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The Variations in Tracheid Length of *Pseudotsuga menziesii* (Mirb.) Franco Wood in Relation to Cambium Age, Site, and Growth

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Abstract: This study investigated the variations in tracheid length of *Pseudotsuga menziesii* (Mirb.) Franco from three sites in Croatia in relation to cambium age, within- and between-site differences, and growth rate. Tracheids are the main structural element in *P. menziesii* wood, varying in length following different patterns that should be precisely determined. After the maceration procedure, earlywood tracheid length (EWTL), latewood tracheid length (LWTL), annual growth ring tracheid length (RTL), earlywood ring width (EWW), latewood ring width (LWW), and annual ring width (ARW) were measured in selected annual growth rings. The significant effect of annual growth rings and zone interaction for EWTL and LWTL, as well as of annual growth rings, trees, and sites for RTL, was determined. The results conclude on the differences between the trends in EWTL and LWTL from pith toward the bark. In addition, the correlation analysis between the tracheid length and different growth patterns was investigated, and very weak or no association between the variables was detected. This research contributes to better understanding the degree of wood uniformity of *P. menziesii* from the technological perspective, as well as the variability factor in the optimization of forest management with favoring overall wood quality.

Keywords: *P. menziesii*; tracheid length; wood anatomical variations; earlywood; latewood; tree ring parameters; tracheid length-to-growth correlations

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1. Introduction

Pseudotsuga menziesii (Mirb.) Franco, as a softwood species, is one of the most ecologically important and valuable timber species globally [1]. It has become a major economic species because of its fast growth rate and good-quality timber. It is now the most abundant non-native tree species cultivated in Central European forests [2]. Recently, there has been growing economic interest in *P. menziesii*, which is less vulnerable to drought than *Picea abies*, becoming a valid softwood alternative on plantations at lower altitudes or in response to climate change [3,4]. As a result of its wide climatic amplitude, *P. menziesii* is both a minor and a major component in many regional ecosystems (climatic or vegetation zones). The timber of this species meets all the requirements where strength is the primary factor [5,6]. Due to its great versatility, its wood can be used for various applications, especially in construction. It is also used for veneer, fibers, or particle panels and in the pulpwood industry [7].

In general, the softwood structure is relatively uniform in comparison to hardwoods. Tracheids are long cells that are often more than 100 times longer (1 to 10 mm) than wider and are the primary component of softwoods [8]. Longitudinal tracheids are four- to -six-sided prismatic cells with closed ends and constitute over 90% of the volume of the softwoods [9]. The difference between the earlywood and the latewood tracheid morphology is in the radial diameter and the thickness of the cell walls [9]. This contributes to a more or less pronounced transition from the earlywood to the latewood of the same growth ring.

The supremacy of wood as a raw material for pulp and paper is unquestioned. Specific characteristics of wood directly affect the quality of raw materials for that specific purpose. Tracheid length is among the most important wood quality characteristics for pulp [10,11] and solid wood end use [12,13]. Consequently, it is evident that the anatomical wood structure largely determines its properties and quality.

Although the wood structure of a specific species is determined by its genetic constitution, the structural characteristics of the wood within the population still vary [14]. Understanding the extent of wood variability is important because the use of wood is related to certain of its characteristics. Different patterns of wood variability can be described, including variations in the radial direction (within and between annual growth rings from pith to the bark), between individual trees of the same species within the site, and between sites of different characteristics. The structure of wood varies as a result of the tree growth. Cross-sections of stems show nonuniform width of the growth rings from the pith to the bark. In addition to the ring width, variations are exhibited by growth ring structure and cell morphology [9,14].

One of the major causes of wood variability is the presence of juvenile and mature wood [15]. Juvenile wood is more pronounced in softwoods compared to hardwoods [16]. The transition between the juvenile and mature wood in *P. menziesii* is defined in the first 10 to 20 years of tree age [7,17]. The usual pattern in softwoods is to have short tracheids near the tree center followed by a rapid increase through the juvenile zone and then a decrease in length [15,18]. Tracheid length can be as much as four to five times greater near the bark than near the pith [19]. Tracheid length in softwoods increases from pith to the bark with much more change than the tracheid diameter and the cell-wall thickness [9]. The general pattern refers to the influence of age on the wood structure [14].

Changes in the ring width mainly describe the variation between growth rings. The relationship between the ring width and the specific characteristics of the wood cells is of great importance. The effects of changing ring width concerning the proportion of latewood and the cell length have been investigated [20,21]. Intra-ring wood variability is explained by differences in the cell size from earlywood to latewood, where latewood tracheids are longer than those of the earlywood [22,23]. In softwoods, the shapes of the curves representing variation in cell lengths across the growth increment are related to the character of the transition from early to late wood [24,25]. Abbreviation titles for investigated anatomical characteristics are given in Table 1. It was determined in softwoods that earlywood width (EWW) is more correlated to the annual ring width (ARW) than latewood width (LWW) [26]. Differences in wood structure occur between sites, with or without regard to geographical localities, altitudes, and latitudes [14,27,28]. In a particular site, the variation is very high, generally higher than between sites [14]. However, the effect of the site on the tracheid length has been poorly investigated so far.

