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A contribution to the rate of xylem cell formation and differentiation of tracheids in *Pinus silvestris* L.

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The seasonal course of the annual ring formation in trees has been the object of numerous investigations of different authors which showed either the gradual decrease of cambial activity during the vegetation season after the spring maximum of radial growth of tree trunk or two maxima of radial increment divided by a period of weak cambial activity at the mid-summer (works reviewed by Grossenbacher 1915, Priestley 1930, Ladefoged 1952, Trendelenburg 1955). Recently, the careful study of cambial activity in *Thuja* presented by Bannan (1955) added further evidence that the rate of formation of elements of wood decreases slowly towards the end of the season. Bannan did not observe in this species any second period of more intensive formation of cells of wood after the spring maximum of radial growth.

The author has been already touched on this question in his investigation of wood formation in larch (Wodzicki 1960). In contrast to Bannan's results there was noticed some significant radial increment of tracheids in plants collected in the second part of vegetation season. Another interesting finding of this work was the clearly observed correlation between changes of width of cambial zone and the type of wood formed, especially the cell wall thickness of tracheids. It was presumed that this correlation might express some causal relation of the type of wood formed with the duration of growth and duration of differentiation of cells in the cambial zone.

Further research was carried out with old pine trees. This paper reports the results of preliminary investigations carried out on two parts of the vegetation season and concerning especially the following questions: a) rate of completion of the differentiation of tracheids, b) rate of xylem cell formation from the cambium, c) width of cambial zone (the above being the elements which permit to deduce the duration of the life period of cells differentiating into tracheids), and finally, d) determination of the changes in the type of wood formed at different times of the vegetation season.

METHODS

Investigations were carried out with four 44-year old *Pinus silvestris* L. trees in Experimental Forests of S.G.G.W. in Rogow. Samples from the trunk of each tree at the breast height were collected three times during the vegetation season of 1960 and once in winter of 1960/61 using a cylindrical chisel of 5 mm diameter.

For microscopic examination, transverse, free-hand sections were taken of samples, stained with safranin and light green and mounted in Canada balsam for permanent preparations.

On the transverse sections a number of fully differentiated tracheids (from the boundary of last year late wood) and a number of cells in the cambial zone, along ten arbitrarily chosen rows of cells in radial direction were determined. Three layers were distinguished in the cambial zone: a) cambium, b) layer of radial diameter growth of cells, c) layer of differentiation, as described in the above mentioned work on Larch (W o d z i c k i 1960).

On the transverse sections of wood from the sample which was collected in winter, the radial diameter and cell wall thickness of all tracheids were measured along four, equally long, radial rows of successive tracheids formed in vegetation season of 1960 (from the boundary of the previous year's annual ring of wood to the dormant cambium layer).

RESULTS AND DISCUSSION

Considering the radial increment of the total number of fully differentiated tracheids and cells in the cambial zone at different periods of vegetation season, the rate of wood cell formation from cambial fusiform initials in these periods may be deduced.

As follows from the data in Table 1, in all the trees, increment of the total cell number per one day was greater in the second part of vegetation season than in July. In spite of the few observations presented in this paper, the results show still very intensive formation of xylem elements at this time. The results seem to show that there were two periods of cambial activity in the investigated trees during the vegetation season and they are in accordance with the results of other authors who observed two maxima of radial growth in different species of trees (M i s c h k e 1890, J o s t 1892, F r i e d r i c h 1897, B r o w n 1915, K o r s t i a n 1921, L o d e w i c k 1925, K i e n h o l z 1934).

On the contrary, the analysis of the increment of fully differentiated tracheids alone indicates, that in all trees the completion of differentiation was slower in the second part of vegetation season. The increase of xylem cell formation from cambium and a simultaneous slowing

down of protoplasm disappearance at the end of tracheid differentiation process caused a marked increase of cells in the cambial zone in September. These observations conform with the results of earlier investigation on *Larix decidua* and *Larix polonica* (Wodzicki 1960), and by inference with the data presented by Mork (1960) in his study concerning the annual ring of wood formation in *Picea abies*.

