Quantitative analysis of cambium growth in *Thuja*

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The increase in girth of a nonstoried cambium is accomplished by an intrusive growth of fusiform initials, by occurrence of oblique (pseudotransverse) anticlinal divisions and by a rather slight increase in width of the initials. However, the intensity of these processes far exceeds the requirements to accommodate the cambium to increasing girth of the wood cylinder. They are balanced by loss or partial decline of the initials. Many aspects of these phenomena have been described by Bannan (1956, 1964, 1965; these papers contain references to other relevant publications of Bannan), Hejnowicz (1961), Srivastava (1963). However, the quantitative relations among them need further studies. There is also a problem of variation of these processes especially in respect to cambium age.

MATERIAL AND METHODS

The developmental changes in cambium were reconstructed by following the radial files of tracheids. The validity of this indirect method is based on the fact that xylem in *Thuja* replicates the cell pattern in cambium (Bannan 1956).

The material used was a disc of wood from a straight stem of 29 years old *Thuja occidentalis* L. grown in Kórnik Arboretum. The disc was sawed off at a distance 3 m from the stem base. Serial tangential sections 40 μ in thickness were cut from the wood sample covering 19 rings beginning with the first section at the pith. The sections were placed in succession on slides and mounted in water glass solution which enables obtaining of optimal contrast of the cell walls. Before placing on the slide each section was immersed in boiling diluted water glass solution to get rid off air bubbles. The sections were projected by using the Zeiss's „Documator” onto high contrast photographic paper and the negatives were prepared.

The analysis depended on localization the tips of tracheids in respect to xylem rays as constant points. The following groups of radial tiers of the tracheids were investigated: the derivatives of two fusiform initials present in one year old cambium and of their descents formed during the next 7 years, the derivatives of four initials in 12 years old cambium and of their descents from the next 6 years, the derivatives of 50 initials and their descents formed during the 4th year of cambium life. similarly during the 12–13th years and 15–17 years.

RESULTS AND DISCUSSION

First we would like to answer the question what is the mean rate of intrusive growth of fusiform initials in different age of cambium. For this purpose we traced sequences of the tracheids along radial distance from the 2nd to the 7th and from the 12th to the 19th annual rings. The length of successive tracheids originating from one fusiform initial follows a line with many rather small fluctuations which certainly are due to variation in intrusive growth during tracheid differentiation. These fluctuations obviously can be ignored. The average rate of intrusive growth of one initial was calculated in the following way: we took the positive displacement (increasing the cell length) of the both tips Δl which occurred between the two successive pseudotransverse partitions and divided it by the linear distance between the partitions in mm along radius of the stem Δr (thickness of the xylem layer). This way we obtained the rate of intrusive growth of an initial $\frac{\Delta l}{\Delta r}$ in mm per mm of xylem increment.

In calculating of the mean rate only not declining initials were taken into account. The results are presented in Table 1.

Table 1

Mean rate of intrusive growth of fusiform initials expressed as the increment of cell length during the production of 1 mm of xylem

Age of cambium	Number of investigated initials	Mean rate of intrusive growth	Minimal and maximal observed rates	
During formation of rings no. 2—7	35	0.28	0.10	0.58
During formation of rings no. 12—19	34	0.33	0.10	0.43

As it may be seen the average rates of intrusive growth of the fusiform initials are quite high and there is no sign that they become lower with the age of the cambium. It is easy to show that if the initials grow with such rate as shown in Table 1 then some of them must be lost or undergo decline to keep the cambium surface equal to the surface of the xylem cylinder, especially in older cambium. Namely, if the cambium surface increased only by intrusive growth of its initials and there was no decline then the following relation should be obeyed:

$$\frac{\Delta l}{\Delta r} = \frac{1}{r} \quad (1)$$

and the rate of intrusive growth would depend upon the r and l as shown in Table 2. In the relation $1/r$ is radius of cambium cylinder, Δr is increment of r , l is mean length of the initials and Δl is increment of l during formation of xylem layer Δr thick.

This relation may be obtained in the following way: the relative increase of cambium surface due to increase of radius is

$$\frac{\Delta s}{s} = \frac{2\pi(r + \Delta r) - 2\pi r}{2\pi r} = \frac{\Delta r}{r} \quad (2)$$

while the relative increase of cambium surface caused by intrusive growth is: $\frac{\Delta s}{s} = \frac{n\Delta lw}{nlw} = \frac{\Delta l}{l}$ (3)

Equalling 2 and 3 one obtains the 1.

Symbols: s and Δs — investigated surface of the cambium and its increment

n — number of the initials in s

w — mean width of the initials

It will be noted that the calculated values of $\frac{\Delta l}{\Delta r}$ are clearly lower than the measured rates. The necessity for decline is then obvious.