P. menziesii was first introduced to Croatia more than 100 years ago. However, only after 1960 did it begin to be used more massively in forestry. Early research on the growth and increment of *P. menziesii* was started by Klepac [29] to determine the conditions in which this species is highly productive. Previous studies on *P. menziesii* in Croatia were carried out by the Croatian Forestry Institute within the IUFRO research program of this species and focused on the suitability of establishing *P. menziesii* cultures in free forest and non-forest areas [30–33]. The mentioned studies pointed to the conclusion about the suitability of establishing *P. menziesii* cultures in free forest and non-forest areas in Croatia. Consequently, *P. menziesii* could become superior to Norway spruce, which is currently Europe's most important economic species.

P. menziesii wood is considered coarse-textured. It is characterized by an abrupt transition from earlywood to latewood, and visible resin canals typically occur [34]. Wood structure or wood properties, as well as different patterns of wood variation of *P. menziesii* in Croatia, have not been investigated so far. Rathgeber et al. [35] investigated intra-tree-ring variation in tracheid diameter. The variation in the relationship between the earlywood tracheid length and the earlywood tracheid width, as well as the latewood tracheid length and the latewood width in this species, has not been studied to date. Understanding the size and the volume of wood variability is essential for end use. The data from this research will provide insight into the technical quality of *P. menziesii* wood from three sites in Croatia.

To contribute to the existing knowledge on different patterns of variations in *P. menziesii* wood, this research aimed to determine the preliminary tracheid length, one of the essential softwood anatomical characteristics, of *P. menziesii* wood from three sites in Croatia.

Table 1. Abbreviation titles for investigated anatomical characteristics.

Acronym	Description
RTL	Ring tracheid length
EWTL	Earlywood tracheid length
LWTL	Latewood tracheid length
ARW	Annual ring width
EWW	Earlywood width
LWW	Latewood width

The specific objectives of this study were (a) to determine the tracheid length (RTL, EWTL, and LWTL) in examined annual growth rings of *P. menziesii* wood from three sites in Croatia, (b) to examine the variation in the tracheid length between earlywood and latewood, (c) to investigate variations in the tracheid length in the direction from pith to the bark, between individual trees within each site, and between sites, and (d) to investigate different correlations between ARW (including EWW and LWW) and tracheid length (including EWTL and LWTL).

2. Materials and Methods

2.1. Site and Study Materials

For the purpose of this research, three sites (two from the continental region and one from the maritime region) in Croatia were selected. The first site was located within the Forest Office Veliki Grđevac, Management Unit "Grđevačka Bilogora" Department 28g (45°46′35″ N, 17°03′28″ E, elevation: 135 m). The mean annual temperature is 11 °C, and the total annual precipitation is 809 mm. Luvisol soils are found there, characterized by mixed mineralogy, high nutrient content, good drainage, and general fertility. The second site was located within the Forest Office Poreč, Management Unit "Lim", Department 39a (45°9′40″ N, 13°40′39″ E, elevation: 90 m). The mean annual temperature is 17 °C, and the total annual precipitation is 1142 mm. It is characterized by red soil, a well-drained, reddish, clayey to silty soil with neutral pH conditions, typical for the Mediterranean region. The third site was located within the Forest Office Varaždin, Management Unit "Zelendvor", Department 13i (46°20′7″ N, 16°12′34″ E, elevation: 186 m). The mean annual temperature is 10 °C, and the total annual precipitation is 873 mm. Dystric cambisol occurs there on acidic substrates, lacking a well-developed mineral–organic surface horizon. It is widely distributed on parent materials of low base status and typically under forest vegetation.

2.2. Sample Collection and Preparation

From each site, three trees of *P. menziesii* were harvested and sampled in October or November 2019. Before felling, each tree was numbered, and the north side was marked. The age of the selected trees ranged from 44 to 47 years, with the diameter at breast height (DBH) from 46.5 to 57 cm at the first site, in contrast to 48 years and 46–48.5 cm DBH at the second site, and 72–77 years and 48.5–56.5 cm DBH at the third site. After felling, 5 cm thick discs were cut from each tree at breast height (1.3 m). Radial segments with north–south orientation were cut from each disc. Depending on the tree's age, annual growth rings (3, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60, and 70) were selected and marked along one radius.

The separation of individual tracheids was necessary for measuring tracheid length. A small wood chip from earlywood and latewood was extracted from each of the previously selected annual growth rings. The maceration was performed using a standardized procedure by Franklin [36]. Prepared wood chips were placed in test tubes, filled with a mixture of acetic acid and hydrogen peroxide (1:1) used as a reagent, and placed in an oven for 48 h at 60 °C until the middle lamella of the tracheids was dissolved. Furthermore, the material in the test tubes was rinsed with distilled water and ethanol, stained with Astrablue, and mounted on microscope slides with glycerin.

