

VARIATION IN TRANSVERSE SECTION AREA OF PINE  
TRACHEID WALLS (*PINUS SYLVESTRIS L.*)

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A variation in the total transection area of walls in a single radial row of tracheids as well as the dependence of the transection area of walls of single tracheids on the cambial age of growth rings and on the tree growth rate in a 52-year even-aged pine stand were determined. The total area of transection walls of tracheids ranges from  $77 \times 10^3 \mu\text{m}^2$  in the core wood annual growth rings to  $5 \times 10^3 \mu\text{m}^2$  in the outer rings of the stem. This value changes with the cambial age of the growth ring according to a negative exponential curve. Due to the worsening of the conditions of tree growth in a stand, the total area of transection of walls in a single row of tracheids for a given growth ring increases. There is a linear dependence between the total area of transection of walls in a single row of tracheids and the number of tracheids in the growth ring. The mean area of transection of walls of a single tracheid is constant within  $\pm 10\%$ , irrespective of the type of tracheid (early or late), of the tree growth class, and of the zone of the stem cross-section.

#### INTRODUCTION

One of the important factors affecting formation of xylem is a tree location in a stand. However, knowledge of the annual ring formation in view of its microstructure is far from complete; particularly its dependence on tree growth rate in an even-aged stand requires further study. Our previous papers on this subject [3] provided results on studies on the effect of the thickness of pine tracheids walls on cambial age of tree growth rings for various tree growth classes in an even-aged stand (for dominant, intermediate, and suppressed trees). The goal of the present paper is to study the influence that the variation in pine growth in an even-aged stand, with the cambial age of annual growth ring also considered, has on the total area of tracheid walls transection formed during the growth period. This paper does not only have a cognitive, but also practical aspect, as the total area of transection of tracheid walls subsequently formed in annual ring is considered a synthetic indicator describing the amount of wood substance deposited in the radial row of tracheids in the growth period [7].

### MATERIALS AND METHODS

Experimental trees from the classes of dominant, intermediate, and suppressed trees were cut in a unispecies and 52-years even-aged pine stand (stand qualification I) on the site of Stęszewko Forestry (Zielonka Forestry District Administration) which belongs to Experimental Forests of the Agricultural University in Poznań. Breast height diameter in a bark was 28, 22, and 14 cm for the dominant, intermediate, and suppressed tree respectively.

Discs were taken at a 1/6 height level of the tree. Along the northern-southern radius of each disc, strips 20 mm in width along the tangential direction and 20 mm in depth along the longitudinal direction were cut out. For micromorphometric measurements, microtome transections taken from the following annual rings along the northern radius: 3, 6, 9, 12, 15, 20, 25, 30, 35 and 40 were prepared; they were immersed in Canadian balsam. Both the diameter of tracheids and their walls thickness were measured using the prototype measuring system [3]. For the annual growth considered, all tracheids falling within the growth ring width and along the selected measuring lines were measured. In each microtome transection such a band of tracheids within an intermediate zone such a row of tracheids was selected which comprises the whole width of the mentioned growth ring. Within this band three representative rows of tracheids were chosen, for each of them radial tracheids diameter ( $D_r$ ) and tangential thickness of their walls ( $T$ ) were measured, the tracheids ranging from the first early one till the last late one for each of a given growth rings. The annual growth ring was divided into the early and late tracheids according to definition of late tracheids by Mørk [5]. Following this definition, the late tracheids are those, a double wall thickness of which is equal to or bigger than the diameter of tracheid lumen.

The area of transection of walls of individual tracheids ( $A$ ) was calculated from the following relation [8]:

$$A = 2T(D_r + D_t - 2T) \quad (\mu\text{m}^2),$$

where  $D_r$  stands for radial tracheid diameter,  $D_t$  for tangential tracheid diameter, and  $2T$  — double thickness of tracheid wall. The tangential tracheid diameter needed for the calculations ( $D_t$ ) was measured for 15 rows in each growth ring. As followed from the calculations, the tangential tracheid diameter is independent of growth ring age and of conditions of tree growth in the stand, and approximately equals to  $30 \pm 1.5 \mu\text{m}$  ( $\bar{x} \pm \sigma$ ). Since within the whole growth ring width, the tangential tracheid diameter is actually constant, thus for the calculations its mean value was taken:  $D_t$  equals to  $30 \mu\text{m}$ .

