WOOD RESEARCH
62 (1): 2017
168-180

CORRELATION BETWEEN THE STEM HYDRAULIC CONDUCTIVITY RATES IN SCOTS PINE (*PINUS SYLVESTRIS* L.) AND THE LIGNIN CONTENT IN TRACHEID WALLS

Tomasz Jelonek, Witold Pazdrowski
Poznań University of Life Scientes, Department of Forest Utilisation
Poznań, Poland

Magdalena Arasimowicz-Jelonek
Adam Mickiewicz University of Poznan, Department of Plant Ecophysiology
Poznań, Poland

(Received June 2016)

ABSTRACT

This paper is an attempt to evaluate the lignin formation in tracheid walls within the stem circumferential area in mature Scots pine (*Pinus sylvestris* L.), and establish the correlation between lignin content, and diameter at breast height and hydraulic conductivity in mature pine. The independent variables included lignin content (L_c) in tracheid walls within the stem circumferential area, and pine diameter at breast height (DBH), and the dependent variable was the relative conducting surface of stems (S_a/N_{mass}, E_{as}/N_{mass}).

Research material came from the 89-91 year old pine stand in the north of Poland. Chemical analysis included mature wood area, i.e. last ten annual rings at 1.30 m (DBH).

The results show clear interdependence between the relative conductive surface (stem hydraulic conductivity), and tree diameter at breast height and lignin content in tracheid walls within the stem circumferential area. Biometric features of pines grown in fresh coniferous forest (FC) and in fresh mixed coniferous forest (FMC) conditions were functionally linked. The link between these values was clear, although it varied, and could be approximated using the linear function.

KEYWORDS: Hydraulic conductivity, lignin, cell wall, tracheid, diameter at breast height, Scots pine.

INTRODUCTION

Chemical structure of wood, including the system of each organic component, depend on many factors (Krzysik 1978, Rowell 2012, Shmulsky and Jones 2011). Lignin is one of the basic and key wood tissue components. It's a three-dimensional polymer of phenylpropane units, and an important cell wall component subject to the lignification process (Engel and Wegner 1989, Hejnowicz 2012, Surmiński 2006). This correlation reduces wall expanding properties, increases their resistance to compression and microorganisms, in particular fungi (Rowell 2012, Shmulsky and Jones 2011). It appears after cells or particular cell wall components finish growing. It is generally present in all cell wall layers, i.e. primary and secondary cell walls, as well as middle lamella (Enngel and Wegner 1989, Antonova et al. 2014, Tsuyama et al. 2014). In dead cells, lignin protects cell wall polysaccharides against partial hydrolysis during the protoplast death process (O`Brien 1970). From the environmental perspective, cell wall lignification is a very significant process. Without lignin reinforcement, cell walls of anatomical tree structures would be crushed by both turgor pressure in neighbouring living cells, and by vacuum in conducting components following transpiration. Lignification of plant tissue is directly connected to lignin synthesis and its deposition in plant cell walls at about 16% to 30% according Surmiński (2006), 20-30% according to Pereira et al. (2003), 25-30% dry mass according to Miidla (1989), and 18% to 36% according to Sarkanen and Ludwig (1971). High share of lignin, its composition and distribution, particularly in the xylem secondary cell walls, are crucial for developing technical characteristics of produced timber. Lignin in cell walls of anatomical tree structures increases cell wall resistance to deformation and stress when compressed, ensuring the stability of woody plants (Boudet et al. 1995, Santos Abren et al. 1999).

Wood tissue formation process is very complex and has not been fully explored yet (Plomion et at. 2001). According to Wodzicki (2001), wood structure and properties are both influenced by genetic conditions, as much as environmental and anthropogenic factors. The reason why not all the principles behind wood tissue formation have not been fully understood is because of the enormous number of interactions between wood structure on one hand, and genetic, environmental and anthropogenic factors, on the other. This correlation covers various wood structure levels, ranging from macrostructural features through complex cell wall structure to molecular level.

The relation between tree biometric properties, stem hydraulic conductivity and the share of basic cell wall components in parts of xylem anatomy are relatively are less known.

