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THE NOVEL RELATIONSHIP BETWEEN THE MORPHOLOGICAL CHARACTERISTICS OF TREES AND ULTRASTRUCTURE OF WOOD TISSUE IN SCOTS PINE (*PINUS SYLVESTRIS* L.)

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ABSTRACT

The relationship between such tree characteristics as tree height and diameter at breast height and the resulting wood properties has not been investigated in depth to date. The phenotypic variability of Scots pine is associated with high variability of xylem even within one population of this species. Thus it seems advisable to focus in research on the verification of both existing and novel hypotheses concerning a relationship or an interaction between multiple anatomical and morphological traits within individual trees and entire stands. Results of such studies may not only provide insight into the functioning of trees, but also optimize timber management and prevention in predicting damage to trees from the wind.

Based on an analysis of 36 trees this study investigated the relationship between morphological characteristics of Scots pine (*Pinus sylvestris* L.) and micro- and ultrastructure of wood tissue, as expressed by the thickness of tracheid walls, lignin content and crystallinity of cellulose. Analyses indicated numerous and relatively strong dependencies between investigated traits. A particularly strong relationship was found between morphological characteristics of trees and crystallinity of cellulose. It was significantly correlated with height, diameter at breast height and the slenderness ratio.

KEYWORDS: Morphological traits of trees, wood microstructure, lignin, crystallinity of cellulose, cell wall.

INTRODUCTION

The multifunctional character and the highly complex nature of forests suggest that research concerning forests should be conducted bearing in mind something more than just the production, economic and social aspects. This unique nature of forests necessitates investigations concerning the structure of forest communities in order to gain comprehensive insight and describe the greatest possible number of factors modifying it. This approach should facilitate not only an improved model of forest economy, but also provide answers to many questions concerning the functioning of both individual trees and whole stands.

There is a growing interest in predicting wood quality from tree morphology traits, which can be measured using remote sensing techniques such as LiDAR, to enhance forest inventory for operational planning (Lenz et al. 2012). Moreover, in recent years demand for best quality timber has led to the development of novel strategies ensuring the most efficient utilisation of tree resources. This may be provided by greater insight into mutual relationships between morphological characteristics of trees and xylem structure.

Studies are constantly conducted in order to determine wood characteristics and properties based on stand structure, morphological traits of trees as well as the characteristics determined in forest surveys (Houllier et al. 1995, Kellomäki et al. 1999, Mäkinen et al. 2007, Lenz et al. 2012).

To date xylem characteristics have not been included in stand inventories, while its actual quality, which was routinely estimated in standing timber, has been unknown. However, it is generally accepted that quality of timber resources may be estimated based on phenotypic traits of individual trees, i.e. tree height, diameter at breast height and crown structure (Kijidani et al. 2010, Wąsik 2010, Kuprevicius et al. 2013).

As it was reported by Sellier and Fourcaud (2009), morphological traits of trees to a much greater extent modify their resistance to dynamic loads than properties and structure of xylem. A crucial role is played here by the size of the crown as well as stem height and diameter.

It is the tree crown that most likely plays a key role in this respect as it determines xylem properties, since it supplies products of photosynthesis and controls wood production modified by the influence of hormones (Savidge 1996, Kellomäki et al. 1999, Larson et al. 2001). Apart from crown parameters the most frequently determined morphological traits of trees include tree height and diameter at breast height. Indexes applied in predictions concerning stability of trees and stands are often formulated based on biometric characteristics of trees. One of the most commonly used such indexes is the slenderness ratio, which is a ratio of height of a tree to its diameter at breast height. In many studies on resistance of trees and stands to the action of external dynamic loads, tree stability is defined using the slenderness ratio (Erteld and Hengst 1966, Peltola 2006, Jelonek et al. 2013). It is considered to be an appropriate measure in the determination of stability of individual trees and their resistance to wind, since it includes optimisation of biomechanical systems in plants (Peltola 2006).

