Radial Variation in Tracheid Lengths in Dominant Trees of Selected Coniferous Species

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The radial variation was examined for tracheid lengths of Norway spruce (*Picea abies* (L.) Karst.), European larch (*Larix decidua* Mill.), and Scots pine (*Pinus sylvestris* L.) wood from dominant trees coming from an even-aged stand, and growing under identical forest site and climatic conditions. The measurements were completed on macerated material. The variation of tracheid lengths in annual rings from the core to the bark was used for determination of the border between the juvenile and mature wood in the trunk cross-section. The boundary age between the juvenile and mature wood zones established for the examined species was comparable, as it was 25 annual rings for Scots pine and 29 for European larch and for Norway spruce. In the juvenile zone, the tracheid lengths increased 2.2-fold in Norway spruce wood, while in Scots pine and European larch wood it was approximately 1.7-fold. By contrast, in the mature wood zone the tracheid lengths was stabilized at a certain level, showing slight fluctuations. The differences in the tracheids length of early and late wood in the examined annual rings were also determined, and it was established that for the majority of annual rings they are statistically significant ($p<0.05$).

Keywords: Tracheid lengths; Early wood; Late wood; Scots pine; Norway spruce; European larch; Juvenile wood; Mature wood

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INTRODUCTION

The properties of any given material are determined by its structure. For wood, its parameters depend both on the microscopic (*i.e.*, the shape and dimensions of cells) and the submicroscopic structure (the layer structure of the cell walls), the distribution of basic chemical compounds (within particular wall layers), as well as the specific gravity (of the wood substance packing in the unit volume). Due to the structural variability of wood (both inter- and intra-species) its properties have been observed to fall within a wide range of values. Despite the considerable variability in its characteristics, wood is a valuable structural material that is also used as a raw material for the manufacture of wood-based boards and for the pulp and paper industry (Corson *et al.* 2004; Cloutier *et al.* 2007; Almeida *et al.* 2016).

One of the features of wood microstructure that directly affects the quality of final products, whether manufactured from solid wood or from pulp, is the length of the cells. This parameter is frequently used to identify the juvenile and mature wood zones at the cross-section of both hardwood and softwood species (Helińska-Raczkowska and Fabisiak 1991; Zhu *et al.* 2000; Ferreira *et al.* 2011; Mvolo *et al.* 2015a; Palermo *et al.* 2015; Gogoi *et al.* 2018). In deciduous species, the diameter of the vessels is often used for this purpose (Helińska-Raczkowska and Fabisiak 1999; Bao *et al*. 2001). Juvenile wood (JW) is formed in the conditions of the apical meristem influence on the cambium. As the crown rises upwards, this influence (of auxins mainly) on the further parts of the tree ceases and the mature wood (MW) is formed. Some authors call the juvenile wood "crown wood" because it is produced within a living crown (Larson 1962; Larson 1994; Zobel and Buijtenen 1989; Kuprevicius *et al*. 2013).

The determination of the width of the juvenile wood zone is crucial for industrial practice, because softwood cells coming from these annual rings may be as much as 3- to 4-fold shorter than those in mature wood (Mvolo *et al*. 2015b). Moreover, juvenile wood of softwoods contain a relatively low number of late wood cells, while a high share of thin-walled cells causes low density and thus low mechanical strength in this wood compared to mature wood (Koubaa *et al.* 2005; Severo *et al.* 2012). The width of the juvenile zone and duration of its formation time are dependent on many internal and external factors. These factors include genetic factors, growth rate of trees, habitat or forest site type, cambial age, geographical location, as well as the biosocial position of tree in the stand (Zobel and Spraque 1998; Bao *et al.* 2001; Passialis and Kiriazakos 2004; Gapare *et al.* 2006; Boruszewski *et al*. 2017). When compared to mature wood, juvenile wood is characterized by a greater lignin and hemicelluloses content at a lower cellulose content (Gierlinger and Wimmer 2004; Rowell *et al.* 2005). In juvenile wood, the angle of microfibrils in relation to the longitudinal cell axis in the S2 layer of the secondary cell wall is greater in comparison to that in mature wood (Fabisiak *et al.* 2006; Wang and Stewart 2012; Hayatgheibi *et al*. 2018). The mechanical properties of wood are strictly correlated with the value of that angle (Mott *et al*. 2002). A wide microfibril angle indicates lower strength properties of wood (Downes *et al.* 2002), while it also results in a high rate of longitudinal shrinkage of wood and a respectively lower tangential and radial shrinkage of wood (Dumail and Castera 1997; Donaldson 2008; Ivković *et al*. 2009). The presented differences in the properties of juvenile and mature wood cause a heterogeneity of wood raw timber, and changes in sorption and thermodynamic properties (Esteban *et al.* 2015) and the problems posed by the use of juvenile wood, particularly as a structural material (Wu *et al*. 2018). However, it is generally acknowledged that juvenile wood may be used to manufacture paper of a high quality. Corson *et al*. (2004) are of an opinion that the differing properties and strength parameters of pulp obtained from juvenile and mature wood result from the fact that the thinner cell walls in juvenile wood promote greater packing of fibers, leading to increased paper density (reduced porosity) and thus enhanced smoothness and improved optical properties. On the other hand, short tracheids were found to have a negative effect on the tear resistance of paper (Semen *et al*. 2001).

