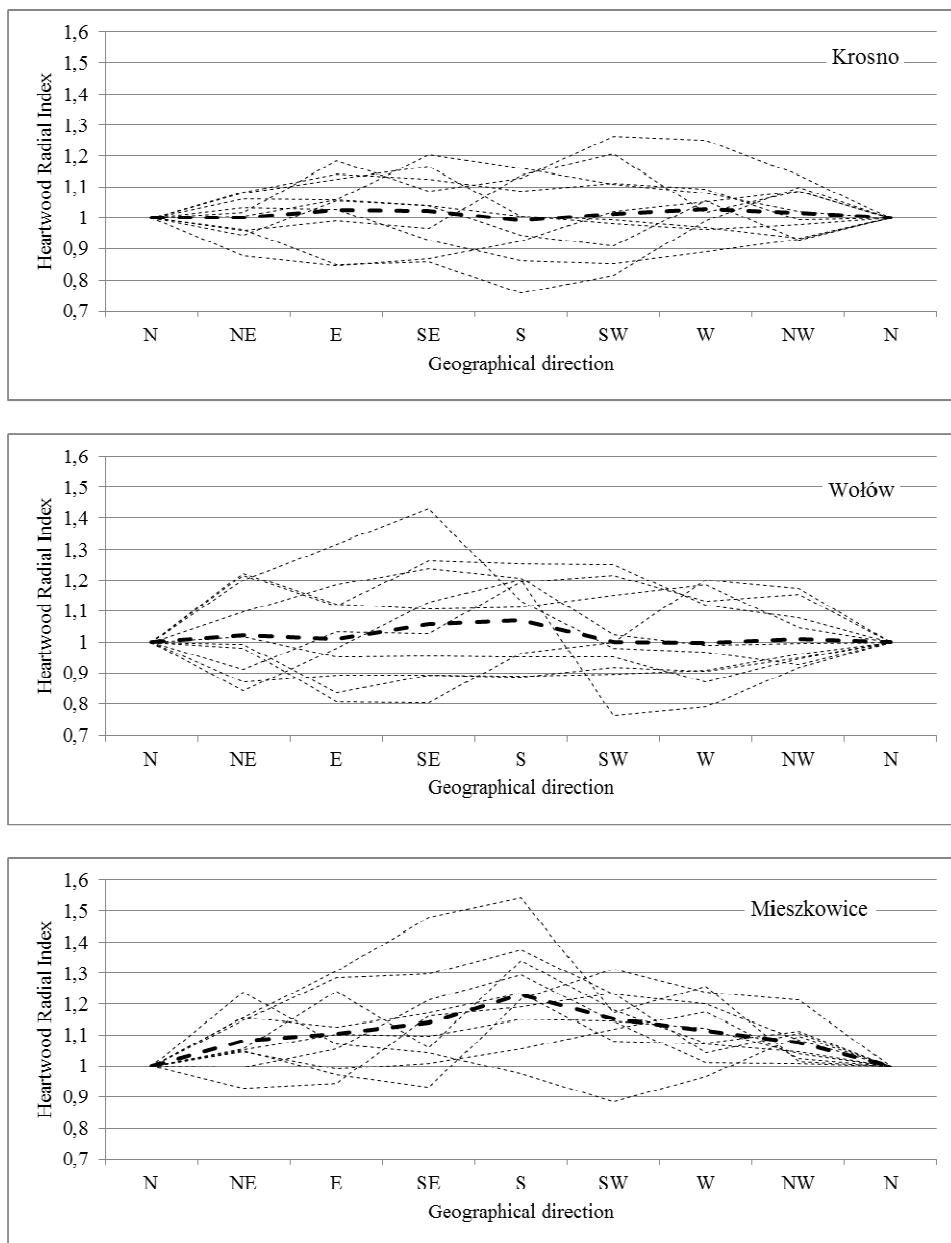


Fig. 3. Circumferential variation in the heartwood radial index (heartwood radius: north radius) for the 10 sample trees. The bold (dotted) line shows the average heartwood radial index of sample trees.