Wood is an anisotropic material. Considerable differences in cell structure are found both within a single tree and between trees (Reme and Helle 2002). Within a single tree xylem characteristics change both during growth (early wood vs. late wood) and with tree age (juvenile wood vs. mature wood). Functioning of trees in terms of their physiology and wood formation was relatively thoroughly described by Zimmermann and Brown (1971) and Chaffey (2002), while

Zobel and van Buijtenen (1989) extensively characterised variability of wood properties at the cellular level. However, xylem itself to a varying degree is optimised in terms of served functions, conditions of tree growth and strategies facilitating its survival (Mencuccini et al. 1997).

Due to the complexity of processes connected with the formation and functioning of wood tissue we still lack insight into all the relationships and interactions occurring between the morphological, anatomical and biomechanical systems of trees. For this reason many characteristics and properties of wood may not be estimated directly based solely on tree architecture. Such a situation to a certain degree limits an efficient development of forest resource inventories, which could potentially contain data concerning wood characteristics (Pitt and Pineau 2009).

It was assumed in this study that dependencies exist between morphological traits of trees and xylem micro- and ultrastructural characteristics. The aim of the study was to determine the power and direction of these dependencies.

MATERIAL AND METHODS

Experimental material included Scots pines (*Pinus sylvestris* L.) grown in mature commercial stands. A total of twelve experimental sites were established in six forest divisions (Tab. 1). In each stand a 1-hectare experimental site was established, in which morphological traits of trees were measured, i.e. tree height, diameter at breast height (DBH), crown length and width. Tree height and crown length were measured using a NIKON Forestry Pro hypsometer, diameters at breast height were measured with electronic callipers by Haglöf, while crown diameter was measured with a Bosch DLE 40 laser distance meter. Tree crown diameters were measured using projections and recording four radiuses.

Tab. 1: Location and a brief description of mean sample plots.

Forest division	Location	Site	Stocking	Quality class	Age (years)
Warcino	N 16 99 12 E 55 17 15	Bśw	0.9	II	94
	N 17 00 10 E 54 19 12		0.9	II	99
Trzebielino	N57 08 13 E 17 09 43	BMśw	1.0	II	95
	N 54 14 48 E 17 01 46		1.0	II	105
Olesno	N 50 56 53 E 18 24 30	LMśw	1.0	I	95
	N 50 56 54 E 18 24 16		1.0	I	95
Drawsko	N 15 53 30 E 53 27 07	BMśw	0.9	II	90
	N 15 53 27 E 53 27 04		0.9	II	92
Kaczory	N 53 10 12 E 16 49 11	Bśw	0.9	II	90
	N 53 9 21 E 16 47 13		0.9	II	102
Szczecinek	N 53 77 10 E 16 91 09	Bśw	1.0	II	95
	N 53 46 05 E 16 53 06		1.0	II	98

Based on biometric traits each of the stands was divided into three classes and in each class one mean sample tree was identified, representing a given group of trees. Mean sample trees were felled and 5 cm discs were collected from a height of 1.3 m and used in analyses of xylem characteristics.

Moreover, for each mean sample tree indicators of its stability were determined, such as:

- The slenderness ratio of trees ($H/D_{1.3}$) – a ratio of tree height to its diameter at breast height,
- The centre of gravity of trees (L_K/H) – the ratio of length of live crown to tree height,
- Crown inclination (D_K/H) – the ratio of mean crown diameter to tree height.

Material for analyses of lignin content, cellulose crystallinity and cell wall thickness was collected from the last five increments in diameter, i.e. samples collected from the mature wood zone from sapwood and oriented in the N-S diameter. Lignin content was determined by spectrophotometry (in three replications) according to Doster and Bostock (1988) with some modifications. First wood from the last five annual growth rings was treated for 48 h with methanol (1 ml methanol per 1 g tissue) and next the samples were dried. From each variant 20 mg dried tissue were collected and mixed with 5 ml 2 N HCl and 0.5 ml thioglycolic acid (Sigma-Aldrich). Samples were incubated at 95°C for 4 h and next they were centrifuged at 3000 g for 20 minutes.