Variation in cell length as well as other wood properties is related to the broadly understood character of the habitat or forest site type, climatic conditions, or biosocial class of tree in the stand and density of the stand (Alteyrac *et al*. 2006). In even-aged stands, the general canopy is not in one plane, because as a result of a different growth rate of trees, some of them have crowns located higher, while others lower. In dominant trees, crowns receive full light from above and partly from the sides and extend above the general level of the crown cover. The dominant trees are the largest in terms of height, breast height diameter and size of the crown, compared to suppressed trees, the lowest, with the smallest crown and breast height diameter. This internal height variation of trees is of great importance for the silviculture and also has an impact on the properties of the obtained wood raw material (Assmann 1970; Mansfield *et al*. 2007).

It may be concluded from past studies that environmental conditions have a greater effect on the structure of annual rings, and thus the width of the juvenile wood zone, than genetic factors (Zobel and Jett 1995; Kijidani *et al.* 2014; Cameron *et al*. 2015; Fernandes *et al*. 2017).

The aim of this study was to determine radial variation in tracheid lengths and to establish the boundary between juvenile and mature wood at the stem cross-section. The differences in the tracheids length of early and late wood in the examined annual rings of each species were also determined. Wood was gathered from trees of selected coniferous species that were from an even-aged stand, the same biosocial class of tree position, and grew under identical forest site and climatic conditions. This research specified the width of the juvenile wood zone in the examined species, which together with data on other wood properties (Czajka and Fabisiak 2016) provided insight into the technical quality of timber from a given geographical region.

EXPERIMENTAL

Materials and Methods

The tested material was comprised of wood from Norway spruce (*Picea abies* L. (Karst.), Scots pine (*Pinus sylvestris* L.), and European larch (*Larix decidua* Mill.). The tests were conducted on wood from the class of dominant trees aged 104 to 106 years. The stand was located in the Łopuchowko Forest Division, in the commune of Murowana Goślina (Poland) (52°26'N, 16°43'E). Three trees of each species were selected for analyses. Next, approximately 5-cm-thick test discs were cut out at the diameter at breast height and then approximately 4-cm-wide slats were cut out from the discs along the north-south radius. It was decided to determine the width of the juvenile wood zone based on radial variability of tracheid length. These measurements were recorded for the following annual rings: 3, 6, 9, 12, and 15, and next at every 10th ring up to the bark. In order to prepare samples for tracheid length measurements in experimental annual rings, early and late wood were collected separately and next they were subjected to tissue maceration. For this purpose, a mixture of acetic acid and hydrogen peroxide at a 1:1 ratio was used. Maceration was run at a temperature of 60 °C for 24 h (Yang *et al.* 2016). In each tested annual ring, the lengths of 30 tracheids were measured in each early and late wood. Various measuring techniques are used to determine the tracheids length (*e.g.* Mvolo *et al.* 2015b; Bouslimi *et al*. 2019). In this work the microstructure of the wood was examined under a light microscope coupled with a computer image analyzer using the Motic Images Plus 2.0 programme (Motic Incorporation, Ltd., Hong Kong, China). The tests were carried out using the direct method, marking with the cursor the length of those tracheids to which there was a certainty that they were undamaged. Only a few tracheids were measured on a single preparation. Thus, from one annual ring, 10 to 16 preparations were prepared. Altogether from each species 1260 tracheids of early wood were measured and the same number for late wood.