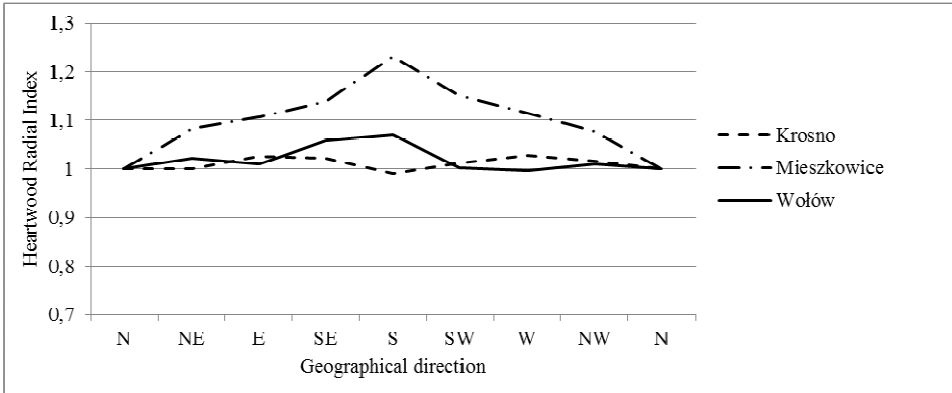


Fig. 4. Circumferential variation in the heartwood radial index (heartwood radius: north radius) for the Krosno, Mieszkowice and Wołów study sites.

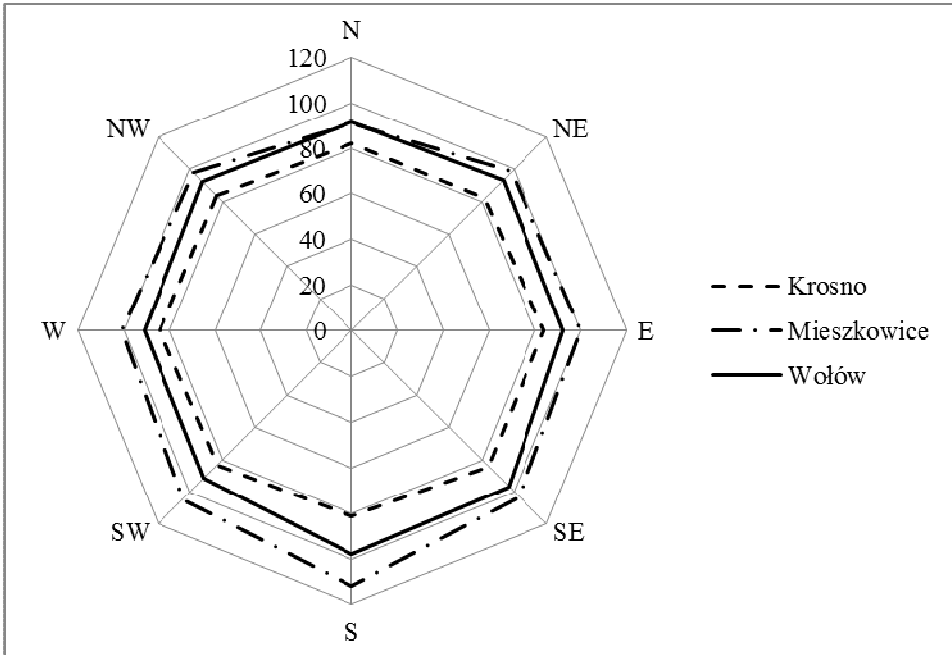


Fig. 5. Circumferential outline of heartwood in relation to compass directions at the Krosno, Mieszkowice and Wołów study sites

Pearson correlation coefficients provided confirmation of the way in which circumferential variation in the cross-sectional shape factor for heartwood and the pith eccentricity index show a dependent relationship with breast-height diameter, total height and crown length. While most of the correlations referred