The precipitate was washed twice with deionised water and incubated with 5 ml 0.5 M NaOH for 18 h at room temperature. After centrifugation at 15 000 g the NaOH extract was collected and the precipitate was washed with 4 ml deionised water and centrifuged again. The supernatant was mixed with the NaOH extract, acidified with 1 ml concentrated HCl and left overnight at 5°C. After centrifugation (15 000 g) the precipitate was dissolved in 5 ml 0.5 N NaOH, centrifuged (15 000 g) and absorbance of the solution was measured at a wavelength of 280 nm using a UV-1202 Shimadzu spectrophotometer. Lignin content was expressed in relative absorbance units.

Cell wall thickness was measured at mid-length of radial walls based on images from an AxioCam MRc5 camera by Zeiss using AxioVision software by Zeiss, following the procedure described by Seo et al. (2012). On each sample thickness of 15 successive cell walls was measured in early- and latewood. Measurements were taken on wood with a maximum moisture content of 4 %, i.e. on absolutely dry specimens. Since each of the measurements comprised thicknesses of walls in two neighbouring tracheids, each of the results was divided by two.

Cellulose crystallinity of samples collected using the procedure described above was determined by X-ray diffraction (Andersson et al. 2003). A Bruker Expert powder diffractometer, equipped with a sealed X-ray tube and a Johanson monochromator tuned into the $CuK_{\alpha 1}$ characteristic-radiation line, was used. The powder patterns were measured in the 2ϑ angle range of 10-40°, with the step of 0.2° and the scanning speed rate of $1°min^{-1}$. The ϑ-2ϑ geometry was applied, with the samples positioned and rotated perpendicular to the scattering vector. An ad-hoc computer program was written to integrate reflections and broad-signal intensity and evaluate the crystallinity ratio.

The STATISTICA 12 software package was used to correlate characteristic data of the samples and analytical results.

RESULTS

This study comprises analyses of all morphological traits of trees and xylem characteristics in thirty six pines growing in twelve locations in different regions of Poland. Mean height of analysed trees was 24.4 m, ranging from 20.4 to 29.5 m, while diameter at breast height was on average 32.8 cm and ranged from 20.5 to 49.0 cm (Tab. 2). Variability in morphological traits of analysed pines was slight. The coefficient of variation for all the tested biometric variables ranged from 10 to 25 %. The smallest variation was observed for tree height, while it was greatest for crown width.

Tab. 2: Descriptive statistics of studied traits.

Characteristics of trees and wood	**N**	**Mean** $\bar{X}$	**Minimum min**	**Maximum max**	**Std dev. σ**	**Coefficient of variation** *V* **(%)**	**Coefficient of skewness** *A*
Tree height (m)	36	24.389	20.400	29.500	2.401	9.85	0.5698
DBH (cm)	36	32.842	20.500	49.000	6.793	20.68	0.4122
Crown width (m)	36	5.283	2.200	8.600	1.342	25.40	0.3055
Crown lenght (m)	36	7.560	4.800	10.116	1.429	18.90	0.0367
$H/D_{1.3}$	36	76.557	51.020	102.326	13.021	17.01	0.1632
L_K/H	36	31.077	20.727	45.455	5.583	17.97	0.2152
D_K/H	36	21.632	10.784	33.036	4.994	23.09	0.2289
Cell wall thickness LW/W (μm)	36	6.852	3.155	11.500	1.574	22.97	0.1772
Cell wall thickness EW/W (μm)	36	2.114	1.095	3.485	0.356	16.87	0.3007
Crystallinity of cellulose (%)	36	69.564	62.355	76.835	3.080	4.43	-0.1336
Lignin content/relative units/10 mg of dry weight	36	0.815	0.745	0.918	0.052	6.42	0.4912

Cluster analysis showed that the characteristics analysed in this study formed three clusters. The first group was composed of two biometric traits, i.e. tree crown length and width, as well as cell wall thickness and lignin content in tracheid walls. The second cluster was formed by biometric traits and tree stability indexes. In turn, the third cluster comprised cellulose crystallinity and slenderness ratio of trees ($H/D_{1.3}$) (Fig. 1).

