In most tree species the xylem consists of two histologically similar but physiologically different wood zones, sapwood and heartwood. Sapwood, i.e. the outer wood zone, is composed of physiologically active, live cells and reserve substances, and the external rings transport water with minerals from roots to the cambium and assimilatory organs. Heartwood, the inner wood zone, is physiologically inactive and does not participate in the conduction of water. With the age of the tree, parenchymal cells die losing their reserve substances, and the wood remains protected by a multicomponent organic complex (heartwood substances). These substances (mostly polyphenols) are responsible for the natural stability of heartwood and its usually darker colour (Hejnowicz 2002; Pinto et al. 2004). The mechanism causing the above-mentioned changes in wood and the physiological functions of heartwood is not fully understood. In the opinion of Shinoazaki et al. (1964) the process of heartwood formation is regulated by the width of the sapwood zone, remaining in a close correlation with the volume of the assimilatory organ (the pipe-model theory). Another concept assumes that after the phase of initiation of heartwood formation, heartwood is formed with more or less constant annual dynamics, which depends on the age of cambium and several external factors affecting the growth of the tree (Wilkes 1991; SELLIN 1994). Recent studies suggest that heartwood is formed as a response to hydraulic impulses and may develop irregularly both in the radial and axial directions in order to maintain a constant, optimal share of sapwood in the stem (Plomion et al. 2001; Berthier et al. 2001).

The quantitative ratio of heartwood to sapwood in tree stems depends first of all on the age of trees, climatic and soil conditions, the height at which the analyzed stem cross-section is located and on the

Dynamics of heartwood formation and axial and radial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.)

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ABSTRACT: The study was an attempt to determine the dynamics of heartwood formation and the radial and axial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.) representing the dominant stand according to Kraft. Correlations were found between the rate of heartwood formation and the social class of tree position in the stand, the age of trees, forest site type and height of trees. Moreover, radial and axial variation was observed in the distribution of analyzed wood zones depending on the height of measurement, the age of cambium and the dimensions of the analyzed tree. Results were analyzed statistically, which facilitated an assessment of the relation between the dynamics of heartwood formation and age, the social class of tree position in the community as well as dimensions, i.e. the thickness of the sapwood ring and the radius of heartwood cylinder. The greatest strength of the relation was determined between the ray of the heartwood and the stem radius ($R^2 = 0.98$), with cambium age and number of heartwood rings ($R^2 = 0.93$). A much smaller relation was determined between the width of the sapwood ring and the stem radius ($R^2 = 0.13$).

Keywords: sapwood; heartwood; dynamics of heartwood formation; social class of tree position; European larch
crown size (Duda, Pazdrowski 1975). Heartwood and sapwood have varying properties and their proportion within the stem has a significant effect on the rational utilization of timber. In practice the share of heartwood in tree stems has a positive effect for some branches of industry due to high stability or aesthetic value, while from the point of view of others this effect is disadvantageous (plywood industry or pulp and paper industry).

European larch (Larix decidua Mill.) is a species which reaches the culmination of its increment in diameter early and maintains it for a long time, forming stands with a large abundance of valuable high-class timber (Chylarecki 2000). In the analyzed forest site types (fresh mixed coniferous forest, fresh mixed forest) in the State Forests larch is recommended to be introduced as an admixture improving stand quality, the aim of which is to increase the value of produced timber.

The aim of the present study was to determine the dynamics of heartwood formation and the distribution of sapwood and heartwood at the cross-section and the axial section of the stem of European larches growing in a fresh mixed coniferous forest and fresh mixed forest, representing three age classes and the dominant stand according to Kraft’s biological classification.