2.3. Tracheid Length Measurement

From each macerated sample (separately earlywood and latewood zone), 30 unbroken tracheids were selected and measured. The measurements of the tracheid length were performed using a light microscope (Carl Zeiss Jena, Germany), a digital camera (Dino-Lite), and DinoCapture 2.0 Software (Dino-Lite Europe, The Netherlands). A total of 5760 tracheids were measured in this study using ×20 magnification.

2.4. ARW Measurement

For ARW measurements, radial segments with north–south orientation were previously dried and sanded using fine granulation. The ARW measurement was performed with a Lintab 6 measuring table (precision 0.01 mm) (Rinntech-Metriwerk GmbH & Co. KG Hardtstr. 20-22 D-69124 Heidelberg, Germany). WinDENDRO (Regent Instruments Inc., 7140 Bd Wilfrid-Hamel, Québec, QC G2G 1B5, Canada) software was used to precisely measure ARW, EWW, and LWW. Both stem radii were measured, and mean values were calculated.

2.5. Statistical Analysis

Statistical analysis of all the results was carried out in Statistica 14.0 (TIBCO Soft Inc., 3307 Hillview Avenue Palo Alto, CA 94304. USA, 2020). Repeated-measures analysis of variance (ANOVA) was used to test the effect of the annual growth rings, tree, site, annual growth rings, and zone interaction. Statistical significance was determined by p-value. If the p-value was ≤0.05, the null hypothesis was rejected, and the differences were declared statistically significant. In contrast, at $p \geq 0.05$, the null hypothesis was not rejected, and the differences were not statistically significant. In the second stage of variance analysis, a post hoc test (Tukey test) was used to identify significant differences between pairs of means (site). The differences were declared statistically significant for a p-value ≤0.05. In addition, a correlation analysis was performed to investigate the relationship of ARW, EWW, and LWW with RTL, EWTL, and LWTL until the 40th annual growth ring in wood from each site. The correlation coefficient (r) was used to indicate the strength of the relationship.

3. Results

3.1. Effect of Annual Growth Rings, Tree, and Site on Tracheid Length and Changes in Earlywood and Latewood

Mean values and the standard deviation of the tracheid length (EWTL, LWTL, and RTL) for all annual growth rings selected in *P. menziesii* wood from three sites are given in Table 2. Radial trends of the *P. menziesii* tracheid length (EWTL, LWTL, and RTL) for all annual growth rings selected in wood from each site are presented in Figure 1. The trees from each site were not of the same age. For better prediction of the radial trends, more annual growth rings were selected in wood from Veliki Grđevac and Varaždin sites. In addition, Table 2 includes all data until the 40th annual growth ring per site.

At the Veliki Grđevac site, EWTL rapidly increased from the third to the 30th annual growth ring, decreased until the 40th, and increased again until the 45th (Figure 1a). At the Poreč site, EWTL increased until the 15th annual growth ring, and then fluctuated until the 35th annual growth ring, which slowly decreased toward the bark (Figure 1c). Similar trends were observed for LWTL at the Veliki Grđevac (Figure 1b) and the Poreč site (Figure 1d), with only a few different fluctuations. At the Varaždin site, EWTL steadily increased from the third to the 25th annual growth ring, which steadily fluctuated toward the bark (Figure 1e). However, LWTL rapidly increased until the 15th annual growth ring, after which significant fluctuations toward the bark were noticed (Figure 1f).

When considering changes in RTL until the 40th annual growth ring in wood from each site, the most pronounced changes were determined until the 25th annual growth ring at the Veliki Grđevac site and until the 20th annual growth ring at both the Poreč and the Varaždin sites. Therefore, from these three sites, this could be interpreted as the juvenile wood boundary between the 20th and the 25th annual growth ring in *P. menziesii* wood.