Table 2

Relation between radius of the cambium cylinder, length of the fusiform initials l and rate of intrusive growth $\frac{\Delta l}{\Delta r}$ calculated from the relation 1.

In last column the measured rates $\frac{\Delta l}{\Delta r}$ are shown

r mm	l (measured) mm	$\frac{\Delta l}{\Delta r}$ calculated mm/mm	$\frac{\Delta l}{\Delta r}$ measured mm/mm
10	1.74	0.17	} 0.28
20	2.24	0.11	
30	2.68	0.09	
40	2.96	0.08	} 0.33
50	3.10	0.06	

To obtain a more complete picture of what had happened in cambium one must consider intrusive growth, decline and pseudotransverse divisions jointly. For this purpose we took 3 series of sections covering about 4 mm thick layer of xylem each. On the first section in the series 50 tracheids were chosen. They correspond to 50 fusiform initials which were present in cambium at the moment of formation of these tracheids. By following the radial files of tracheids produced by these initials we measured total intrusive growth, total decline and total length of partition walls which occurred in the initials and in their descent initials during the production of 4 mm thick layer of xylem.

As total intrusive growth we understand the sum of positive shifts of the tips, i.e. upward shift of the upper tip and downward shift of the lower tip, obtained by comparison of the initial position of the tips, i.e. on the first section in the investigated series or on the section where the tip formed in pseudotransverse division

first appeared, with their final position, i.e. on the last section in the series or on the last section before pseudotransverse division. As the total decline we understand the sum of length of the initials which were lost completely from the cambium, measured on the first section in the series or on the section where the cell formed in pseudotransverse division first appeared, and the sum of negative shifts obtained by comparison the initial position of the tip with its final position as defined previously. The total length of pseudotransverse partitions is defined as the sum of distances between upper and lower ends of the partitions measured along the axis of the initials.

The pseudotransverse divisions and the intrusive growth already include the growth in width of the initials as a factor increasing cambium surface. Namely, the pseudotransverse divisions and the intrusive growth contribute to the increase of cambium surface due to growth in width of the narrow parts of the initials either along the partition walls or at tips formed by intrusive growth. The mean width of the tracheids (tangential diameter) was the same on the extreme sections of one series so it was not necessary to take into consideration the increase of the mean width with age of the cambium as a factor increasing cambium surface in the present studies.

The results of the measurements are shown in Table 3.

Table 3

Results of measurements on serial tangential sections of xylem related to fusiform initials which produced the considered tiers of tracheids

Measurement		Annual ring		
		no. 4	no. 11—12	no. 15—17
A.	initial and final distance of the fusiform initials from the pith (mm)	6.0—9.9	37.4—41.5	44.9—48.9
B.	initial and final number of the considered fusiform initials	50—69	50—53	50—53
C.	initial and final total length of the initials (mm)	73.1—116.4	143.7—155.1	156.6—161.6
D.	Total intrusive growth (mm)	56.2	47.0	69.6
E.	Total decline (mm)	39.4	53.8	93.1
F.	Total length of pseudotransverse partitions (mm)	28.1	21.3	30.1
G.	number of pseudotransverse partitions	51	35	48
H.	mean rate of intrusive growth per cell:			
a.	per 1 mm of xylem increment (mm/mm)	0.24	0.24	0.33
b.	per year	0.93	0.46	0.40

As may be seen the total intrusive growth as well as the total decline attained comparatively high values, 30—75% of the initial total length of cambial cells during the formation of 4 mm of xylem. As they counteracted each other we can conclude that there were intensive exchanges of cells in the cambium. In the youngest of the investigated samples of cambium the intrusive growth exceeded considerably the decline, in the two older the decline surpassed the intrusive growth.

However, the sum of intrusive growth and of pseudotransverse partitions surpassed the decline in each case.

Let us check if the net increase of total length of cambial initials, which is proportional to increase of cambium surface, fits to the requirement due to increase of girth of the cambium. The increment of cambium surface during the production 4 mm thick layer of xylem was 65%, 11% and 9% in the three investigated samples. The increase in total length of cambial initials was 59%, 8% and 3% respectively, so the agreement is fairly good.

The total intrusive growth of 50 initials and of their descents was kept on the similar level in the three samples differing in age of the cambium. The amount of intrusive growth was similar on the upper and lower tips.

Dividing the total intrusive growth by mean number of the initials and by width of xylem layer, mean rate of intrusive growth per cell per 1 mm of xylem increment was obtained, line Ha, Table 3. The rates are consistent with these shown in Table 1 and did not decrease with age of cambium.