MATERIAL AND METHODS

Investigations were conducted in stands of age classes II, III and IV growing in the Choszczno Forest Division (The Regional Directorate of State Forests in Szczecin), where larch was found as an admixture (in at least group mixtures) in a fresh mixed coniferous forest (BMśw) and fresh mixed forest (LMśw). In selected compartments mean sample plots of 0.5 ha were established, where breast height diameters of all trees of the analyzed species were measured and presented in terms of 2 cm diameter sub-classes. The next height was measured in proportion to the frequency of trees in adopted diameter sub-classes. Based on the height and diameter characteristics of trees a total of 18 model trees were selected (3 for each mean sample plot) according to Hartig (Grochowski 1973) and Kraft’s biological classification (1884) – only the first three classes, i.e. the dominant stand, were taken into consideration. This classification, based on the quality assessment of the crown and height of a tree in relation to the immediate surroundings, describes quite well the crown of a tree and its biological position in the community. Those trees were felled and their stems were divided into 2 m sections, from the centre of which discs were cut in order to analyze selected properties of wood macrostructure. The discs were used to measure the width of sapwood rings and the radius of the heartwood cylinder, and to determine the number of heartwood and sapwood rings at two perpendicular diameters oriented in the north-south and east-west directions. The ratio of the number of heartwood rings to the number of all wood rings in a given disc (H/A) made it possible to determine the dynamics of heartwood formation. Results of analyses were expressed in absolute and relative values and presented in the form of tables and graphs. Statistical analysis was conducted using a computer software package Statistica 6.0 PL (Kala 2002).

RESULTS AND DISCUSSION

Biometric traits of model trees are presented in Table 1. Fig. 1 illustrates the dynamics of heartwood formation depending on the height at which the site of measurement was located. The dynamics of heartwood formation decreased with tree height in all investigated age classes. In relation to the analyzed forest site types the dynamics of heartwood formation was found to be higher in the fresh mixed forest (Figs. 1, 2c).

The mean value of the H/A ratio in all age classes was 0.47 in age class II, 0.55 in age class III, and

<table>
<thead>
<tr>
<th>Measured trait</th>
<th>Age class II BMśw</th>
<th>Age class II LMśw</th>
<th>Age class III BMśw</th>
<th>Age class III LMśw</th>
<th>Age class IV BMśw</th>
<th>Age class IV LMśw</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breast height diameter (cm)</td>
<td>21.4 (4.9)</td>
<td>25.6 (6.5)</td>
<td>29 (5.3)</td>
<td>32.3 (6.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of rings at breast height diameter</td>
<td>25</td>
<td>41</td>
<td>68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height of tree (m)</td>
<td>18.6 (1.02)</td>
<td>24.2 (1.36)</td>
<td>28.4 (3.2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of live crown (m)</td>
<td>6.13 (0.96)</td>
<td>13.5 (0.5)</td>
<td>6.3 (0.3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crown level (% total height)</td>
<td>32.9 (3.77)</td>
<td>55.7 (2.17)</td>
<td>22.4 (3)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

BMśw – fresh mixed coniferous forest, LMśw – fresh mixed forest
0.67 heartwood ring/year in age class IV (Fig. 2a). In Kraft’s biological classes the value of this index in Kraft’s class III (codominant trees) was 0.55, while in class II (dominant trees) it was 0.56 and in class I (predominant trees) it was almost 0.61 (Fig. 2b). When comparing the dynamics of heartwood formation within the forest site types a higher value of the H/A ratio, and thus a faster process of heartwood formation, were found in the fresh mixed forest – 0.58, compared to the fresh mixed coniferous forest – 0.54 (Fig. 2c).

The dynamics of heartwood formation in European larch decreases with an increase in the height at which the measurement site is located on the stem, which is probably connected with the age of parenchymal cells, which did not reach the boundary age in higher parts of the stem, i.e. the process of their death initiating the transformation of sapwood into heartwood did not start (Hejnowicz 2002). Analysis of variance was conducted for the H/A ratio in relation to age classes and biological classes according to Kraft. The analysis of variance for the H/A ratio in age classes showed statistically significant differences (Table 2). For this reason Tukey’s honestly significant difference (HSD) test was conducted (Ta-
ble 3). As a result of the test it was found that all age classes differed statistically significantly in terms of the dynamics of heartwood formation described in the study using the H/A ratio (Table 3).