Statistical analysis was performed using Statistica 10.0 software (Dell, Round Rock, TX, USA). The nonlinear estimation was used for determining the boundary between the juvenile and mature wood zones. The descriptive statistics and one-way analysis of variance (ANOVA) were applied. The values of all properties analyzed in this study were means from measurements taken along the northern and southern rays. All tests were performed at the significance level of $p < 0.05$.

RESULTS AND DISCUSSION

The measured tracheid lengths in the function of cambial age in annual rings of Scots pine, European larch, and Norway spruce wood are presented in Fig. 1a through 1c. The cambial age corresponds to the age of the annual ring in which the ring was formed. Each point represents a mean value of 90 measurements of that parameter. The statistical analysis of the recorded results showed that the coefficients of variation for the measured value were comparable and their means for individual species amounted to 17% for Scots pine, 9% for European larch, and 7% for Norway spruce. Numerical values for these coefficients fell within the ranges of coefficients of variation for lengths of prosenchymatic elements in coniferous species (Panshin and De Zeeuw 1980).

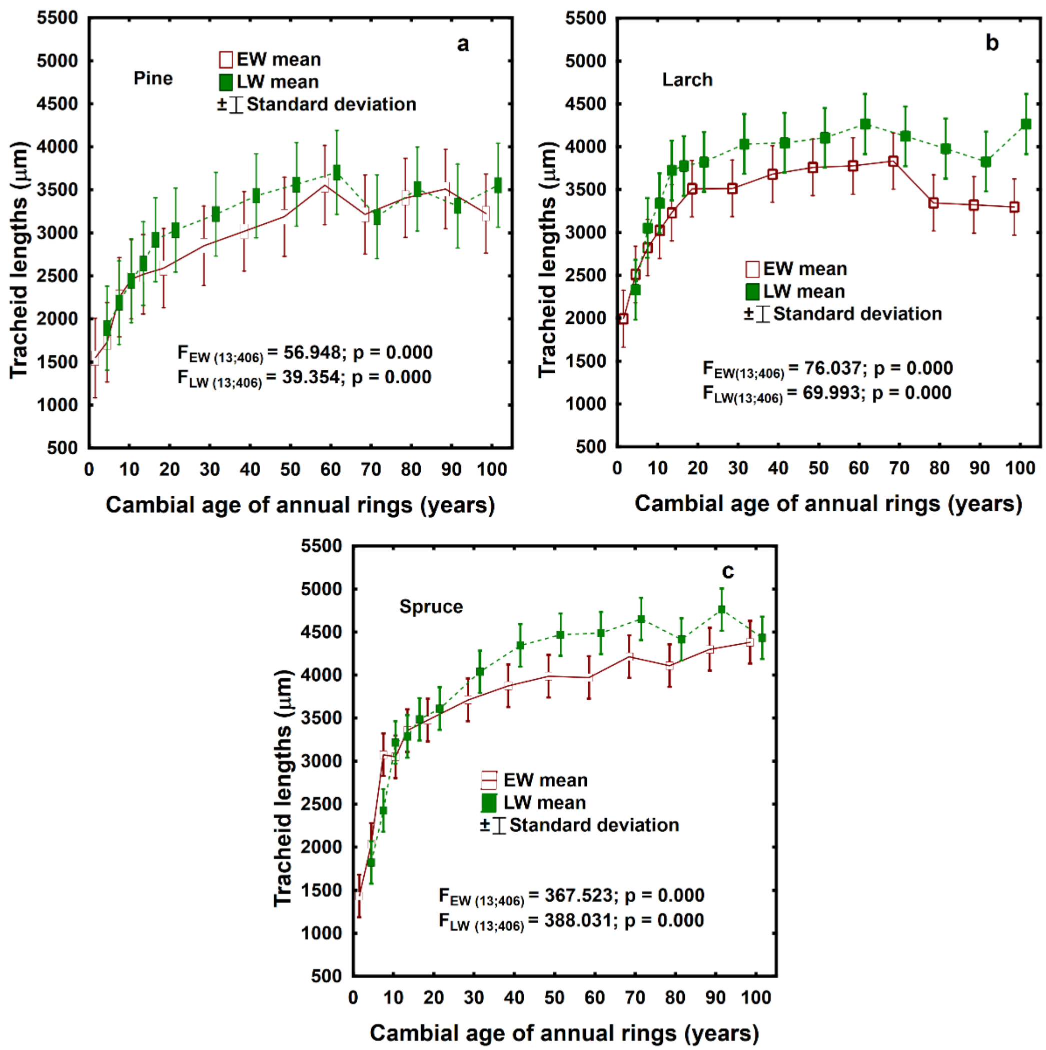

Fig. 1. Relationship between cambial age of annual rings and tracheid lengths (EW - early wood, LW - late wood) in dominant trees of a) Scots pine, b) European larch, and c) Norway spruce