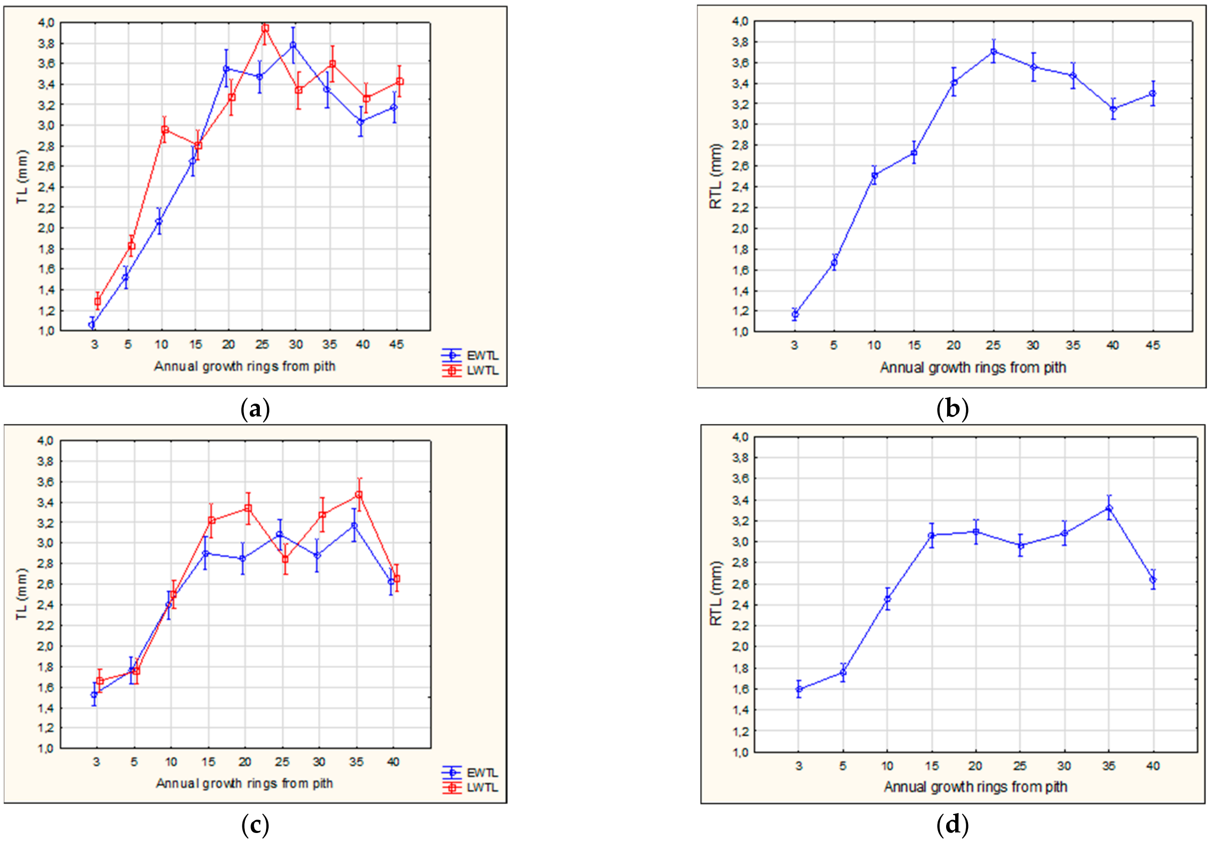
Table 2. The mean and standard deviation of the *P. menziesii* tracheid length (earlywood, latewood, and the annual ring) for all annual growth rings selected in wood from each site (Part 1) and for all data until the 40th annual growth ring from each site (Part 2).

Part 1—for All Annual Growth Rings per Site							
Site	**Annual Growth Ring**	**Property**					
		EWTL (mm)		**LWTL (mm)**		**RTL (mm)**	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
VG	3	1.05	0.29	1.28	0.49	1.17	0.42
	5	1.52	0.49	1.83	0.54	1.67	0.54
	10	2.07	0.61	2.96	0.63	2.51	0.76
	15	2.65	0.70	2.80	0.68	2.73	0.69
	20	3.55	0.65	3.26	1.00	3.41	0.85
	25	3.47	0.78	3.94	0.70	3.71	0.78
	30	3.78	0.93	3.34	0.79	3.56	0.89
	35	3.35	0.88	3.60	0.81	3.47	0.85
	40	3.04	0.55	3.27	0.80	3.15	0.69
	45	3.17	0.68	3.44	0.76	3.30	0.73
PO	3	1.53	0.50	1.66	0.56	1.59	0.53
	5	1.76	0.55	1.76	0.66	1.76	0.61
	10	2.40	0.53	2.51	0.76	2.45	0.66
	15	2.90	0.58	3.22	0.94	3.06	0.80
	20	2.85	0.71	3.34	0.77	3.09	0.78
	25	3.08	0.49	2.85	0.87	2.97	0.72
	30	2.88	0.72	3.28	0.85	3.08	0.81
	35	3.17	0.68	3.47	0.85	3.32	0.78
	40	2.62	0.51	2.66	0.73	2.64	0.63
VŽ	3	1.5	0.36	1.68	0.54	1.59	0.47
	5	1.74	0.42	1.93	0.5	1.83	0.47
	10	2.57	0.71	2.59	0.62	2.58	0.66
	15	2.66	0.64	3.13	0.61	2.9	0.67
	20	2.81	0.66	3.00	0.71	2.91	0.69
	25	3.05	0.66	2.61	0.64	2.83	0.69
	30	2.86	0.67	3.11	0.87	2.99	0.79

35	2.84	0.65	3.15	0.94	2.99	0.82
40	2.58	0.77	2.69	0.69	2.63	0.73
45	2.86	0.66	3.00	0.72	2.93	0.69
50	2.69	0.65	3.54	0.98	3.12	0.93
60	2.83	0.54	2.83	0.75	2.83	0.65
70	2.92	0.80	2.98	0.61	2.95	0.71
Part 2—All Data until the 40th Annual Growth Ring per Site						
Site	**Property**					
	EWTL (mm)		**LWTL (mm)**		**RTL (mm)**	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
VG	2.72	1.14	2.92	1.08	2.82	1.11
PO	2.58	0.80	2.75	1.00	2.66	0.99
VŽ	2.51	0.80	2.65	0.85	2.58	1.00

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin; SD—standard deviation.