Table 2. Analysis of variance for the H/A ratio in age classes at the significance level 0.95 ($P < 0.05$)

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>Test $F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>H/A</td>
<td>1.433391</td>
<td>2</td>
<td>0.716695</td>
<td>63.74205</td>
<td>0.000000</td>
</tr>
</tbody>
</table>

SS – sum of squares, MS – quadratic mean, df – degrees of freedom, $P$ – significance level

Table 3. Tukey’s honestly significant difference test for the H/A ratio in analyzed age classes

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class II</td>
<td>0.000133*</td>
<td>0.000022*</td>
<td></td>
</tr>
<tr>
<td>Age class III</td>
<td>0.000133*</td>
<td>0.000022*</td>
<td></td>
</tr>
<tr>
<td>Age class IV</td>
<td>0.000022*</td>
<td>0.000022*</td>
<td></td>
</tr>
</tbody>
</table>

*Denoted differences are statistically significant at $P < 0.05$

Table 4. Analysis of variance for the H/A ratio in Kraft’s biological classes at a 0.95 significance level ($P < 0.05$)

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>Test $F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>H/A</td>
<td>0.131926</td>
<td>2</td>
<td>0.065963</td>
<td>3.825886</td>
<td>0.023284</td>
</tr>
</tbody>
</table>

SS – sum of squares, MS – quadratic mean, df – degrees of freedom, $P$ – significance level

The analysis of variance was conducted for the H/A ratio in relation to Kraft’s biological classes. Differences in the investigated index turned out to be statistically significant (Table 4). It was followed by Tukey’s honestly significant difference (HSD) test between Kraft’s classes and the H/A ratio (Table 5). Statistically significant differences in the dynamics of heartwood formation defined in this study using the H/A ratio were found between the trees representing Kraft’s class I (predominant trees) and codominant trees from Kraft’s class III (Table 5).

Table 5. Tukey’s honestly significant difference (HSD) test for the H/A ratio in analyzed Kraft’s biological classes

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Kraft’s class III</td>
<td>0.914220</td>
<td>0.030618*</td>
<td></td>
</tr>
<tr>
<td>Kraft’s class II</td>
<td>0.914220</td>
<td>0.073390</td>
<td></td>
</tr>
<tr>
<td>Kraft’s class I</td>
<td>0.030618*</td>
<td>0.073390</td>
<td></td>
</tr>
</tbody>
</table>

*Denoted differences are statistically significant at $P < 0.05$

It was also decided to investigate the effect of the age of cambium on the number of heartwood rings at individual heights of measurement sites in stems of trees (Fig. 3). The high coefficient of determination $R^2 = 0.93$ shows that the number of heartwood rings in 93% is determined by the age of cambium, while in 7% the process of this transformation is determined by other factors.

Fig. 4 presents the percentages of heartwood at the radius of cross-sections coming from different heights on the stems. The heartwood percentage shows maximum values at the butt end of a tree while minimum values are at its top (Fig. 4).

The width of a sapwood ring measured at the radius of the cross-section decreases slowly along with the increasing distance from the butt end moving toward the tree top (Fig. 5). Up to a certain point of height on the stem the width of sapwood shows more or less similar values, afterwards it decreases mark-
edly. In age class II such a marked decrease occurred at a height of approximately 14 m, in class III up to 20 m, while in class IV – up to 24 m. The maximum value of sapwood width was recorded in age classes II and III at the butt end, while in age class IV at the point preceding a decrease of its value (Fig. 5a). The heartwood radius (and thus the width) has the maximum value at the butt end of a tree, followed by a gradual decrease, reaching its minimum in the tree top zone (Fig. 5b).

The study was an attempt to analyze the effect of the stem radius (inside bark) on the width of the sapwood ring (B) and on the heartwood radius (A). Statistical analysis showed a marked correlation between the stem radius and the heartwood radius, which is confirmed by the high coefficient of determination \( R^2 = 0.98 \). Thus, the heartwood radius in 98% is determined by the size of the stem radius (Fig. 6a). The relationship between the radius of the cross-section and the width of the sapwood ring is opposite (Fig. 6b). The low value of the coefficient of determination \( R^2 = 0.13 \) indicates that the width of the sapwood ring is determined by the size of the stem radius only in 13% (Fig. 6b). Thus, the width of the sapwood ring is determined by other factors to a greater extent (87%).