This paper evaluates the lignin formation in tracheid walls within the stem circumferential area in mature Scots pine (*Pinus sylvestris* L.), and establishes the correlation between the diameter at breast height (DBH), lignin content (*Lc*), and stem hydraulic conductivity using two indicators. The independent variables included diameter at breast height and lignin content in tracheid walls, while the dependent variable was the stem hydraulic conductivity (S_a/N_{mass}, E_{as}/N_{mass}).

MATERIAL AND METHODS

Research focused on mature pine stands grown in the following forest types: fresh coniferous forest and fresh mixed coniferous forest at Tuchola Forest District in northern Poland (53°36‘N 17° 51‘ E) under the administration of Regional Directorate of National Forests in Toruń, Poland. 1ha testing areas were located at four Scots pine (*Pinus sylvestris* L.) sites within the natural range of this forest forming tree species in Europe. Tab. 1 shows general characteristics of tested wood stands.

Tab. 1: Characteristics of wood stands under study.

Coordinates	Division section	Forest site type	Age	Index of stoking	Site class	Description of the soil
53.36538 N 17.56339 E	154c	FC	89	0.9	II	rusty spodic soils formed in loose sands
53.36445 N 17.56298 E	155c	FC	89	0.9	II	rusty spodic soils formed in loose sands
53.37079 N 17.56542 E	117b	FMC	89	0.9	I	rusty spodic soils formed in firm sands
53.36260 N 17.55075 E	125m	FMC	94	0.9	I	rusty spodic soils formed in firm sands

All pine trees were measured in diameter at breast height and height, and compared in proportion to 2 cm increments. Once tree thickness and height characteristics at each testing site were established, DBH and height values for model trees were calculated. Test trees were selected using Ulrich II dendrometric method for thickness class levels (Grochowski 1973) and classification method of Kraft (1884) for main stand, i.e. pre-dominant, dominant and codominant trees. Nine sample trees were indicated for each test site. In total, 36 trees were selected. After trees were cut, sampling discs were cut from each tree at breast height (1.30 m). Additionally, fresh needles were weighed for each sample tree.

Discs were used to determine sapwood area (S_a) and sapwood earlywood area (E_{as}). Using fresh needle mass (N_{mass}) from sample trees, sapwood area and sapwood earlywood tracheid area, the relative conductive surface, i.e. stem hydraulic conductivity at breast height, was established. The value was calculated by dividing the sapwood area and earlywood tracheid area at this particular stem section zone by the fresh needle mass S_a/N_{mass} ($mm^2 \cdot kg^{-1}$), E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$).

Material used for lignin measurement was sampled from the last ten annual growth rings, i.e. sapwood part of mature wood area.

Every disc was carefully sanded to see growth rings and borders between early and latewood. Two perpendicular lines were marked on sanded surface, crossing at the core. The lines were drawn through the maximum and minimum disc diameter. Measurements were taken along radius of four sample disc using the Preisser Digi-Met readout caliper and the Grube Comm software. Sapwood and heartwood width were measured along the radius, starting from the core. Each growth ring was measured for sapwood earlywood width. Sapwood earlywood area was calculated as the total area of all annual growth rings.

Lignin content (L_c $mg \cdot g^{-1}$ dry mass) was evaluated spectrophotometrically (three repetitions were made) using a modified Doster and Bostock method (1988). The first step was to treat wood produced in the last ten annual rings with methanol for 48 hours using 1 ml of methanol per 1 g of wood tissue, the second step was drying. Dry wood samples (20 g) were mixed with 5 ml of 2N HCL and 0.5 ml of thioglycol acid (Sigma-Aldrich). Samples were incubated for 4 hours at 95°C, and then centrifuged for 20 minutes at 3000 g. Sludge produced was washed with deionised water and incubated for 18 hours at ambient temperature using 5 ml of 0.5 N NaOH. After centrifugation at 15000 g was completed, NaOH extract was collected, and the sludge was washed with 4 ml of deionised water and centrifuged again. The resultant supernatant was then combined with extracted NaOH, acidified with 1 ml of concentrated HCL and left overnight at 5°C. After centrifugation 15000 g, the resulting supernatant was dissolved in 5 ml of 0.5 N NaOH, centrifuged 15000 g, and the absorbance of the solution was measured at 280 nm, using Shimadzu UV-1202 spectrophotometer. Lignin content is expressed as relative absorbance units.