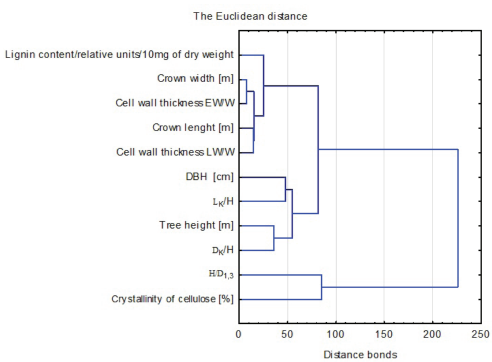

Fig. 1: Cluster analysis of investigated tree traits and xylem characteristics in Scots pine (Pinus sylvestris L.).

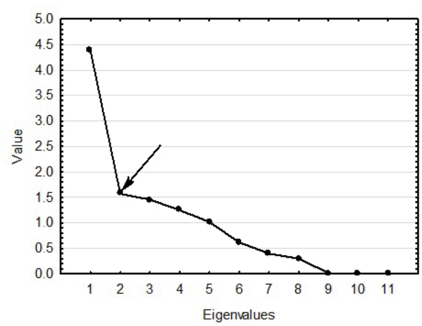

Fig. 2: A scree plot for eigenvalues of factors for morphological traits of trees and xylem characteristics.

Since the analysed traits did not have a normal distribution, the dependencies were analysed applying Spearman's rank correlations (Tab. 3). Morphological characteristics of the trees were treated as the response variable while the ultrastructural characteristics of wood as an explanatory variable.

Tab. 3: Spearman's rank correlations for analysed traits.

	Lignin content/ relative units/10 mg of dry weight	**Cell wall thickness EW/W (μm)**	**Cell wall thickness LW/W (μm)**	**Crystallinity of cellulose (%)**
Tree height (m)	0.012051	0.089310	0.097178	-0.350121
DBH (cm)	0.114026	0.119497	0.357162	-0.367166
Crown width (m)	0.357902	0.185894	0.209869	-0.097797
Crown lenght (m)	0.168276	0.123849	0.207931	-0.205254
$H/D_{1.3}$	-0.083660	-0.069241	0.406976	0.430804
L_K/H	0.161786	0.037838	0.199369	-0.127438
D_K/H	0.366629	0.128717	0.217674	-0.013904

Correlation coefficients are statistically significant at the level of $p < 0.05$.

When investigating first the dependencies found between morphological traits of trees and their wood structure, a relationship was observed between cell wall thickness in late wood and diameter at breast height of trees (**0.357**) andslenderness ratio (**0.407**). Moreover, a strong relationship was also found between cellulose crystallinity and tree height (**-0.350**) and diameter at breast height (**-0.367**), while a much stronger relationship was recorded between cellulose crystallinity and slenderness ratio of trees $H/D_{1.3}$ (**0.431**).

Moreover, a statistically significant relationship was detected between lignin content in xylem and crown width (**0.358**) and crown inclination index D_K/H (**0.367**).

In turn, strong dependencies were found between biometric traits of trees. Diameter at breast height and tree height were strongly correlated with each other and with morphological characteristics of tree crown investigated in this study. In contrast, in the group describing xylem characteristics only cell wall thickness was positively correlated with lignin content.

Factor analysis showed that the first factor explained as much as 40 % common variation, while the second factor as little as 13 % (Fig. 2).

The hierarchical oblique factor analysis indicated a secondary factor probably affecting morphological characteristics of trees, particularly crown width and diameter at breast height, which is not directly connected with the other traits.

At the same time the above analysis showed that the morphological traits of trees and xylem characteristics discussed in this study belong to two areas, of which one covers biometric traits of trees excluding diameter at breast height and tree height, while the other comprises wood characteristics analysed in this study as well as diameter at breast height and tree height.