A dependence of the dynamics of heartwood formation on the width of the sapwood ring and the radius of the heartwood cylinder was also investigated. It results from the analyses that the dynamics of heartwood formation was correlated with the radius of the heartwood cylinder to a higher degree (0.82) than with the width of the sapwood ring (0.08). Calculated correlation coefficients are significant at a significance level \( \alpha = 0.05 \). Equations of linear regression were also calculated. In the first case the width of the sapwood ring was assumed as the independent variable and the calculated regression turned out to be statistically non-significant (at the correlation coefficient between traits 0.08). In the other case the radius of the heartwood cylinder was taken as the

\[
y = 0.0031x^2 + 0.491x - 1.0393 \quad R^2 = 0.9315
\]
independent variable. Here the regression turned out to be statistically significant ($P < 0.0001$) and the variation of the radius of the heartwood cylinder explains the variation of the $H/A$ ratio in 69%, at the correlation coefficient 0.82. Graphic representations of equations of linear regression are presented in Figs. 7a,b.

An increase in the volume of heartwood is a function of time, thus we talk of a process determining its dynamics (rate). The number of heartwood rings decreases with tree height. According to Hejnowicz (2002), the tree as a whole is composed of sapwood until the age of the stem exceeds the boundary of life for parenchymal cells. With an increase in the height of the stem (trunk) the age of cambium decreases, and thus the age of parenchymal cells, the death of which initiates the transformation of sapwood into heartwood. For this reason both the relative proportion of heartwood and the dynamics of heartwood formation decrease starting from the base of the stem (trunk) towards the tree top. This was confirmed by the studies of Pazdrowski and Szaban (2002), who found a reduction in the rate of heartwood formation with tree height in Scots pine ($Pinus sylvestris$ L.) and black pine ($Pinus nigra$ Arnold). In the analyzed age classes the highest dynamics of heartwood formation expressed by the $H/A$ ratio was recorded for trees representing age class IV – mean 0.67, while the lowest for trees from age class II – on average 0.47 heartwood ring/year, which is probably connected with the age of cambium and parenchymal cells. In the analyzed social classes of tree position in the stand the highest $H/A$ ratio was found for predominant trees (Kraft’s class I) – 0.61, while the lowest for codominant trees (Kraft’s class III) – 0.55. A better social class of tree position in the stand is connected with a faster rate of heartwood formation. It results from the studies of Pazdrowski

![Graphical representations of equations of linear regression taking into consideration the effect of the width of sapwood ring (a) and the radius of the heartwood cylinder on the $H/A$ ratio describing the dynamics of heartwood formation](image-url)
and Spława-Neyman (1993) that the social class of tree position in the stand as well as the closely related crown size may be considered as symptoms of maturity for tracheids in Scots pine (Pinus sylvestris L.). Trees occupying inferior social positions in the stand are characterized by a lower proportion of the light crown towards the tree top. Similar results were reported by Knapic et al. (2006) when investigating heartwood formations in a tree.

A more dynamic process of heartwood formation was observed in the fresh mixed forest, i.e. at the more fertile site. Duda and Pazdrowski (1975) found a relationship between site fertility and the share of heartwood in pine stems. Pines growing in associations richer in terms of the species composition (on fertile soils) provide much more heartwood than trees growing on less fertile soils. In 100 years old pines the differences in the percentage of heartwood between the least fertile community (Leucobryo-Carpinetum) and the richest (Galio-Carpinetum) were as much as 16% in favour of the more fertile site.

The rate of heartwood formation expressed as the ratio of the number of sapwood rings to that of heartwood rings was analyzed in Scots pine (Pinus sylvestris L.) and black pine (Pinus nigra Arnold) by Pazdrowski and Szaban (2002). Those authors reported higher dynamics of heartwood formation (i.e. a lower ratio of the number of sapwood rings to that of heartwood rings) in Scots pine. The dynamics of heartwood formation in Scots pine (Pinus sylvestris L.) was analyzed in the same manner by Duda and Pazdrowski (1975). The fastest rate of heartwood formation examined for the height of 2.5 m was recorded by those authors in the Pino-quercetum association (1.28), while the lowest in the Leucobryo-Pinetum clad one (1.94).