The study defines basic statistical characteristics of the independent and dependent variables analysed, as well as their interdependence, reflected with regression equations and correlation coefficients. Resulting empirical material was analysed via Statistica 12.0 analytic tools, using the mathematical statistics method.

RESULTS

Tab. 2 presents patterns of location and dispersion measures of the selected independent variables of pine trees grown in mixed habitat conditions. Diameter at breast height (DBH) in poor soil habitat varied between 20.2 cm and 36.2 cm, while in rich soil habitat (FMC) between 23.8 cm and 41.0 cm. Standard deviation was 4.73 at FC and 5.276 at FMC, and the coefficient of variation of this biometric tree property was similar, with 17.8% and 17.1%, respectively. The average value for pine trees at both of the analysed habitats was 18.7% (Tab. 2).

Tab. 2: Statistical analysis of selected independent variables of researched pine trees grown in mixed habitat conditions.

Forest site type	Variable	Mean	Standard deviation	Minimum	Maximum	Coefficient of variation (%)
FC	DBH (cm)	26.70	4.73	20.2	36.2	17.8
	Lc ($mg \cdot g^{-1}$) dry weight	226.35	17.17	180.52	240.89	7.6
FMC	DBH (cm)	30.90	5.28	23.8	41.0	17.1
	Lc ($mg \cdot g^{-1}$) dry weight	233.33	13.33	205.14	249.36	5.9
Total	DBH (cm)	28.80	5.39	20.2	41.0	18.7
	Lc ($mg \cdot g^{-1}$) dry weight	229.84	15.79	180.5	249.4	6.9

FMC - Fresh Mixed Coniferous Forest
FC - Fresh Coniferous Forest
DBH - Diameter at Brest Height
L_c - Lignin Content

Tracheid wall lignin content (L_c) from the last ten annual growth rings in the sapwood part of mature wood area was between 180.52 $mg \cdot g^{-1}$ and 240.89 $mg \cdot g^{-1}$ in pine trees grown in fresh coniferous forest (FC), and 205.14 m $mg \cdot g^{-1}$ and 249.36 $mg \cdot g^{-1}$ in trees grown in fresh mixed coniferous forest (FMC), the difference, however, did not reach statistical significance. Standard deviation was 17.17 $mg \cdot g^{-1}$ and 13.33 $mg \cdot g^{-1}$, respectively, and the coefficient of variation was 7.6% in pine trees from lower fertility soils, and 5.9% in pine trees from FMC (Tab. 2). The average lignin content variation ratio in tracheid walls was 6.9% in trees from both analysed habitats (Tab. 2).

Tab. 3 presents statistical characteristics of variables studied here. Hydraulic conductivity is expressed using the ratio of sapwood surface to fresh needle mass (S_a/N_{mass}), and by referring tracheid surface in sapwood earlywood area to fresh needle mass (E_{as}/N_{mass}) in all sample trees. The value of S_a/N_{mass} ratio remained between 939.47 $mm^2 \cdot kg^{-1}$ and 2109.22 $mm^2 \cdot kg^{-1}$

in the case of poor soils, and between 736.97 $mm^2 \cdot kg^{-1}$ and 1468.71 $mm^2 \cdot kg^{-1}$ in the case of rich soils. In the case of pine trees grown in the poor soils, the standard error S_a/N_{mass} was 73.90 $mm^2 \cdot kg^{-1}$, standard deviation was 304.70 $mm^2 \cdot kg^{-1}$, and the variation ratio was 19.06%, while in the case of rich soils (FMC), the corresponding values were 64.76 $mm^2 \cdot kg^{-1}$, 266.99 $mm^2 \cdot kg^{-1}$, 23.88% (Tab. 3).

Tab. 3: Statistical analysis of selected dependent variables of researched pine trees grown in mixed habitat conditions.