DISCUSSION

Xylem structure to a varying degree is optimised by its functions, tree growth conditions and strategies facilitating tree survival. Thus the characteristic features of xylem include a complex chemical composition and species-specific anatomical structure, directly determining physical and mechanical properties of wood (Barnett and Jeronimidis 2003).

Although literature sources on the subject relatively often describe dependencies between tree traits and xylem architecture and properties (Meyer 1959, Smith 1968, Lenz et al. 2012) or its characteristics (Jelonek et al. 2009), still scientific papers present the above mentioned system in a simplified or generalised form.

A considerable body of research, describing tree architecture in relation to anatomical characteristics of xylem or its properties, investigates these dependencies and interactions in terms of tree stability and potential tree damage caused by dynamic loading (Ezquerra and Gil 2001, James et al. 2006, Sellier and Fourcaud 2009). Tree size, shape and structure are known to have a considerable effect on tree stability at static and dynamic loading (James et al. 2006). As it is reported by Kim (2000), tree stability is affected by the relationship between stem diameter and tree height, as well as by the allocation of foliage biomass.

Tree architecture changes depending on many external factors (Vanninen et al. 1996, Mäkinen and Isomäki 2004, Cienciala et al. 2006, Jelonek et al. 2009, West 2009) and genetic conditions (Giertych 1997). It is related with characteristics and properties of xylem. As it is reported by Schniewind (1962), changes in the characteristics of anatomical elements result directly from the existence of two overlapping systems in trees, i.e. the physiological and mechanical systems, exemplifying optimisation of tree growth and adaptation to different requirements (Brüchert and Gardiner 2006). Thus we may assume the existence of multifaceted interactions and dependencies between wood structure and morphological traits of trees.

This study analyzed dependencies between traits describing tree morphology as well as allometric indexes of its stability ($H/D_{1.3}$, L_K/H, D_K/H) and xylem characteristics, i.e. tracheid wall thickness, lignin content and cellulose crystallinity. Xylem characteristics were analysed in the circumferential part of the stem. The circumferential part of the stem was examined, because as a result of adaptation radial growth of trees the circumferential area of the stem is the zone where the greatest loads caused by wind are transferred (Kenneth et al. 2006) and where stem rigidity increases (Morgan and Cannell 1994, Telewski 1995). One of the two maximums of stem load is found in the lower butt end (Ancelin et al. 2004), thus the analyses were conducted at breast height.

The basic biometric characteristics investigated in this study included diameter at breast height (33 ± 6.8 cm) and tree height (24 ± 2.4 m), being typical of mature pine trees and comparable to those reported by Meixner et al. (1997).

The index describing crown inclination (D_K/H) and the centre of gravity of trees (L_K/H) amounted to 22 ± 5 and 31 ± 6, respectively, and these values were very similar to those recorded for mature pines by Turski et al. (2012). In turn, the slenderness ratio of mean sample trees was on average 77 ± 13 and as such it fell within the range, in which trees may be classified as stable (Burschel and Huss 1987).

In terms of tree structure the study analysed values of tracheid wall thickness in early and late wood. On average in the investigated pines tracheid wall thickness in early wood was 2.1 μm and in late wood it amounted to 6.9 μm, respectively, with these values being consistent with those given for this species in literature sources (Verkasalo 1992, Hannrup et al. 2001, Martín et al. 2010). Reme and Helle (2002) reported that the thickness of tracheid walls in pine in the circumferential zone of the stem is approx. 3 - 4 μm in late wood and approx. 2 μm in the early wood zone. According to a study by Irbe et al. 2013, the thickness of tracheid walls both in early and late wood increases in the circumferential part of the stem, in the tracheids of late wood amounting to approx. 6 μm.