The highest EWTL was measured in the 30th annual growth ring (3.78 mm) from the Veliki Grđevac site, in the 35th annual growth ring (3.17 mm) from the Poreč site, and in the 25th annual growth ring (3.05) from the Varaždin site. The highest LWTL was measured in the 25th annual growth ring (3.94 mm) from the Veliki Grđevac site, in the 20th annual growth ring (3.34 mm) from the Poreč site, and in the 50th annual growth ring (3.54 mm) from the Varaždin site. Compared to the highest EWTL, the highest LWTL was reached with earlier cambium age from Veliki Grđevac and Poreč site but with much later earlier cambium age in wood from the Varaždin site. The highest RTL was measured in the 25th annual growth ring (3.71 mm) from the Veliki Grđevac site, in the 35th annual growth ring (3.32 mm) from the Poreč site, and in the 50th annual growth ring (3.12 mm) from Varaždin site.



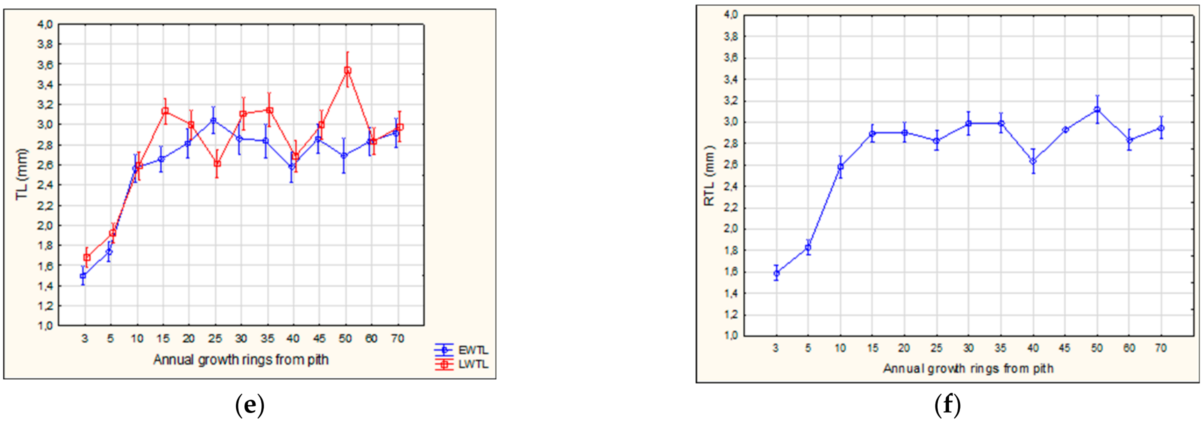


Figure 1. Radial trends of the *P. menziesii* tracheid length (EWTL—earlywood, LWTL—latewood, and RTL—annual ring) for all annual growth rings selected in wood from each site. (**a**,**b**) Veliki Grđevac; (**c**,**d**) Poreč; (**e**,**f**) Varaždin. The vertical bars represent 0.95 confidence intervals.

The annual growth ring-by-zone interaction was highly significant for EWTL and LWTL in wood from all three sites (Table 3). Zones included the earlywood and latewood separately, as presented in Figure 1a,c,e. However, the effect of annual growth rings (age) and trees was tested on the tracheid length of the annual growth ring (RTL).

Table 3. Repeated-measures analysis of variance for the *P. menziesii* tracheid length for zones (earlywood and latewood) in all annual growth rings selected in wood from each site.

Site	Source	SS	d.f.	MS	F	*p*
VG	Annual growth rings × zone	54.93	9	6.10	12.30	0.000000
PO	Annual growth rings × zone	18.58	8	2.32	4.95	0.000005
VŽ	Annual growth rings × zone	45.91	12	3.83	8.22	0.000000

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin; SS—sum of squares; d.f.—degrees of freedom; MS—mean sum of squares.

Annual growth rings affected RTL in wood from all three sites in a highly significant way (Table 4). The effect of trees on RTL was significant in wood from Veliki Grđevac and Varaždin sites, being highly significant in wood from the Poreč site.

Table 4. Repeated-measures analysis of variance for the *P. menziesii* tracheid length for zones (earlywood and latewood) in all annual growth rings selected in wood from each site.

Site	Sources	SS	d.f.	MS	F	*p*
VG	Annual growth rings	1179.66	9	131.07	249.15	0.000000
	Tree	5.75	2	2.88	4.67	0.010522
PO	Annual growth rings	548.69	8	68.59	139.79	0.000000
	Tree	16.18	2	8.09	14.04	0.000002
VŽ	Annual growth rings	463.95	12	38.66	92.43	0.000000
	Tree	7.83	2	3.92	7.54	0.000719

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin; SS—sum of squares; d.f.—degrees of freedom; MS—mean sum of squares.