Table 1 also specifies data concerning the rate of the transition of cells in the cambial zone from cambium into a radial growth layer and into a differentiation layer. Analogically, comparing the rate of these two processes, it may be concluded that, though the rate of transition of cells from cambium into the radial diameter growth layer was higher in the second part of the vegetation season than in July, completion of cell growth and the beginning of differentiation were even faster. It produced a narrowing of the radial diameter growth layer in September and probably a decrease of the duration of the radial diameter growth period of these cells.

The rate of transition of the cells from the layer of radial diameter growth into the differentiation layer was nearly the same in July as the increment of fully differentiated tracheids in this time. Yet, in the second part of the season, the increment of cells in the differentiation layer was about three times that of the increase of tracheids after their differentiation process was completed. It caused approximately a fivefold enlargement of the differentiation layer in September as compared with June and July. These observations seem show that near the end of the vegetation season, cells in the cambial zone began to differentiate earlier, but the completion of the differentiation process was slower, and the period of differentiation of cells was significantly longer than in July.

It is rather doubtful whether the latter conclusion equally applies to all the cells observed in the differentiation layer of the sample collected in September. But this question cannot be clarified yet, since no exact dates, of the full completion of annual ring formation in the examined trees, were ascertained.

The investigations, treated as a preliminary survey, were based on the observations made on samples collected only three times during the vegetation season and once in winter. Although, this reduces the side effects of wounding on wood formation it renders difficult to examine the gradual changes of the rate of the investigated processes in the cambial zone.

It proved most interesting to campare the observations made in the cambial zone with the radial diameter and cell wall thickness of tracheids examined successively as they were formed starting from the boundary of the last year late wood to the cambium in radial direction.

Table 1

Increment of tracheids and cells in individual layers of cambial zone at the various periods of vegetation season

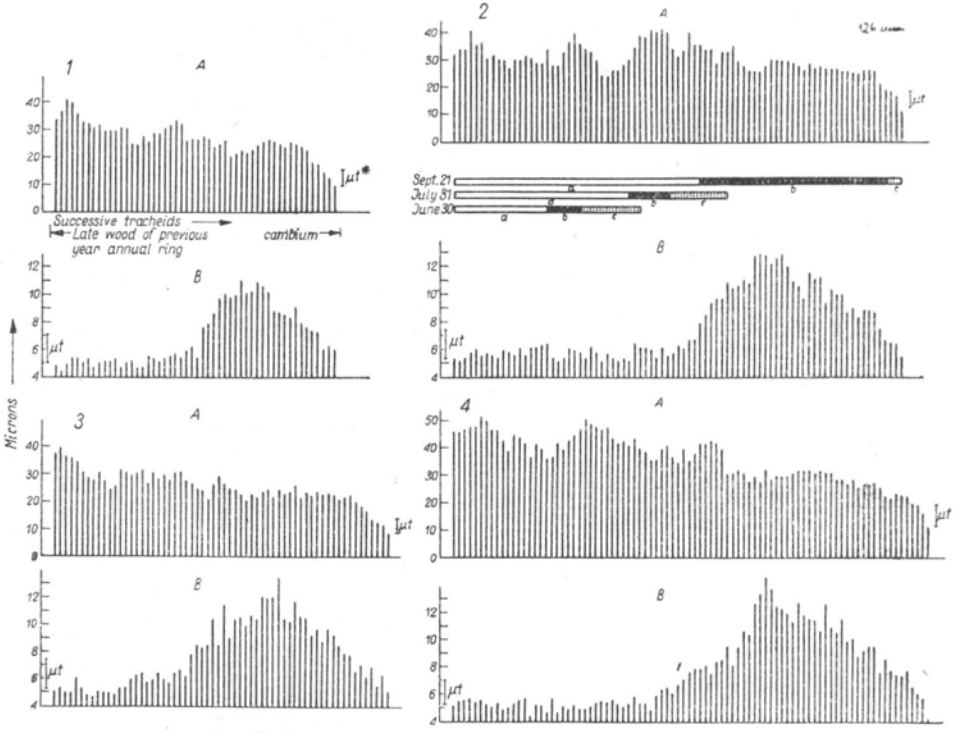
No. of tree and girth of trunk at the breast height (cm)	Date	Number of cells								Increment					Increment of cells per one day			
		Fully differentiated tracheids — T	Cambium — C	Layer of radial diameter growth — G	Layer of differentiation — D	Cambial zone (total) C + G + D	Cambial zone plus tracheids T + D + G + C	Tracheids plus growth and differentiation layers T + D + G	Tracheids plus differentiation layer T + D	Days	T	T + D + G + C	T + D + G	T + D	T*	T + D + G + C**	T + D + G***	T + D****
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
No. 1	30.VI	16.2	3.7	12.3	7.5	23.5	39.7	36.0	23.7									
										31	10.1	6.5	6.4	7.9	0.33	0.21	0.21	0.25
	31.VII	26.3	3.8	10.8	5.3	19.9	46.2	42.4	31.6									
78										52	7.5	19.2	17.7	25.9	0.14	0.37	0.34	0.50
	21.IX	33.8	5.3	2.6	23.7	31.6	65.4	60.1	57.5									
	30.VI	18.4	5.0	11.3	6.1	22.4	40.8	35.8	24.5									
No. 2										31	14.6	16.0	16.0	15.5	0.47	0.52	0.52	0.50
	31.VII	33.0	5.0	11.8	7.0	23.8	56.8	51.8	40.0									
84										52	13.4	31.8	31.5	40.2	0.26	0.61	0.61	0.77
	21.IX	46.4	5.3	3.1	33.8	42.2	88.6	83.3	80.2									