Also lignin content in cell walls and cellulose crystallinity in wood of analysed pines fell within the range given by literature sources (Barnett and Jeronimidis 2003, Antonova et al. 2014). In wood of these pines crystallinity ranged from 70 to 77 % and was characterised by limited dispersion (4.4 %). It is commonly assumed that in softwood approx. 70 % cellulose is its crystalline form with a polymerisation rate of approx. 10 000 (Barnett and Jeronimidis 2003). With an increase in crystalline areas and length of cellulose chains wood will exhibit better strength parameters, lower shrinkage and greater density.

Sellier and Fourcaud (2009) in their study on tree stability in relation to the action of wind stressed the role of the crown and changes in the geometric tree axis as more important than properties and anatomical traits of wood. In turn, studies conducted by Lenz et al. (2012) indicated a significant relationship between wood structure and morphological traits of trees, at a much weaker or no relationship between xylem characteristics at the cellular level (cell wall thickness and cellulose crystallinity as well as the microfibril angle).

Results presented in this study indicate the existence of a significant relationship between tree morphology and the structure of their wood. Tree height, its diameter at breast height and the slenderness ratio resulting from these variables were significantly correlated with the share of crystalline cellulose, which plays a significant role by modifying mechanical properties of anatomical xylem elements (Barnett and Jeronimidis 2003). The relationship found between lignin content in cell walls and tree crown parameters also indicates the role of lignin in the modification of biomechanical tree stability. Wider crowns, with a greater inclination coefficient, will exert greater compressive forces on tracheid walls, which in turn will require greater rigidity to resist this pressure. The high share of lignins in xylem enhances resistance of cell walls to deformations and provides the tree with mechanical stability (Boudet et al. 1995, Santos Abreu et al. 1999). A significant relation was also found between diameter at breast height as well as slenderness ratio ($H/D_{1.3}$), and cell wall thickness in late wood.

The dependence found between tracheid wall thickness and slenderness ratio of trees is confirmed by the relationships stressed in literature, which are observed between tree form and xylem characteristics and properties (Cannell 1993, Pretzsch 1995). Results recorded in this study may to a certain degree indicate the direction of adaptation changes in xylem. A dependence was found between tracheid wall thickness, cellulose crystallinity and slenderness ratio of trees, the latter being a major indicator of tree resistance to dynamic load caused by wind, thus suggesting adaptation changes aiming at the maintenance of internal balance in the mechanical system of the stem. Such changes were partly described by Mencuccini et al. (1997) and concern mainly relationships in the mechanical and hydraulic systems within plants. Such results indicate the complexity of adaptation processes in trees, aiming at the optimisation of their growth and xylem structure. At the same time, those authors also stressed the importance of anatomic xylem elements, which apart from the conductivity and storage functions also comprises the biomechanical system ensuring survival of individual specimens (Mattheck and Bethge 1998, Niklas et al. 2006). At the same time it needs to be remembered that the recorded results refer to a relatively small group of trees. Thus to ensure their more extensive application it seems advisable to conduct further studies on the dependencies and interactions found between the morphological structure of trees, xylem characteristics and wood properties.

CONCLUSIONS

The limited understanding of all laws governing xylem formation results first of all from the great number of interactions between wood structure and genetic, environmental and anthropogenic factors. At the same time, this network of dependencies refers to all levels of wood structure, starting from macrostructural traits through the complex structure of cell walls and finally the molecular level.

This study analysed the relationship between tree architecture and xylem characteristics at the micro- and ultrastructural levels. A dependence was found between morphological traits of Scots pine (*Pinus sylvestris* L.) and its xylem characteristics expressed in the thickness of cell walls, lignin content in cell walls and cellulose crystallinity. The strongest dependence was observed between slenderness ratio of trees and cellulose crystallinity, as well as slenderness ratio of trees and cell wall thickness in the late wood zone. Moreover, a significant relationship was found between tree crown width as well as crown inclination index and lignin content in tracheid walls.

It may be assumed that multifaceted interactions and dependencies found between the morphological structure of trees and their xylem characteristics provide evidence for the existence of a complex optimisation mechanism in individual trees. Adaptation growth of trees is probably based on the formation of xylem with characteristics and properties ensuring the best survival strategy thanks to the maximum adaptation to served functions.

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