Forest site type	Variable	N	Mean	Median	Minimum	Maximum	Standard deviation	Coefficient of variation (%)	Standard error
FC	S_a/N_{mass} ($mm^2 \cdot kg^{-1}$)	17	1589.98	1586.37	939.47	2109.22	304.70	19.06	73.90
	E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$)	17	936.42	942.98	545.46	1327.79	197.55	21.10	47.91
FMC	S_a/N_{mass} ($mm^2 \cdot kg^{-1}$)	17	1118.17	1216.16	736.97	1468.71	266.99	23.88	64.76
	E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$)	17	702.15	795.58	462.17	929.96	176.29	25.11	42.76

S_a/N_{mass} ($mm^2 \cdot kg^{-1}$) – ratio between the sapwood area to fresh needle mass
E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$) – ratio between the sapwood earlywood area to fresh needle mass

This ratio was 1598.98 $mm^2 \cdot kg^{-1}$ in FC pine trees, and 1118.17 $mm^2 \cdot kg^{-1}$ for pine trees in the rich soil (Tab. 3).

The second of the indicators analysed, i.e. E_{as}/N_{mass} was expressed by the ratio of the sapwood earlywood area in the stem cross section cut at breast height to fresh needle mass, and varied between 545.46 $mm^2 \cdot kg^{-1}$ and 1327.79 $mm^2 \cdot kg^{-1}$ in pine trees from FC habitat, and between 462.17 $mm^2 \cdot kg^{-1}$ and 929.96 $mm^2 \cdot kg^{-1}$ in trees from FMC. Standard error for this ratio was 47.91 $mm^2 \cdot kg^{-1}$, standard deviation was 197.55 $mm^2 \cdot kg^{-1}$ and the content variation ratio was 21.10% for pine trees in the poor soil, while the corresponding values for trees in the rich soil were 42.76 $mm^2 \cdot kg^{-1}$, 176.29 $mm^2 \cdot kg^{-1}$ and 25.11%.

The average value of this dependent variable was 936.42 $mm^2 \cdot kg^{-1}$ in trees from FC, and 702.15 $mm^2 \cdot kg^{-1}$ in pine trees from FMC (Tab. 3).

Considering the hydraulic conductivity of pine stems grown on richer soils (FMC), the median value for both of the ratios discussed is significantly above average. Asymmetric left distribution of properties indicates, that the bottom quarter of stem hydraulic conductivity indicators show very low values, and significantly lower the average value. This is not the case with the indicators for trees grown in the FC conditions, where both the median value and the average value are similar (Tab. 3).

Conducted analysis of variance (Tab. 4) indicated statistically significant differences between DBH cross sections of pine trees, and S_a/N_{mass} and E_{as}/N_{mass} depending on habitat conditions (Tab. 4). DBH values of pine trees in fresh coniferous forest conditions were significantly smaller compared to trees from a fresh mixed coniferous forest, while stem hydraulic conductivity rates displayed inverse relationship, where the relative conductive surface in the first group was significantly bigger compared to pine trees grown in the rich soil habitat.

Tab. 4: Analysis of variance on the properties and indicators of pine trees grown in rich soil (FMC) and poor soil (FC) conditions.

Variable	SS	df	MS	SS	df	MS	F	p
S_a/N_{mass} ($mm^2 \cdot kg^{-1}$)	3375353	1	3375353	5851751	34	172110.3	19.61157	0.000093
E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$)	978520	1	978520	2900627	34	85312.5	11.46982	0.001800
DBH (cm)	162	1	162	854	34	25.1	6.43762	0.015928
Lc [$mg \cdot g^{-1}$] dry weight	439	1	439	8285	34	243.7	1.80083	0.188506

differences statistically significant at the significance level p<0.05 are marked

The correlation between the analysed hydraulic conductivity indicators (S_a/N_{mass} and E_{as}/N_{mass}) at DBH and the lignin content (L_c) within the stem circumferential area in pine trees grown in FC and FMC conditions was expressed using the calculated correlation ratios, equations, and regression lines (Tab. 5, Figs. 1- 4).

Tab. 5: Correlation ratios between the relative conductive surface (S_a/N_{mass} $mm^2 \cdot kg^{-1}$, E_{as}/N_{mass} $mm^2 \cdot kg^{-1}$, and DBH and lignin content in tracheid walls (Lc (mg/g) dry weight) in pine trees grown in various habitat conditions.