c.d. tabl. 1

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	30.VI	8.7	4.4	7.3	5.1	16.8	25.5	21.1	13.8									
No. 3										31	9.0	11.8	11.7	9.9	0.29	0.38	0.38	0.32
	31.VII	17.7	4.5	9.1	6.0	19.6	37.3	32.8	23.7									
84										52	11.6	34.3	33.0	39.9	0.22	0.66	0.63	0.77
	21.IX	29.3	5.8	2.2	34.3	42.3	71.6	65.8	63.6									
	30.VI	23.8	4.1	18.0	5.7	27.8	51.6	47.5	28.5									
No. 4										31	12.7	10.5	9.9	14.6	0.41	0.34	0.32	0.47
	31.VII	36.5	4.7	13.4	7.5	25.6	62.1	57.4	43.1									
81										52	19.6	46.3	46.1	55.0	0.38	0.89	0.89	1.06
	21.IX	56.1	4.9	5.4	42.0	52.3	108.4	103.5	98.1									

* Rate of the formation of fully differentiated tracheids,
** Rate of xylem cell formation from cambial fusiform initial,
*** Rate of transition of cells into the layer of radial diameter growth of cells in the cambial zone,
**** Rate of transition of cells into the layer of differentiation in the cambial zone.

Radial diameter of the tracheids was subject to considerable variation. In spite of this there were observed alternate periods of tracheid formation either with larger or smaller radial diameter in all trees during the vegetation season (Figs. 1*A*—4*A*). The method of measurement employed did not eliminate the possibility of an error arising from the fusiform shape of tracheids. Taking into account this reservation, it may be presumed, that the observed essential changes of radial diameter within the individual radial groups of tracheids reflect the periodical differences in the rate of growth of these cells after their formation through the tangential division of cambial initials. The radial diameter of tracheids formed shortly before the cessation of cambial acitivity was distinctly smaller. Some reduction of the radial diameter of tracheids



* Statistical computations by Snedecor's method, t — test at 5 per cent level.