The total area of the transection of walls from the radial row of tracheids in the growth ring ( $\Sigma A$ ) was calculated as a sum of transection areas of individual tracheids ( $A$ ) for the whole width of annual growth ring, from the first early tracheid ( $A_1$ ) to the last late tracheid ( $A_n$ ):

$$\Sigma A = A_1 + A_2 + A_3 + \dots + A_n.$$

## RESULTS

As expected, the total transection area of tracheid walls is varied considerably for the whole annual growth ring, depending on the cambial age of tree growth rings and the tree class; it ranges from  $77 \times 10^3 \mu\text{m}^2$  in the core wood growth rings to  $5 \times 10^3 \mu\text{m}^2$  in the outer growth rings of a stem. The effect of cambial age of growth rings on the total transection area of tracheid walls is illustrated in Fig. 1a. It shows regression curves calculated from the equation  $y = ax^{-b}$ . Parameters of this equation are compiled in Table 1. Taking into account the results of previous studies [6, 9] in the growth rings under consideration the following three zone may be distinguished: the core zone, or juvenile wood zone (<10 rings), intermediate zone (from 10 to 20 annual rings), and the outer zone or mature wood zone (>20 rings). A border between these zones is marked with a dotted line in Fig. 1.

The total transection area of walls in one row of tracheids in the growth rings varies, depending on the cambial age of growth rings and the tree growth rate. Decrease in the total transection area of tracheid walls along with the increase in the annual ring age is the more pronounced, the better the conditions of tree growth in a stand. The decrease in the total area of transection of tracheid walls within the range of the annual rings considered (from 3 to 40 rings) for the dominant tree is 90%, for the intermediate tree 80%, and for the suppressed tree — 70%. The highest decrease in the total area of transection of tracheid walls was found to occur in the first zone, till the 10th annual ring around the pith, i.e. in the juvenile wood, and it attains the value of 54 to 56% of the total decrease in total area of transection of tracheid walls. In the intermediate zone (>10 to <20 rings) this decrease ranges from 16 to 32%, and in the mature zone (>20 rings) is only from 7 to 15%. In the growth rings which are closest to the pith, the total area of transection of tracheid walls does not reveal significant differences with respect to the tree growth classes. These differences tend to increase with the age of the growth ring by about 10 rings, and then remain more or less on the same level.

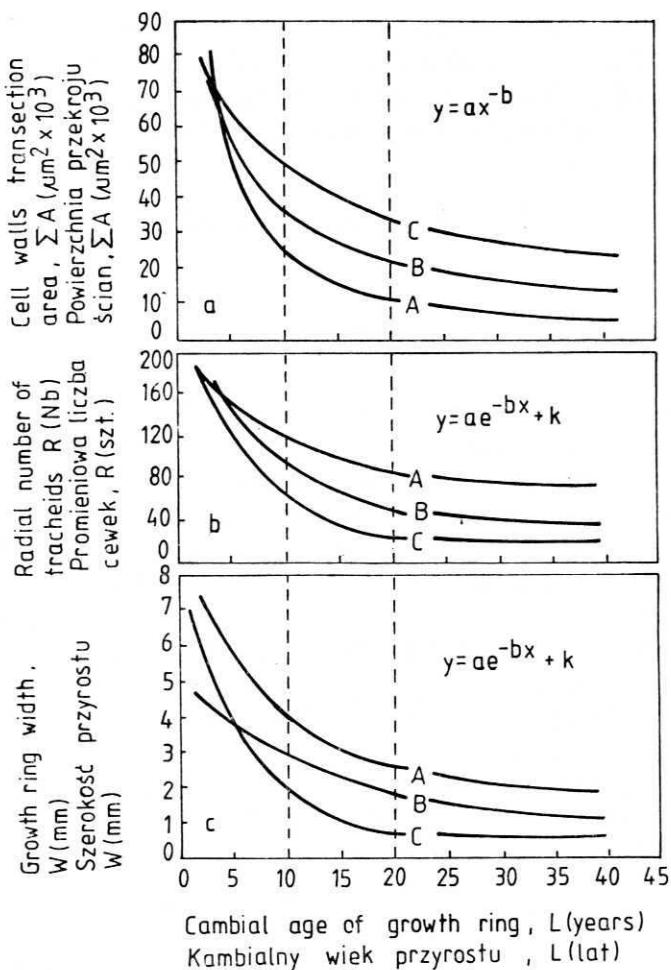


Fig. 1. Effect of annual growth rings age on the total area of transection of walls of a single radial row of tracheids (a), on a radial number of tracheids in growth ring (b), and on growth rings width (c), for pines belonging to dominant (A), intermediate (B), and suppressed (C) classes of trees