	Variable	S_a/N_{mass} ($mm^2 \cdot kg^{-1}$)	E_{as}/N_{mass} ($mm^2 \cdot kg^{-1}$)
FC	DBH (cm)	-0.500671	-0.508134
	Lc ($mg \cdot g^{-1}$) dry weight	0.495377	0.491830
FMC	DBH (cm)	0.416346	0.379107
	Lc ($mm^2 \cdot kg^{-1}$) dry weight	-0.311488	-0.327709

correlation significance at the level p < .05

Conducted statistical analysis indicated clear link between diameter at breast height (DBH) and lignin content (L_c) in tracheid walls within the stem circumferential area, and the conductivity ratio of pine trees grown in both types of forest habitats (FC and FMC). Statistically significant correlation between all of the analysed variables was observed in the FC conditions (Tab. 5).

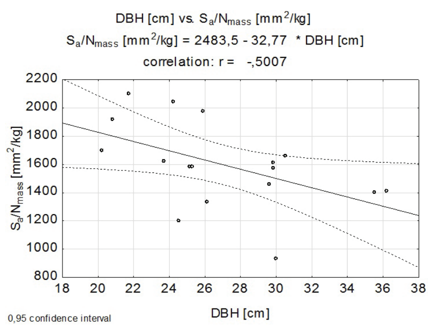

Fig. 1: Patterns on S_a/N_{mass} in relation toDBH in pine trees grown in the FC conditions.

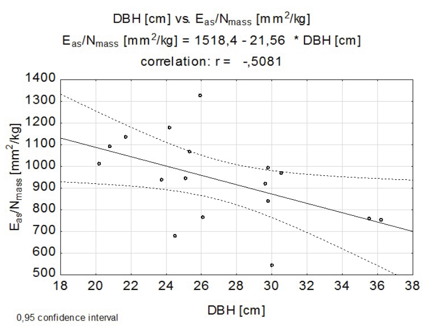

Fig. 2: Pattern of E_{as}/N_{mass} in relation toDBH in pine trees grown in the FC conditions.

In the case of pine trees grown on poor soils, the correlation of sapwood area relative to fresh needle mass (S_a/N_{mass}) against diameter at breast height (DBH) was negative. Correlation ratio at the significance level of $p < 0.5$ was r = - 0.5007 (Fig. 1). Earlywood area of sapwood compared to fresh needle mass (E_{as}/N_{mass}), at the same significance level of $p < 0.5$ was r = - 0.5007 correlated negatively, with the correlation ratio value of r = - 0.5081 (Fig. 2). Hydraulic conductivity measured by these two indicators was also determined by the statistical significance of lignin content in tracheid walls (L_c) within the stem circumferential area. In the first case, the correlation ratio value was r = + 0.495, and the second case it was r = + 0.4918 (Fig. 3 and 4).

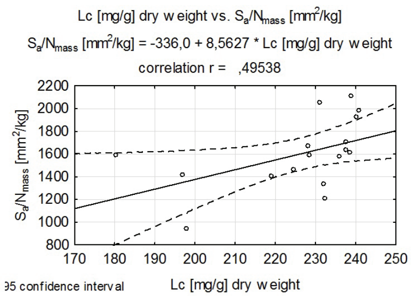

Fig. 3: Pattern of S_a/N_{mass} in relation to Lc in pine trees grown in the FC conditions.

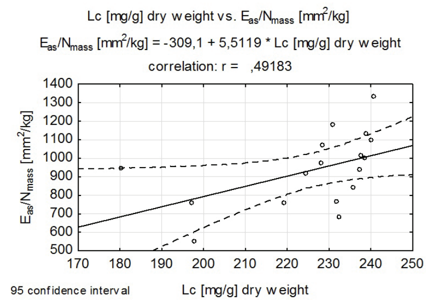

Fig. 4: Pattern of E_{as}/N_{mass} in relation to Lc in pine trees grown in the FC conditions.

In rich soil habitat (FMC), the analysed variables correlated positively, as it was the case with the trees from FC, whereby the calculated correlation indicators had lower values and were not statistically significant, considering that the assumed statistical level was $p < 0.5$.