The results of the ANOVA with Tukey post hoc test for RTL at the three sites until the 40th annual growth ring are given in Table 5.

The results from Table 2 (Part 2) indicate smaller mean values of EWTL in comparison to LWTL in wood from all three sites. All three properties (EWTL, LWTL, and RTL) had the highest values in wood from the Veliki Grđevac site, following the Poreč site, with the Varaždin site having the lowest values. According to the IAWA Committee [37], tracheids of *P. menziesii* wood from those three sites could be classified as short (tracheid length less than 3000 μm). However, the same authors pointed out that tracheids of *P. menziesii* could fall into at least two categories (overlap): 2500–4500–5600 μm.

Table 5. Repeated-measures analysis of variance for the *P. menziesii* tracheid length (annual ring) among three sites until the 40th annual growth ring.

Source	SS	d.f.	MS	F	*p*	Tukey Post hoc		
						Site		*p*
Site	47.29	2	23.65	42.29	0.000000	VG	PO	0.000022
							VŽ	0.000022
						PO	VG	0.000022
							VŽ	0.006616
						VŽ	VG	0.000022
							PO	0.006616

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin; SS—sum of squares; d.f.—degrees of freedom; MS—a mean sum of squares.

Similar to previous results on the effect of the annual growth rings and growth rings-by-zone interaction, the effect of site was highly significant for RTL. The significance was determined by the interaction among all individual sites (Veliki Grđevac, Poreč, and Varaždin).

3.2. Different Patterns of Correlations between Tree Ring Parameters and Tracheid Length

The mean values and standard deviations of EWW, LWW, and ARW until the 40th annual growth ring are given in Table 6.

The results in Table 6 detected different variations of the radial growth-related parameters. Fluctuations in inconsistent radial patterns of EWW, LWW, and ARW characterized wood from all three sites. In summary, the narrowest EWW (1.80 mm), LWW (1.63 mm), and ARW (3.43 mm) were determined in wood from the Varaždin site.

The widest EWW was measured in the fifth annual growth ring from the Veliki Grđevac site (4.76 mm), in the 10th annual growth ring from the Poreč site (5.06 mm), and in the third annual growth ring from Varaždin site (3.38 mm). The widest LWW was measured in the 10th annual growth ring from the Veliki Grđevac site (4.00 mm), in the fifth annual growth ring from the Poreč site (3.99 mm), and in the 20th annual growth ring from the Varaždin site (2.02 mm). The widest ARW was measured in the fifth annual growth ring from the Veliki Grđevac site (7.47 mm), in the 10th annual growth ring from the Poreč site (8.54 mm), and in the third annual growth ring from Varaždin site (5.00 mm). The greatest values of EWW, LWW, and ARW were detected within the juvenile wood (until the 20th annual growth ring) from all three sites.

Table 6. The mean and standard deviation of the *P. menziesii* earlywood width (EWW), latewood width (LWW), and annual ring width (ARW) from all three sites.

Site	Annual Growth Ring	Property					
		EWW (mm)		LWW (mm)		ARW (mm)	
		Mean	SD	Mean	SD	Mean	SD
VG	3	2.91	3.34	1.84	0.44	6.13	2.09
	5	4.76	1.26	2.92	1.79	7.47	0.43
	10	1.84	0.74	4.00	1.00	6.25	0.24
	15	2.70	0.20	2.73	0.76	5.52	0.20
	20	3.44	0.66	2.64	0.57	5.75	0.47
	25	1.81	0.17	2.01	0.81	3.87	0.15

	30	2.22	0.13	3.08	0.75	5.34	1.75
	35	1.52	0.31	1.39	0.48	2.73	0.29
	40	1.09	0.28	0.62	0.35	1.59	0.28
	All	2.60	1.57	2.36	1.21	4.96	2.24
PO	3	2.61	0.39	1.77	1.12	4.38	1.16
	5	2.91	1.17	3.99	3.19	6.90	4.22
	10	5.06	0.93	3.47	0.84	8.54	0.40
	15	2.16	0.87	1.69	0.19	3.86	1.01
	20	2.93	0.90	2.48	1.14	5.42	1.78
	25	3.62	0.09	3.28	1.12	6.90	1.16
	30	2.69	0.77	1.57	0.60	4.25	1.34
	35	2.76	0.22	1.62	0.48	4.38	0.69
	40	1.76	1.29	1.05	1.01	2.81	2.28
	All	2.94	1.14	2.33	1.49	5.27	2.36
VŽ	3	3.38	1.19	1.62	1.66	5.00	1.47
	5	1.23	0.69	1.39	1.30	2.63	1.99
	10	1.14	0.51	1.08	0.56	2.22	0.88
	15	1.33	0.49	1.65	0.95	2.98	1.43
	20	1.96	1.05	2.02	0.89	3.98	1.92
	25	2.06	0.56	1.65	0.57	3.71	1.06
	30	1.45	0.38	1.60	0.93	3.05	0.91
	35	1.77	0.62	1.71	0.17	3.48	0.73
	40	1.87	0.44	1.97	0.58	3.83	0.99
	All	1.80	0.88	1.63	0.83	3.43	1.37

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin; SD—standard deviation.