Rys. 1. Wpływ wieku przyrostu na sumaryczną powierzchnię przekroju poprzecznego ścian jednego promieniowego rzędu cewek (a), na promieniową liczbę cewek w przyroście (b) i na szerokość przyrostu (c) w drzewach sosny należących do grupy drzew dominujących (A), średnich (B) i opanowanych (C)

The curves in Fig. 1a are similar to relation characterizing the influence of the annual ring age on the radial number of tracheids in the growth and on the growth ring width (Fig. 1b and 1c, and Table 2 and 3).

Our choice of the regression equation describing the relation between the annual growth ring age and the radial number of tracheids in the growth ring, and the growth ring width was partially determined not only by the value of determination coefficient ( $R^2$ ) but also by Fritts [4] view according to which the dependence in question can be well

Table 1  
 Parameters of regression equations  $y = ax^{-b}$  characterizing the dependence between the total value of transection of walls in a single radial row of tracheids ( $y$ ,  $\mu\text{m}^2$ ) and growth ring age ( $x$ , years)  
 Parametry równań regresji  $y = ax^{-b}$  opisujących zależność między sumaryczną powierzchnią przekroju poprzecznego ścian pojedynczego promieniowego rzędu cewek ( $y$ ,  $\mu\text{m}^2$ ) i wiekiem przyrostów ( $x$ , lat)

Tree growth class Grupa wzrostowa drzew	Equation parameters Parametry równania		Determination coefficient Współczynnik determinacji $R^2$
	$a$	$b$	
Dominant	23.341	-1.07	0.90
Dominującé			
Intermediate	16.032	-0.66	0.85
Średnie			
Suppressed	14.485	-0.49	0.84
Opanowane			

described by regression equation of the negative exponential function type. The dependencies there of are no identical though, because the total area of transection of tracheid walls, besides radial number of tracheids in the growth ring and their diameter, also depends on the thickness of their walls.

As follows from the comparison of curves in Fig. 1a and 1b, the growth ring width and the radial number of tracheids in a given growth ring increase with increasing rate of trees growth in a stand, while between the area of transection of one row of tracheids and the trees growth rate a reversed relation is observed (Fig. 1a). As the rate of tree growth diminishes, the area of transection of one row of tracheids in a given growth ring tends to increase. In other words, along with the decrease in the number of tracheids in growth ring, due to worsening conditions of tree growth, the total area of transection of walls in one radial row of tracheids increases. This indicates that there is a linear dependence between the total area of transection of walls in one

Table 2  
 Parameters of regression equations  $y = a \exp(-bx) + k$  describing a relation between the radial number of tracheids in a growth ring ( $y$ , Nb) and the growth ring age ( $x$ , years)

Parametry równań regresji  $y = a \exp(-bx) + k$  opisujących zależność między promieniową liczbą cewek w przyroście ( $y$ , szt.) i wiekiem przyrostów ( $x$ , lat)

Tree growth class Grupa wzrostowa drzew	Equation parameters Parametry równania			Determination coefficient Współczynnik determinacji $R^2$
	$a$	$b$	$k$	
Dominant	131.41	-0.113	71.00	0.78
Dominującé				
Intermediate	205.10	-0.113	30.75	0.90
Średnie				
Suppressed	271.31	-0.193	19.69	0.80
Opanowane				

Table 3

Parameters of regression equations  $y = a \exp(-bx) + k$  describing a dependence between growth rings width ( $y$ , mm) and their age ( $x$ , years)

Parametry równań regresji  $y = a \exp(-bx) + k$  opisujących zależność między szerokością przyrostów ( $y$ , mm) i ich wiekiem ( $x$ , lat)

Tree growth class Grupa wzrostowa drzew	Equation parameters Parametry równania			Determination coefficient Współczynnik determinacji $R^2$
	$a$	$b$	$k$	
Dominant	6.544	-0.105	1.739	0.56
Dominując	4.037	-0.086	1.050	0.62
Intermediate	7.886	-0.182	0.565	0.72
Średnie				
Suppressed				
Opanowane				

radial row of tracheids and the radial number of tracheids (Fig. 2). The value of determination coefficient testifies to the fact that in as many as 99% cases, the variation in the total area of transection of tracheid walls results from a varied number of tracheids in growth ring. For