DISCUSSION

Wood is optimised to a different degree depending on performed functions, growing conditions, and survival strategies. Consequently, it features a sophisticated chemical composition and anatomical features typical to specific tree species, which directly define physical and mechanical properties of wood (Barnett and Jronimidis 2003). Differences in the structure and properties of wood may occur even between the single species, e.g. depending on geographical location (Fabijanowski 1961), habitat conditions (Pazdrowski and Spława-Neyman 1997), age, or biosocial position in a tree stand (Pazdrowski and Spława-Neyman 1993). This has impact on forest management and the timber market(Adamowicz 2010; Adamowicz et al. 2016).

This study is an attempt to analyse the xylem hydraulic conductivity in stems against lignin content in the circumferential area and diameter at breast height in Scots pine (*Pinus sylvestris* L.) grown on two types of soil. Hydraulic conductivity was expressed with two indicators combining physiologically active surface and the size of assimilation and transpiration apparatus. The first indicator was the total sapwood surface in relation to fresh needle mass (S_a/N_{mass}), and the second one was the earlywood area of sapwood in relation to fresh needle mass (E_{as}/N_{mass}). The analysis covered mature stand grown under optimum habitat conditions, i.e. fresh coniferous forest and fresh mixed coniferous forest. In total, research was carried out on 36 pine trees (*Pinus sylvestris* L.) between 89 and 91.

Lignin content, the significant structural component of tracheid walls ranged between 180.52 and 249.36 ($mg \cdot g^{-1}$), which is similar to the results by other authors (White 1987, Santos Abreu et al. 1999).

Attention should be drawn to the observed correlation between the hydraulic conductivity of stems, and the lignin content in tracheid walls of sapwood and the diameter at breast width. The correlation was positive in the first case, a negative in the second case. As the hydraulic area increased in size, so did the lignin percentage in tracheid walls within the circumferential zone. This regularity was confirmed for both habitat types, i.e. poor and rich soil. In the poor soil location (FC), the correlation was statistically significant, whereas it was non-significant in the rich soil location (FMC). This regularity might be related to the intensity of water conductivity in xylem. Mass water flow rate through wood conductive components from the roots up to the assimilation apparatus (long-distance transport), as well as short-distance transport and transpiration move from the locus of greater potential to the locus of lesser potential. Long-distance water transport against gravity within xylem is probably the result of vacuum caused by transpiration and root pressure supported by the forces of cohesion and adhesion and the capillary action (Kopcewicz et al. 2012).

The analysis of lignin content in tracheid walls playing active part in water transport was just as important. This is because lignin is one of the main tracheid wall components that have critical structural significance. Lignification of plant tissue is connected to lignin synthesis and its deposition in plant cells at about 16% to 30% according Surmiński (2006), 20-30% according to Pereira et al. (2003), 25-30% of dry mass according to Miidla (1989). Such significant lignin percentage in wood increases cell wall resistance to deformation and ensures its mechanical stability (Boudet et al. 1995, Santos Abreu et al. 1999). Lignin therefore enables water movement within xylem even at considerable heights, and protects wall polysaccharides against partial hydrolysis during the protoplast death process (O'Brien 1970, Hejnowicz 2012, Hatfield and Vermerris 2001).

The studies conducted showed significant differences between average values of the relative conductive area, expressed by means of two indicators, i.e. S_a/N_{mass} and E_{as}/N_{mass}. The trees grown in poor soil habitat (FC) demonstrated higher values of the relative conductive area S_a/N_{mass} = 1598.98 $mm^2 \cdot kg^{-1}$fresh needle mass and E_{as}/N_{mass} = 936.43 $mm^2 \cdot kg^{-1}$, while the same values for trees grown in the rich soil (FMC) were 1118.17 $mm^2 \cdot kg^{-1}$ and 702.15 $mm^2 \cdot kg^{-1}$, respectively.

This might be explained by the pipe-model theory of Shinozaki et al., (1964a, 1964b), where physiologically healthy trees optimise xylem conductive area, which is directly correlated with the size and efficiency of the assimilation apparatus of the tree, as well as with its height (Jelonek et al. 2008).

Referring directly to the results, the reasons for such significant differences between the indicators analysed might also be explained by the growth dynamics of annual rings within the stem sapwood zone of the pine trees that were tested. Growth rings in pine trees from the poor soil habitat were more narrow (average width of 2.43 mm), and in pine trees grown in richer soil habitat they were considerably wider, with average width at 2.69 mm.