The correlation coefficients (*r*) between RTL and ARW, between EWTL and EWW, and between LWTL and LWW are given in Table 7. RTL was weakly negatively correlated with ARW at the Veliki Grđevac site, while the correlation at the Poreč and Varaždin sites was almost negligible. EWTL was weakly negatively correlated with EWW at the Veliki Grđevac and Varaždin sites. However, a positive but negligible correlation between EWTL and EWW was determined at the Poreč site. A very weak or almost negligible correlation was detected between LWTL and LWW at all three sites, but this correlation was negative at the Veliki Grđevac and Poreč sites and positive at the Varaždin site.

Table 7. Correlation coefficients of the *P. menziesii* tracheid length (RTL, EWTL, and LWTL) and ring width (ARW, EWW, and LWW).

Site	Correlation Coefficient		
	RTL–ARW	**EWTL–EWW**	**LWTL–LWW**
	r	***r***	***r***
VG	−0.4495	−0.4765	−0.1798
PO	−0.1492	0.0358	−0.2328
VŽ	−0.2163	−0.3836	0.1277

Notes: VG—Veliki Grđevac; PO—Poreč; VŽ—Varaždin.

4. Discussion

The dimensions of tracheids are a major determinant of the usefulness of softwood timber [38,39]. In softwoods, the rate of increase in the tracheid cross-section dimensions is considerably lower than that for length increases [9]. Concerning that, different patterns of tracheid length variations contribute to a better understanding of within- and between-ring wood heterogeneity. Variations in wood properties occur concerning growth conditions, silviculture, the genetic origin of the trees, and the location of the wood within the tree [7].

The wood of coniferous species Is relatively homogeneous in its characteristics, which makes it especially suitable for mass-production applications as building construction materials [9]. However, the variability of wood characteristics within individual trees is fundamentally related to changes resulting from the genetically controlled age of the cambium effect [38] and modifications imposed on the cambial activity by environmental conditions [9]. The patterns of cell size change with these structural variations were first described by Sanio [40]. Changes in the cambial initials with the aging tree are an important cause of radial variation in cell length [14,38]. An additional major influence on the radial variations (pith to bark) is the post-cambial development of cells [9].

The most pronounced change in the RTL, and similarly in both EWTL and LWTL, was determined between the 20th and the 25th annual growth rings in *P. menziesii* wood from these three sites. This could be defined as the transition threshold from juvenile to mature wood. In line with this, Acuna and Murphy [17] and Blohm et al. [41] reported on the mature wood forms around the age of 18–20 in *P. menziesii* trees. The results of this research pointed out that the juvenile period of growth reflects the pronounced increase in tracheid length. In the early period of tree growth, the cambial fusiform initials divide at a high frequency [9]. As a result, short initials are formed near the pith, but their length increases with tree age. Studies on other softwood species, such as *P. glauca* [25,39], *P. contorta* [42], and *P. brutia* [43], reported on the most rapid changes in the tracheid length over the first 10–25 annual growth rings.

Cambial age was the most crucial predictor of tracheid length. It was hard to conclude the deviations in the radial trend patterns in *P. menziesii* tracheid length from all three sites. This was due to differences in the age of the trees, with those from the Varaždin site being the oldest. Nevertheless, the results indicate that RTL in wood from all three sites similarly decreased in the 4^{0}h annual growth ring. Despite that, only *P. menziesii* wood from the Veliki Grđevac site showed typical leveling off in the tracheid length toward the bark after reaching the maximum value. However, only the first 45 annual growth rings were considered here. Usually, in coniferous species, the fusiform cambial initials may increase in length from 100% to 400% within the first 40–60 years [9].

Earlywood and latewood differ, above all, in cell size [14]. In relation to that, Zheng et al. [44] confirmed differences in tracheid diameter between earlywood and latewood. Longer latewood than earlywood tracheids were measured in this study. Similar results were confirmed in *P. menziesii* by Gartner et al. [45]. This is supported by a few sources on different softwood species [39,46,47]. A specific curvilinear radial pattern was determined in EWTL and LWTL of *P. menziesii* wood from the Varaždin site. RTL changed at a similar rate toward the bark. Studies confirm that wood anatomical characteristics change in a single annual growth ring between earlywood and latewood [48,49]. The pattern in EWTL and LWTL from the Veliki Grđevac site was more linear, and RTL pattern stabilized much earlier, while that from the Poreč site was somewhere in between. More fluctuations were determined in LWTL radial trends. This does not agree with Mvolo et al. [39], who predicted whole-ring values of wood properties based on earlywood and latewood properties. Significant effect of annual growth ring and zone interaction for EWTL and LWTL from all sites concludes on similar differences in EWTL and LWTL radial patterns. Most changes occurred after the 1^{0}h annual growth ring.