to did not achieve statistical significance, the relationships in question were observed to differ from one site to another. In the case of the site with the youngest stand, Krosno, the correlations between the two indices and the biometric features of the trees assumed values close to zero. In contrast, in the case of the older stand at Wołów, both the cross-sectional shape factor for heartwood and the pith eccentricity index showed moderately negative correlations with breast-height diameter. Finally, in the Mieszkowice stand (the oldest of all, and with the most diversified age structure, given the presence of trees aged 44–47 years), the opposite trend could be observed, with both indices correlating with breast-height diameter in a moderately positive way (table 3). The lack of any more distinct dependent relationship between the height and the analysed indices characterising the dynamic for radial growth was in fact in line with the authors' expectations. In turn, the variable nature of the dependent relationships observed between the indices and the breast-height diameters of the trees is most probably conditioned by the marked scatter present in the results. Where the number of samples is low (10 sample trees per site), this fact may exert an unfavourable influence on the correlation coefficient values. Only the correlation with the crown length in the trees at Wołów emerged as statistically significant, albeit with values for both the cross-sectional shape factor and the pith eccentricity index being moderately negative (-0.6917 and -0.6828, respectively). This confinement to just one of the stands of any statistically significant relationship between the crown length and indices of circumferential variation in heartwood may reflect the influence of habitat conditions on the development of sapwood. The stand in question was in the poorest of the studied habitats – fresh mixed/coniferous forest, while the remaining two stands were in the habitat optimal for the Black locust, which is to say, fresh mixed/broadleaved forest. The relationship between the dynamic to the development of sapwood and heartwood and habitat conditions (fertility and humidity) has been remarked upon by many authors in the case of both broadleaved trees [Pazdrowski et al. 2009, Rybniček et al. 2006, Szymański et al. 2008] and coniferous species [Jakubowski 2004, Jelonek et al. 2006, Nawrot et al. 2008, Spława-Neyman, Pazdrowski 2001]. The previously mentioned study confirmed the influence of habitat conditions on the shares of sapwood and heartwood, albeit without going into the relationship concerning circumferential variation.

Table 3. Pearson's correlation coefficients between the cross-sectional shape factor for heartwood or the pith eccentricity index and DBH, total height and crown length (p-values given in brackets).

Stand	Stand-quality traits	Cross-sectional shape factor for heartwood	Pith eccentricity index
Krosno	DBH	-0.0981 (0.7875)	-0.1277 (0.7251)
	Total height	-0.1225 (0.736)	-0.2482 (0.4892)
	Crown length	0.0986 (0.7864)	0.2006 (0.5784)
Wołów	DBH	-0.2465 (0.4923)	-0.4092 (0.2403)
	Total height	0.1204 (0.7405)	0.1291 (0.7222)
	Crown length	-0.6917 (0.0267)	-0.6828 (0.0295)
Mieszkowice	DBH	0.411 (0.2381)	0.1713 (0.6362)
	Total height	0.1854 (0.6081)	-0.1899 (0.5992)
	Crown length	-0.0572 (0.8752)	0.3018 (0.3967)

The issue of the circumferential variation in the share of heartwood in the context of an eccentric position for the pith in the cross-section was analysed at length in the Maritime pine [Stokes, Berthier 2000; Berthier et al. 2001; Knapic et al. 2014]. The matter was also addressed by Stringer and Olson [1987], who considered 12-year-old Black locust trees characterised by unstabilised radial growth. However, these studies did not address the relationship between circumferential variation in the heartwood and the biometric features. Only in the work by Knapic et al. [2014] was a comparison made between the indices for pith eccentricity and heartwood in trees of different heights. The authors of these studies stressed the stronger development of the heartwood zone in a north-easterly direction, at a height above the ground corresponding with DBH, as well as in a south-easterly direction at the base of the crown. The explanation of the axial differences in heartwood generation assigned a key role to the tree crown, at the time the process generating heartwood is initiated. Such observations support the assumption that Black locust resembles Maritime pine in featuring axial circumferential variation in the share of heartwood.

Conclusions

The share of heartwood in the trunk cross-section is very much more dependent on the age of a given tree than on the fertility of the habitat in which it occurs. As middle-age approaches, the trees in a stand will have greater and great shares of heartwood. At the same time, with age, trees manifest more and more distinct circumferential differentiation in the share of heartwood, with generation being most marked in an easterly direction. In turn, values for the development of heartwood along radii in different directions, as expressed in terms of an index comparing this with development in a northerly direction, point to prevalent growth in a southerly direction in the two older stands of Black locust (in Wołów and Mieszkowice). Leaving aside the particularly marked southerly direction to heartwood growth, it was also possible to note a generally high level of variation from tree to tree in terms of the heartwood radial index. The lack of statistically significant correlations between the cross-sectional shape factor for heartwood or the pith eccentricity index, and either height or breast-height diameter, may reflect the considerable dispersion of results, in the face of a sample size representing each stand that is relatively small. At the same time, the significant correlation between the coefficients of circumferential variation mentioned and crown length – at the Wołów research site only – points to the key influence of crown architecture on the development of sapwood and heartwood. Given the high technical quality of the trees representing the stands under analysis, it would seem astonishing that there is such a high degree of circumferential variation for heartwood. Insight into the causes of this phenomenon will only be forthcoming if there is both an augmentation of research to include the analysis of cross-sections at different heights up the trunk, and consideration through analysis given to factors other than those conditioned by the environment (i.e. genetic structure of the stand).

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