Annual ring growth in conifer species takes place by increasing earlywood width in tree stem (Barnett and Jerominidis 2003, Shmulski and Jones 2011, Rowell 2012). As a result, trees grown in the poor soil habitat conditions (deeper water deposits, highly permeable soils) had to develop considerably more sap and tracheid surface in the conducting sapwood area in the cross-sectional area of wood in order to ensure balance between the processes of conductance and transpiration than trees grown in the richer soil habitat. This regularity is most probably caused by different soil properties typical for fresh forests and fresh mixed forests, and the resulting access to groundwater by the root systems. Groundwater is much deeper in the poor soil habitats, which forces trees to the natural biomodification of wood involved in the vertical water transport in stem, while maintaining biomechanical stability at the same time.

CONCLUSIONS

1. Properties and indicators related to the pine tree stem hydraulic conductivity were different in both types of studied forests, whereby independent variables were more uniform in comparison to dependent variables.
   DBH variation ratio was 17.8% in trees grown in the poor soil habitat (FC), and 17.1% in trees grown in the rich soil habitat (FMC). The variation ratio of lignin content in tracheid walls was 7.6% and 5.9%, respectively. The variation ratios S_a/N_{mass} and E_{as}/N_{mass}, i.e. dependent variables, were 19.0% and 21.1% in trees grown in the poor soil, and 23.9% and 25.1% in trees grown in rich soil.
2. Trees grown in both types of forest habitat types demonstrated clear correlation between the relative conductive surface expressed by S_a/N_{mass} and E_{as}/N_{mass} ratios, and DBH and lignin content (L_c) in tracheid walls within the stem circumferential area. The correlation was negative in the first case, a positive in the second case. Conductive surface decreased with larger DBH, and increased with higher lignin content in tracheid walls (L_c). Correlation coefficients of the above were statistically significant only in the case of trees grown in the poor soil habitat (FC).
3. Biometric properties of trees analysed in this paper were functionally connected. The correlation between the characteristics was clear, but varied, and it was possible to describe it by a linear function.

REFERENCES

1. Adamowicz, K., 2010: Cenowa elastyczność popytu na drewno na pierwotnym lokalnym rynku drzewnym w Polsce (Lumber demand price flexibility on the primary Polish lumber market), Sylwan 154 (2): 130–138.
2. Adamowicz, K., Szramka, H., Starosta–Grala M., Szczypa P. 2016: Eksport i import surowca drzewnego w wybranych krajach Unii Europejskiej (Timber import and export in the selected EU countries), Sylwan 160 (3): 179–186.
3. Antonova, G.F., Varaksina T.N., Zheleznichenko T.V., Stasova, V. V. 2014: Lignin deposition during earlywood and latewood formation in Scots pine stems, Wood Science and Technology 48(5): 919-936.
4. Barnett, J.R., Jeronimidis, G., 2003: Wood quality and its biological basis. Oxford: Blackwell, 226 pp.
5. Boudet, A. M., Lapierre, C., Grima-Pettenati, J., 1995: Biochemistry and molecular biology of lignification, New Phytology 129: 203-236.
6. Doster, M., A., Bostock, P. M., 1988: Quantification of lignin formation in almond bark in response to wounding and infection by *Phytophtotra* species, Phytopathology 78: 473- 477.
7. Fabijanowski, J., 1961: Kilka uwag o badaniach dotyczących rasy sosny zwyczajnej w Polsce oraz o sośnie mazurskie) (Some observations on Scots pine species research in Poland and Masurian pine), Sylwan 105 (4): 21-27.