The rate of heartwood formation (its dynamics) determines the share of both types of wood in the stem (trunk) of a tree (Pazdrowski, Szaban 2002). It was found in this study that the highest relative proportion of heartwood was contained in the butt end of larch trees and it gradually decreased towards the tree top. Similar results were reported by Knapić et al. (2006) when investigating heartwood in Australian blackwood (Acacia melanoxylon) and by Yang et al. (1994), who investigated Japan cedar (Cryptomeria japonica). In the opinion of Duda and Pazdrowski (1975), who studied Scots pine (Pinus sylvestris L.), the highest share of heartwood, and thus the lowest proportion of sapwood, for different sites was found at 5.5–9.5 m tree height. The maximum width of sapwood in analyzed larch trees was either recorded at the butt end (age classes II and III) or at the point preceding a sudden decrease in its value (age class IV). Knapić et al. (2006) reported the biggest width of the sapwood ring in Australian blackwood (Acacia melanoxylon) at approximately 75% of total tree height, i.e. similarly like in the case of larches from age class IV. In turn, Yang et al. (1994) reported the biggest width of the sapwood ring at the butt end of Japan cedar (Cryptomeria japonica), i.e. similarly like in larches from age classes II and III. Yang et al. (1994), Pinto et al. (2004) and Knapić et al. (2006) recorded similar results in relation to the dependence between the width of wood and the width of the sapwood and heartwood zones in stems of Australian blackwood (Acacia melanoxylon) and Japan cedar (Cryptomeria japonica) as in the case of European larch (Larix decidua Mill.) investigated in this study. Bauch and Dünisch (2000), who studied Carapa guianensis Ablu. in the central Amazon River basin, found a percentage increase in the proportion of heartwood at the cross-section with an increase in the area of the analyzed cross-section expressed in cm², i.e. a similar trend to that in European larch, where a larger radius of a tree determined to a high degree (in 98%) a larger heartwood ray.

CONCLUSIONS

1. Dynamics of heartwood formation increases with the age of a tree and with the improved social class of tree position in the stand. Greater dynamics of heartwood formation was found in trees growing in a more fertile site – fresh mixed forest.

2. Dynamics of heartwood formation decreased in stems of European larch from the butt end towards the tree top.

3. Radial and axial variation was found in the distribution of sapwood and heartwood in stems of the analyzed forest-forming species.

4. Relationships were observed between the width of the sapwood ring and the radius of the heartwood cylinder, and the dimensions of a given wood type and the dynamics of heartwood formation.

5. Based on the conducted statistical analyses it was found that the dynamics of heartwood formation, expressed as the H/A ratio, showed statistically significant differences between all analyzed age classes. In relation to the social class of tree...
position in the stand statistically significant differences were recorded only between trees representing Kraft’s class I (predominant trees) and codominant trees (Kraft’s class III). Thus the H/A ratio varied more markedly in age classes than in Kraft’s biological classes, which was confirmed by the statistical analyses.

(6) Due to the complexity of the problem it is advisable to conduct further studies on the subject.

References


Received for publication April 10, 2008
Accepted after corrections July 3, 2008

Dynamika tvorby jadrového dreva a axiálna a radiálna distribúcia beľového a jadrového dreva na kmeňoch smrekovca európskeho (Larix decidua Mill.)

ABSTRAKT: Práca je snahou o určenie dynamiky tvorby jadrového dreva a axiálnej a radiálnej distribúcie beľového a jadrového dreva na kmeňoch smrekovca európskeho (Larix decidua Mill.), reprezentujúcich hlavnú úroveň porastu podľa Krafta. Našli sa závislosti medzi výskytom jadrového dreva a stromovými triedami v poroste, vekom stromov, typom lesného stanovišia a výšky stromov. Taktiež sa sledovala aj radiálna a axiálna variabilita v distribúcii analyzovaných zón dreva v závislosti od meranej výšky, veku kambia a rozmerov analyzovaného stromu. Výsledky sa štatisticky analyzovali, čo umožňuje odhad závislosti medzi dynamikou tvorby jadrového dreva a veku, stromovej triedy ako aj dimenzií, t.j. hustoty letokruhov beľového dreva a polomeru valca jadrového dreva. Najväčšie závis-
losti sa určili medzi stržňovými lúčmi jadrového drevä a polomerom kmeňa ($R^2 = 0,98$), vekom kambia a počtom letokruhov jadrového drevä ($R^2 = 0,93$). Oveľa slabšie závislosti sa určili medzi šírkou letokruhov beľového drevä a polomerom kmeňa ($R^2 = 0,13$).

Kľúčové slová: beľové drevä; jadrové drevä; dynamika tvorby jadrového drevä; stromová trieda; smrekovec európsky

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