The mean rate of intrusive growth of an initial can be also expressed in mm per year, Table 3, Hb. It will be noted that the rate of intrusive growth per year tends to decrease with age of the cambium.

Some numbers presented in Table 3 can be compared with these which can be found in Bannan's papers. According to Bannan (1956) mean intrusive growth of the newly formed initials was 0,55 mm during the first year after their origin in pseudotransverse division in cambium of *Thuja* trees with diameter of stem more than 15 cm. The growth was smaller in the next years. Mean rate can be estimated on basis of Bannan's data as 0.32 mm per year what is less than the mean intrusive growth per cell per year in our oldest cambium which however is much younger than the cambium to which Bannan's data are relevant. This is consistent with the trend of changes in intrusive growth observed by us.

The amount of intrusive growth during the production of 1 mm of xylem (the rate in mm per 1 mm of xylem) determined by us for *Thuja* is similar as calculated by Bannan (1965) for different species of *Pinus* in rings wider than 1 mm. According to Bannan the amount of intrusive growth per 1 mm of xylem drops as ring width increases, particularly in the range of width below 2 mm. However this intrusive growth was not measured directly but calculated from the frequency of anticlinal divisions, cell length and length of partitions. This way the trend in intrusive growth showed by Bannan reflected the trend in frequency of pseudotransverse divisions. To say if this trend in intrusive growth in respect to ring width can be showed by direct measurements accordingly to our method more extensive studies are needed.

SUMMARY

Quantitative relations between intrusive growth, pseudotransverse divisions and decline of fusiform initials in about 4 year, 11—12 and 15—17 years old cambium of *Thuja occidentalis* L. were investigated. There was significant overproduction of the initials by intrusive growth and by pseudotransverse anticlinal divisions in the investigated cambium. Namely, total length of the cell parts which were formed by intrusive growth (total intrusive growth) and by

pseudotransverse divisions in 50 fusiform initials and in their descent initials during the production of 4 mm of xylem was 114%, 47% and 63% in the three investigates cases, while the requirement for increment of total length of initials due to increase of girth of the cambium was 65%, 11% and 9% respectively. The total intrusive growth was greater than total decline in 4 year old cambium but not in the 11—12 and 15—17 year old. However the sum of the intrusive growth and the partitions formed in pseudotransverse divisions was greater than the decline in each case and the difference representing the net increase in total length of the initials was fitting to the requirement.

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Ilościowa analiza rozrostu miazgi u *Thuja*

Streszczenie

W miazdze niepiętrowej jaką reprezentuje *Thuja* komórki inicjalne wrzecionowate rosną końcami wciskając się między komórki sąsiednie (wzrost intruzywny) oraz dzielą się antyklinalnie skośnie. Intensywność tych procesów jest większa niż to jest potrzebne dla zwiększania obwodu miazgi. Nadmiar wzrostu kompensowany jest przez eliminowanie części komórek z miazgi. W niniejszej pracy badano ilościowe stosunki zachodzące między wzrostem intruzywnym, podziałami skośnymi eliminowaniem komórek i wzrostem obwodu miazgi 4-letniej, 11—12-letniej i 15—17-letniej. Stwierdzono, że łączna długość tych części komórek inicjalnych, które w okresie odkładania pokładu drewna o grubości 4 mm powstały w rezultacie wzrostu intruzywnego, wynosi 76%, 32% i 44% łącznej długości komórek inicjalnych w poszczególnych wypadkach. Przyrost łącznej długości komórek na skutek podziałów skośnych w tym okresie wyniósł 38%, 15% i 19%. Łączny efekt wzrostu intruzywnego i podziałów skośnych był 2 razy większy w miazdze 4-letniej oraz 5 i 7 razy większy w miazdze 11—12-letniej i 15—17-letniej niż zapotrzebowanie określone wzrostem średnicy cylindra miazgi. Ten nadmiar został skompensowany eliminacją odpowiedniej ilości komórek. W miazdze 11—12-letniej i starszej łączna długość komórek wyeliminowanych przekraczała łączny wzrost intruzywny. Przyrost netto długości komórek inicjalnych w badanych grupach zgadza się z zapotrzebowaniem określonym wzrostem średnicy cylindra miazgi. Przeciętna szybkość wzrostu intruzywnego przypadająca na jedną komórkę inicjalną wrzecionowatą wynosiła 0.24—0.33 mm na 1 mm warstwy odkładanego drewna. Wzrost intruzywny na 1 mm warstwy drewna nie zmniejszał się z wiekiem miazgi, zmniejszała się jednak szybkość wzrostu intruzywnego obliczona w stosunku do czasu (na jeden rok).