8. Fengel, D., Wegener, G., 1989: Wood: chemistry, ultrastructure, reactions. De Gruyter, Berlin, 613pp.
9. Grochowski, J., 1973: Dendrometria (Dendrometry). PWRiL, Warszawa.
10. Hatfield, R., Vermerris, W., 2001: Lignin formation in plant. The dilemma of linkage specificity, Plant Physiology 126: 1351-1357.
11. Hejnowicz, Z., 2002: Anatomia i histogeneza roślin naczyniowych (Vascular plant anatomy and histogenesis). Wyd. Nauk. PWN, Warszawa.
12. Jelonek, T, Pazdrowski, W., Arasimowicz, M., Tomczak, A., Walkowiak, R., Szaban, J., 2008: The applicability of the pipe model theory in trees of Scots pine (*Pinus sylvestris* l.) of Poland, Journal of Forest Science 54(11): 519-531.
13. Kopcewicz, J., Lewak, S., 2012: Fizjologia roślin (Plant physiology). Warszawa: Wydawnictwo Naukowe PWN.
14. Kraft, G., 1884: Beiträge zur Lehre von den Durchforstungen, Schlagstellungen und Lichtungshieben. Klindworth's, Hannover.
15. Krzysik, F,. 1978: Nauka o drewnie. (Wood science), PWN, Warszawa.
16. Miidla, H., 1989: Biochemistry of lignin formation. In: The formation of lignin in wheat plants and its connection with mineral nutrition. E. Padu (Ed.). Tartu State University, Tartu: 11- 23.
17. O'Brien, T. P., 1970: Further observations on hydrolysis of the cell wall in the xylem, Protoplasma 69(1): 1-14.
18. Pazdrowski, W., Spława–Neyman, S., 1993: Badania wybranych właściwości drewna sosny zwyczajnej (*Pinus sylvestris* L.) na tle klas biologicznych w drzewostanie (The study of selected wood properties in Scots pine (*Pinus sylvestris* L.) against biological classes in the stand), Folia Forestalia Polonica, Ser. B, 24: 133–145.
19. Pazdrowski, W., Spława – Neyman, S., 1997: Macrostructure of Scots pine wood from unripe forest stands grown in conditions of fresh forest, Folia Forestalia Polonica, Ser. B. 28: 41–46.
20. Pereira, H., Graça, J., Rodrigues, J., 2003: Wood chemistry in relation to quality. In: Wood quality and its biological basis. J.R. Barnett, G. Jeronimidis (Ed.). Blackwell, Oxford, Pp 53-86.
21. Plomion, C., Leprovost, G., Stokes, A., 2001: Wood formation in trees, Plant Physiology 127: 1513–1523.
22. Rowell, R. M., 2012: Handbook of wood chemistry and wood composites, second edition, CRC Press Taylor and Francis Group. London, New York, 703 pp.
23. Santos, Abreu, H., Nascimento, A. M., Maria, M. A., 1999: Lignin structure and wood properties, Wood and Fiber Science 31(4): 426-433.
24. Sarkanen, K. V., Ludwig, C. H., 1971: Lignins: Occurrence, formation, structure and reactions, Eds., John Wiley & Sons, Inc., New York 1971, 916 pp.
25. Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964a: A quantitative analysis of plant from: the pipe model theory. I. Basic analyses, Japanese Journal of Ecology 14: 97-105.
26. Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964b: A quantitative analysis of plant form: the pipe model theory. II. Further evidence of the theory and its application in forest ecology, Japanese Journal of Ecology 14: 133-139.
27. Shmulsky, R., Jones, D. P., 2011: Forest products and wood science an introduction, sixth edition, Wiley-Blackwell, Pp 426-433.
28. Surmiński, J. 2006: Zarys chemii drewna (Basics of wood chemistry). Wyd. AR, Poznań.

29. Tsuyama, T., Takabe, K., 2014: Distribution of lignin and lignin precursors in differentiating xylem of Japanese cypress and poplar, Journal of Wood Science 60(5): 353–361.
30. Wodzicki, T. J., 2001: Natural factors affecting wood structure, Wood Science and Technology 35(1): 5–26.
31. White, R. H., 1987: Effect of lignin content and extractives on the higher heating value of wood, Wood and Fiber Science 19(4): 446-452.

Tomasz Jelonek*, Witold Pazdrowski
Poznań University of Life Scientes
Department of Forest Utilisation
Wojska Polskiego 71A
60-625 Poznań
Poland
Corresponding author: tomasz.jelonek@au.poznan.pl

Magdalena Arasimowicz-Jelonek
Adam Mickiewicz University of Poznan
Department of Plant Ecophysiology
Umultowska 89
61-614 Poznań
Poland