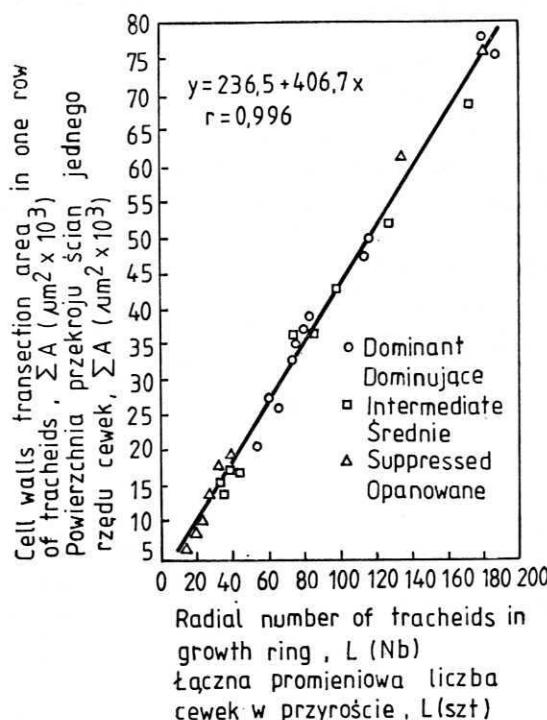


Fig. 2. Relation between the total area of transection of walls of a single radial row of tracheids and the radial number of tracheids in pine growth ring  
Rys. 2. Zależność między sumaryczną powierzchnią przekroju poprzecznego ścian jednego promieniowego rzędu cewek a promieniową liczbą cewek w przyrostach rocznych sosny

the same reasons, a similarly close dependence was observed between the total area of transection of tracheid walls and growth ring width ( $y = 2716.8 + 12.3x$ ;  $R^2 = 0.99$ ), as growth ring width is a function of the number of tracheids in growth ring. The studies on growth ring formation of odd-aged pines which grow in different conditions showed that the relation between the total area of transection of tracheid walls and the radial number of tracheids may be also described by the parabolic equation [8]. This equation describes well the results obtained by the above mentioned authors, and it comprises from 15 to 79 tracheids in the growth ring width ( $R^2 = 0.91$ ). For a higher radial number of tracheids this equation fails short.

The analysis of the variation in the mean area of transection of walls of single tracheids permitted a conclusion that the mean value is only slightly smaller for early tracheid, for which  $V = 11\%$  ( $V_{\min} = 6\%$ ,  $V_{\max} = 22\%$ ), than for late tracheids, for which  $V = 16\%$  ( $V_{\min} = 8\%$ ,  $V_{\max} = 33\%$ ).

When comparing for given growth rings, the mean areas of transection of tracheid walls it can be noticed that the area for early and late tracheids is almost identical, as the difference between the there of

Table 4

Mean area of transverse section of walls of single tracheids (both early and late) of pine trees at their different growth stages

Średnia powierzchnia przekroju poprzecznego ścian pojedynczych cewek wczesnych i późnych drzew sosny należących do różnych grup wzrostowych

Tree growth class Grupa wzrostowa drzew	Tracheid kind Rodzaj cewek	
	Early Wczesne	Late Późne
	Wall transection area, $A$ ( $\mu\text{m}^2$ ) Powierzchnia przekroju ścian, $A$ ( $\mu\text{m}^2$ )	
Dominant	402 $\pm$ 53 <sup>a)</sup>	422 $\pm$ 86
Dominując		
Intermediate	400 $\pm$ 60	408 $\pm$ 82
Srednie		
Suppressed	419 $\pm$ 50	419 $\pm$ 77
Opanowane		

<sup>a)</sup>  $\bar{x} \pm \sigma$  (mean  $\pm$  standard deviation)

<sup>b)</sup>  $\bar{x} \pm \sigma$  (średnia  $\pm$  odchylenie standardowe)

values for 83% of the studied growth rings does not exceed  $\pm 10\%$ . Such a conclusion also follows from data given in Table 4. Actually, already in 1975 for 25-year-old *Pinus radiata*, Cowan [2] observed a practical lack of any differences in the mean value of transection area of walls of early and late tracheids. According to this author, the

mean area of transection of walls for both early and late tracheids equals to  $420 \mu\text{m}^2$ .