In each analyzed species, tracheids formed in the first part of the vegetation period were shorter than those formed in the summer, irrespective of the location of the annual increment at the stem cross-section. The smallest differences in tracheid lengths between early and late wood were recorded in Norway spruce and Scots pine, as they amounted to approximately 9% and 10%, respectively, while they were the greatest in European larch, reaching approximately 14%. The confirmation of these differences is the performed ANOVA analysis of variance (Table 1), which shows that for most of the studied annual rings, the differences in the tracheids length of late and early wood were statistically significant ($p < 0.05$). A cursory analysis of data given in Fig. 1a through 1c indicates that tracheid length initially increased in the direction from the pith towards the bark dynamically, and after reaching a certain value it stabilized at a relatively steady level, showing slight fluctuations in the successive annual increments.

The effects of cambial age on mean tracheid length in the analyzed growth increments in Scots pine, Norway spruce, and European larch wood are presented in Fig. 2. A detailed analysis of variation in the mean tracheid lengths in the investigated species using nonlinear regression made it possible to determine a demarcation line on the ray length of tree between the zone of juvenile and mature wood. The nonlinear estimation module enables to determine the breakpoint (P) of the regression line. The segment regression model is estimated by the software and has a form as follows:

$$y = (a_1+b_1\,x)(x<=P)+(a_2+b_2\,x)(x>P) \tag{1}$$

The obtained regression model indicates that it is a two-segment regression (Abdel-Gadir and Krahmer 1993). For the segment corresponding to juvenile wood, the equation takes the form $y_1 = a_1 + b_1$ x, while for that corresponding to mature wood it is $y_2 = a_2 + b_2$ x. Parameters of regression equations for tracheid lengths in those zones in the stem cross-section in the analyzed species are given in Table 2. The boundary between juvenile and mature wood is indicated by the abscissa of the breakpoint (P) of the regression lines. The length of juvenile growth of the examined trees is comparable, as it is 25 annual rings for Scots pine and 29 for European larch, and for Norway spruce. These relationships are also shown graphically in Fig. 2.

Table 1. ANOVA of Early and Late Tracheid Lengths for Annual Rings of Scots Pine, European Larch, and Norway Spruce Wood

Source of Variation	Cambial Age of Annual Rings	Species					
		Scots Pine		European Larch		Norway Spruce	
		Results of Variance Analysis					
		$F_{(1;58)}$	p	$F_{(1;58)}$	p	$F_{(1;58)}$	p
Kind of Tracheids (Early, Late)	3	16.989	0.000	38.767	0.000	163.357	0.000
	6	10.796	0.001	33.562	0.000	144.504	0.000
	9	2.590	0.112*	56.636	0.000	4.079	0.048
	12	2.159	0.147*	115.992	0.000	23.362	0.000
	15	11.283	0.001	123.882	0.000	5.331	0.024
	20	10.5405	0.001	10.300	0.002	3.771	0.057*
	30	8.761	0.004	30.242	0.000	13.506	0.000
	40	13.398	0.000	17.487	0.000	32.431	0.000
	50	7.974	0.006	12.261	0.000	39.178	0.000
	60	1.585	0.213*	16.141	0.000	54.668	0.000
	70	0.054	0.816*	8.902	0.004	37.531	0.000
	80	0.705	0.404*	45.415	0.000	28.389	0.000
	90	2.591	0.112*	33.689	0.000	97.978	0.000
	100	5.935	0.017	114.566	0.000	0.761	0.386*

*Non-significant differences

In the juvenile zone, the tracheid length increased 2.2-fold in Norway spruce wood, while in Scots pine and European larch wood it was approximately 1.7-fold. By contrast, in the mature wood zone, the length of the tracheids was stabilized at a certain level, showing slight fluctuations. In the mature wood zone, the smallest fluctuations in tracheid lengths were observed in Scots pine and European larch wood, because the ranges in that parameter (*i.e.*, the difference between the longest and shortest tracheids) were practically identical, amounting to 429 μm and 447 μm, respectively. In turn, in Norway spruce wood, this difference was 50% greater. Moreover, in the last vegetation periods (over the 80th annual ring) in Norway spruce wood, a further increase in tracheid lengths was observed, particularly in late wood, whereas in the other species a downward trend was found. The trend for the tracheid lengths to decrease and an analogous trend also for other properties (*e.g.*, wood density) in old trees was confirmed for many tree species (Pearson and Ross 1984; Zobel and Spraque 1998).