Figs 1—4. Radial diameter (*A*) and cell wall thickness (*B*) of the successive tracheids from the boundary of the previous year's late wood to the cambium, after the annual ring formation was completed. Mean values obtained by the measurement of the tracheids along four rows across the annual ring of wood formed in 1960

Fig. 1 — tree No. 1, Fig. 2 — tree No. 2 (*a* — fully differentiated tracheids, *b* — differentiation layer, *c* — layer of radial diameter growth of cells in the cambial zone); Fig. 3 — tree No. 3, Fig. 4 — tree No. 4.

might be also observed somewhat earlier in spite of the above mentioned variation.

On the contrary, the graphs of cell wall thickness of tracheids give a regular picture (Figs. 1*B*—4*B*). After the period of thin-walled tracheid formation (early wood), the cell walls of tracheids successively formed were growing thicker until they reached the maximum and then began to grow thinner again. Owing to the formation of tracheids with increasingly thinner cell walls, the cell wall thickness of the last tracheids in the annual ring of wood was approximately te same as those of early wood.

Exact comparison of the width of individual layers in the cambial zone with the radial diameter and cell wall thickness of corresponding tracheids was made on tree No. 2 (Fig. 2). A similar comparison could be made on other trees, although not so accurately owing to a greater variability of the cell number in the individual samples. The limits of each layer are shown in Fig. 2 (fully differentiated tracheids, layer of differentiation, and layer of radial diameter growth) for three separate samples collected during the vegetation season. It is seen that the tracheids which were formed from the cells situated in the differentiation layer of two samples collected in June and July were thin-walled, which corresponds to the small width of differentiation layer in the two samples and to the short period of differentiation at that time. Cell walls of the tracheids formed later were thicker. It is quite clear that these tracheids were formed from cells observed in the wide differentiation layer of the sample collected in September. At the beginning of the second part of vegetation season, cell walls of the successive tracheids were gradually growing thicker which presumably corresponds to the gradual extension of differentiation period of cells in the cambial zone (this period was shown to be much longer in the second part of vegetation season than in July). Near the completion of cambial activity, the period of differentiation of tracheids was probably gradually reduced again due to the narrowing of the differentiation layer and the disappearance of the entire cambial zone except for the initial cells of cambium. It is seen that, the cell walls of following tracheids, differentiated from the cells situated closer to the cambium in the differentiation layer, were growing thinner again.

An analogous comparision of changes in the width of radial diameter growth layer with the radial diameter of fully differentiated successive tracheids is somewhat more difficult owing to the greater instability of radial diameter. However, the diminishing of the radial diameter of tracheids near the end of the vegetation season corresponds to the narrower layer of radial diameter growth of cells in the cambial zone.

The results seem to substantiate the author's earlier suggestion concerning the connection between the type of wood formed in Conifers and the length of the periods of radial diameter growth and differentiation of cells in the cambial zone, which vary during the vegetation season. However, the investigation showed also marked differences between individual trees with respect to the rate of new xylem cell formation from the cambium (observed also by earlier authors, Weiler 1898, Brown 1915 and others), and rate of completion of their growth and differentiation processes. (Table 1). This fact seems to indicate that the intensity of these processes was probably different in individual trees, although the differences in the cell wall thickness and the radial diameter of tracheids were not so distinctive. This points to the correlation between the type of wood formed and the changes of the length of growth and differentiation periods in the cambial zone being more complicated which should be taken into account in further study.

SUMMARY

The rate of radial diameter growth and differentiation of cells in cambial zone and the rate of formation of xylem cells from the cambium were investigated in 44-year old *Pinus silvestris* L. trees. It was shown that the rate of xylem cell formation from cambial fusiform initials in the second part of vegetation season was higher than in July. On the contrary, the rate of formation of fully differentiated tracheids was lower. These opposing trends in the rate of the two processes led to the extension of the differentiation period, and the reduction the radial diameter growth period, in the second part of the vegetation season.

These changes in the relative length of periods of growth and differentiation of cells in the cambial zone seem to be in a causal connection with the different cell wall thickness and radial diameter of tracheids in the wood formed at different times of the vegetation season.

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