The presented data seem to suggest that the mean area of wall transection of a single tracheid is approximately constant ( $\pm 10\%$ ), irrespective of the type of tracheid (early or late), of the tree growth class in a stand, and of the cross-section zone of the stem (Table 5).

**Table 5**  
**Influence of growth class and of the zone of cross-section of stem of pine trees on the mean area of transection of walls of single tracheids**  
**Wpływ grupy wzrostowej i sfery przekroju poprzecznego strzały drzew sosny na średnią powierzchnię przekroju poprzecznego ścian pojedynczych cewek**

Type of tracheid Rodzaj cewek	Tree growth class Grupa wzrostowa drzew	Zone of the stem cross-section Sfera przekroju poprzecznego strzały		
		Juvenile wood Drewno młodociane (<10 rings) (<10 przyr.)	Intermediate zone Sfera pośrednia (10 ... 20 rings) (10 ... 20 przyr.)	Mature wood Drewno dojrzale (>20 rings) (>20 przyr.)
		Wall transection area, A ( $\mu\text{m}^2$ ) Powierzchnia przekroju ścian, A ( $\mu\text{m}^2$ )		
Early Wczesne	Dominant	402	418	379
	Dominujące	410	376	413
	Intermediate			
	Średnie	420	424	390
Late Późne	Suppressed			
	Opanowane			
	Dominant	409	430	415
	Dominujące	383	434	401
	Intermediate			
	Średnie			
	Suppressed	428	421	374
	Opanowane			

These data support an opinion expressed by Bethel [1] that at coniferous tracheid the amount of wood substance that can be used for wall development at the stage of tracheid development is practically constant and does not depend on the degree of lumen increase following division.

#### CONCLUSIONS

1. The total area of transection of walls in one radial row of tracheids in the growth rings is affected by the cambial age of growth rings, and the growth class of pine trees; ranging from  $77 \times 10^3 \mu\text{m}^2$  in the core wood to  $5 \times 10^3 \mu\text{m}^2$  in the outer rings of the stem.

2. The total value of transection of walls in one radial row of tracheids decreases with the cambial age of growth rings according to this relation:  $y = ax^{-b}$  ( $R^2 = 0.84 \dots 0.90$ ).

3. Due to the worsening of the conditions of tree growth in a stand, the total value of transection of walls in one radial row of tracheids in a given growth ring increases.

4. There is a linear dependence between the total value of transection of walls in one radial row of tracheids in growth ring and the radial number of tracheids ( $R = 0.99$ ).

5. The mean area of transection of walls of a single tracheid is by approximately 10% a constant value, independent of the type of tracheid (early or late), of the tree growth class, and of cross-section zone of the stem.

Received in January 1992

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**ZMIENNOSC POWIERZCHNI PRZEKROJU POPRZECZNEGO SCIAN CEWEK SOSNY (*PINUS SYLVESTRIS* L.)****S t r e s z c z e n i e**

Oznaczano zmienność sumarycznej powierzchni przekroju poprzecznego ścian w pojedynczym promieniowym rzędzie cewek oraz powierzchnię przekroju poprzecznego ścian pojedynczych cewek w zależności od wieku kambialnego przyrostów rocznych i grupy wzrostowej drzew w jednowiekowym 52-letnim drzewostanie sosnowym. Sumaryczna powierzchnia pola przekroju poprzecznego ścian cewek zmienia się w przyroście rocznym od  $77 \times 10^3 \mu\text{m}^2$  w przyrostach przyrodzeniowych do  $5 \times 10^3 \mu\text{m}^2$  w przyrostach zewnętrznych strzały. Wielkość ta zmienia się wraz z wiekiem kambialnym przyrostów według negatywnej krzywej wykładowiczej. Wskutek osłabienia wzrostu drzewa w drzewostanie, sumaryczna powierzchnia przekroju poprzecznego ścian w jednym promieniowym rzędzie cewek w danym przyroście rocznym zwiększa się. Zależność między sumaryczną powierzchnią przekroju poprzecznego ścian jednego rzędu cewek i liczbą cewek w przyroście rocznym jest prostoliniowa. Średnia powierzchnia przekroju poprzecznego ściany pojedynczej cewki jest w granicach  $\pm 10\%$  wielkością stałą, niezależną od rodzaju cewki (wczesne czy późne), od grupy wzrostowej drzew i od strefy przekroju poprzecznego strzały.