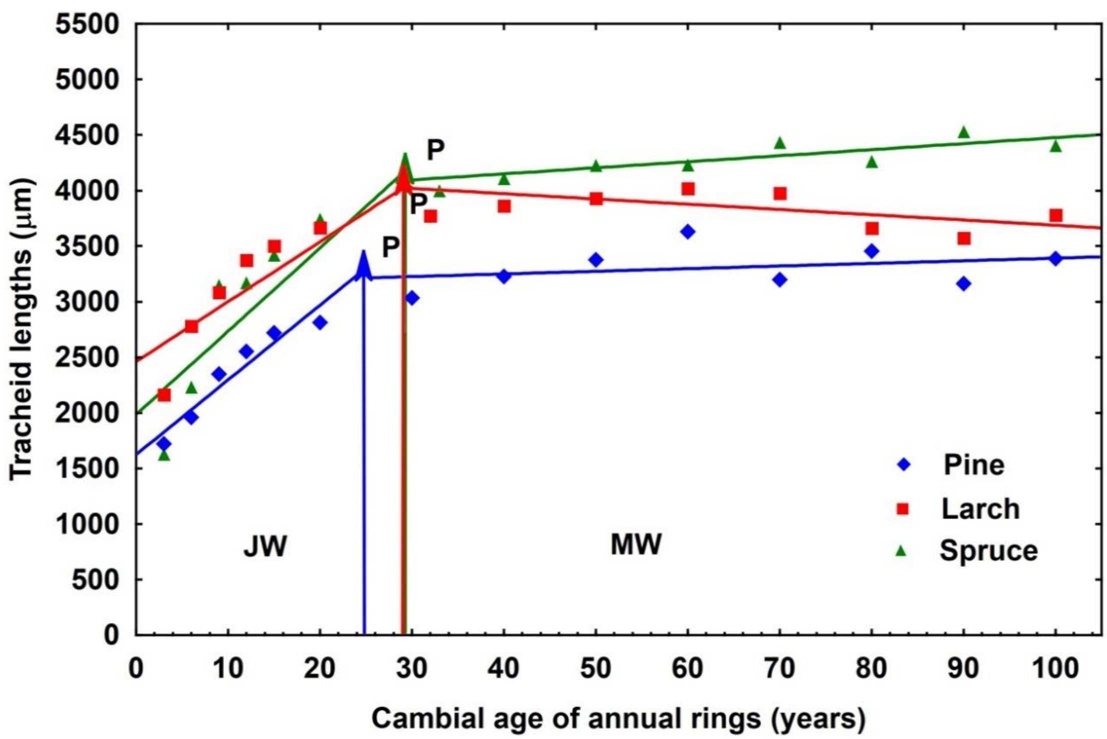

Fig. 2. The effect of cambial age of annual rings on mean tracheid lengths in dominant trees of Scots pine, European larch, and Norway spruce; the demarcation lines between juvenile wood (JW) and mature wood (MW) are marked with vertical lines

Table 2. Parameters of Regression Equations Describing the Relationship Between Tracheid Lengths (*y*, μm) and Cambial Age of Annual Rings (*x*, years) of Scots Pine, European Larch, and Norway Spruce Wood

Regression Parameters	Scots Pine	European Larch	Norway Spruce
a_1	1623	2461	1985
b_1	67.26	53.85	74.87
a_2	3155	4161	3933
b_2	2.367	-4.728	5.436
P	25	29	29

P abscissa of breakpoint of the regression lines

The determined width of the juvenile wood zone in this study was compared with the results of other researchers who conducted research on the wood from dominant trees. It has been found that the width of this zone is similar to that reported by Koizumi *et al*. (2003), who based on the variability in tracheid lengths of *Larix sibirica* identified it as 20 annual rings. Similarly, Karlman *et al.* (2005) assumed the period of juvenile wood formation for pine (*Pinus sylvestris*) and several larch species (*Larix* spp.) to be 20 years based on literature data. Fabisiak (2005) and Fabisiak and Moliński (2002a, 2002b) showed that in 45-year-old dominant trees of Douglas fir and Scots pine, the age of transition of juvenile tissue into mature wood was 25 years, while in European larch it was 20 years. Thus, it may be assumed that the period of juvenile wood formation in the analyzed species coming from the same biosocial class was similar.