This study confirmed the significant tree effect on RTL for all three sites. The analysis of variance results highlights that RTL varied the most among trees at the Poreč site while being somewhat less significant at the Varaždin and Veliki Grđevac sites. This could be explained by the differences in the genetic constitution [50] and in the microenvironment of the trees [14], more precisely, with growing conditions such as competition within the stand or soil fertility [9]. It is also important to account for within-tree variation [14], which can explain the significant tree variation. There is a lack of information on the tree effect on tracheid length in the literature. Mvolo et al. [21] determined no significant tree effect on tracheid length in *P. glauca*.

As previously mentioned in describing the results, RTL from all three sites has been categorized as short [37], with that from the Veliki Grđevac site being the longest. The result highlights this site as possibly better for *P. menziesii* breeding than the other two. The literature reports on tracheid length being important for tensile strength and short tracheids being unfavorable for wood quality [51]. For example, a good paper tear strength demands a minimum average of 2 mm tracheid length [52]. Longer tracheids, with an average length of 3.6 mm, in *P. menziesii* wood from 65 year old trees were reported by Czajka and Fabisiak [53]. The results of this research are in the range of the *P. glauca* juvenile and mature wood tracheid length by Mvolo et al. [25] (earlywood (2.29–3.27 mm), latewood (2.45–3.39 mm), and ring (2.32–3.3 mm)). Adamopoulos et al. [43] report on shorter tracheids in the earlywood (1.65 and 1.67 mm) and latewood (2.10 and 2.13 mm), as well as weighted tracheids (1.74 and 1.78 mm) in younger trees of *P. brutia*, depending on the quality of the site.

Similarly, Duchesne and Zhang [54] reported on the whole-radius *P. glauca* tracheid length, again shorter, ranging from 2.06 to 2.31 mm. Compared to this study, shorter tracheids from the literature generally include younger trees. Considering that RTL results are based on mean values until the 40th annual growth ring, it is likely that more annual growth rings from older trees included would give different results. However, if comparing the mean values of older trees from the Varaždin site (until the 70th annual growth ring), the result would be only somewhat longer tracheids (2.7 mm). Thus, more annual growth rings included would not result in longer tracheids in wood from this site.

Early findings by Panshin and de Zeeuw [9] on tracheid lengths in *P. menziesii* have been related to its wide natural range in latitude and altitude. The significant effect of site on tracheid length has been confirmed [27] and rejected [43] in the literature.

Ring width displayed by *P. menziesii* varies considerably depending on the growth conditions, the silviculture, the genetic endowment of the trees, their age, the crown development, and the juvenile and mature wood [7]. The same authors concluded that the average ring width in European trees is between 2 and 7 mm. The results of ARW from this study correspond to that range. The mean values of EWW were wider compared to LWW in wood from all three sites. As detected in this study, the large radial increment in the first few annual growths rings results from the limited competition between crowns [55]. However, the radial patterns in EWW, LWW, and ARW are not entirely similar to those reported by Lenz et al. [48] in *P. glauca*.

EWW, LWW, and ARW poorly explained the variations in EWTL, LWTL, and RTL in *P. menziesii* wood from all three sites. The investigated correlations were weak, despite both positive and negative prefixes. The findings of no correlation between tracheid length and annual ring width are supported by a study for *P. abies* [56].

Concerning the relationship between the ring width and the cell length, the literature mostly concludes on the negative prefix. According to early findings of Ahmad [57] for *P. abies* and Sudo [58] for *P. densiflora*, wider annual growth rings resulted in shorter tracheids than in wood with narrow annual growth rings. Several recent studies support cognition [20,46,59,60]. Positive or negative relationships between tracheid length and annual ring width suggest that tracheid length depends on growth rate. However, due to weak or no association between the tracheid length and the annual ring width, the results of this study do not support that conclusion.

5. Conclusions

All tested sources of variation (annual growth rings, trees, site, and annual growth ring × zone interaction) affected tracheid length significantly. The longest earlywood, latewood, and ring tracheids were measured in *P. menziesii* wood from the Veliki Grđevac site.

Very weak or weak correlations were determined between the tracheid length (EWTL, LWTL, and RTL) and the growth parameters (EWW, LWW, and ARW) in *P. menziesii* wood from all three sites. The results suggest no relationship between the tracheid length (EWTL, LWTL and RTL) and the ring width (EWW, LWW, and ARW). This provides the opportunity for silvicultural management to improve the growth and tracheid characteristics of *P. menziesii*.

Continuing the research in determining wood's physical and mechanical properties would better characterize and quantify *P. menziesii* wood quality for final utilization and use. This would undoubtedly clarify and improve the understanding of the wood variability for both foresters and technologists. With such knowledge of *P. menziesii* wood, rational wood utilization would become possible to practice to the best advantage.

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