The mean tracheid lengths in the juvenile and mature wood zones in Scots pine, Norway spruce, and European larch are presented in Fig. 3. When investigating intraspecific variation in the measured parameter in the juvenile and mature wood zones, an ANOVA was conducted, which showed that these differences within the investigated species were statistically significant.

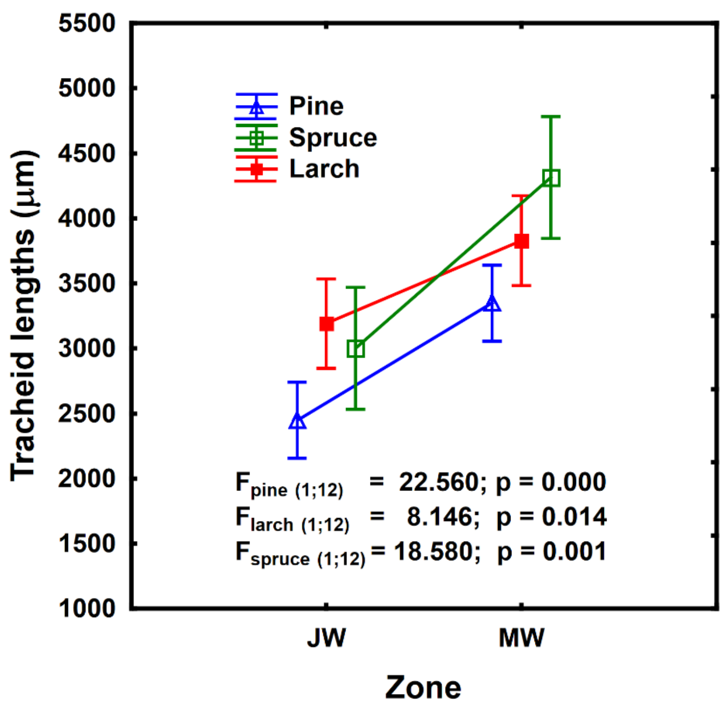

Fig. 3. Mean tracheid lengths in the juvenile (JW) and mature (MW) wood zones in Scots pine, Norway spruce, and European larch wood; vertical bars denote confidence interval of 95%.

In the juvenile wood zone, the mean tracheid lengths were the smallest in Scots pine, and amounted to 2450 µm. In the juvenile wood zone of Norway spruce wood, tracheids reached 2860 µm on average. Tracheids were the longest in European larch wood, with lengths that slightly exceeded 3100 µm. When comparing the increase in the length of analyzed cells in that zone (JW), it was found that in Scots pine and European larch this value increased approximately 75%, while in Norway spruce it was by as much as 120%. In turn, in the mature wood zone, the longest cells were found in Norway spruce wood, as their average length was 4260 µm. In European larch wood, this parameter reached 3820 μm. The shortest tracheids in mature wood (similarly as in the pith annual rings) were observed in Scots pine wood. At their mean length in that part of the stem, the cross-section amounted to 3390 μm.

CONCLUSIONS

1. In each of the analyzed species, the tracheid length increased in the direction from the pith towards the bark, initially dynamically, and stabilized at a relatively steady level. In the successive annual rings, it showed slight fluctuations up to the stem bark.
2. Tracheids that formed in the first part of the vegetation period were shorter than those formed in the summer, irrespective of the species and the position of the annual ring at the stem cross-section. The smallest differences in the analyzed parameter were recorded in Norway spruce and Scots pine wood, as they amounted to approximately 9% and 10%, respectively, while they were the greatest in European larch wood, reaching approximately 14%.
3. The period of juvenile wood formation in the examined species was comparable and was identified as 29 annual rings for Norway spruce, and for European larch, and 25 for Scots pine. In that zone, tracheid length increased 2.2-fold in Norway spruce wood, while in Scots pine and European larch wood it was approximately 1.7-fold, in comparison to mature wood of those species.
4. The shortest cells in the juvenile wood zone were found in Scots pine wood (mean tracheid length of 2450 μm), in Norway spruce and European larch wood these cells were longer by 17% and 24%, respectively, in comparison to Scots pine wood. In the mature wood zone the shortest tracheids were found in Scots pine wood (3390 μm), while they were the longest in Norway spruce wood (4260 μm).

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