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Investigation on the kind of *Larix polonica* Rac. wood formed under various photoperiodic conditions

I. Plants growing in natural conditions

T. WODZICKI

The paper reports the first part of investigations carried out in natural conditions and in greenhouse on the problem of wood formation, with respect to daily rhythm of light. The problem of influence of environmental factors on wood formation has been investigated by many authors but as yet papers dealing with the influence of daylength on cambial activity and wood formation are scanty. According to these works (Wareing 1951, Wareing, Roberts 1956), the activity of cambium in some woody species may be prolonged in the vegetation season by a long day regime and inhibited by short day conditions. New recent findings of Żelawski (1957) seem to show that daylength also influences the type of wood that is formed under various photoperiodic conditions. He showed that typical late wood elements were formed in larch seedlings when the plants were grown under short day conditions, while under continuous illumination (light intensity — 1300 lux during night hours) only thin walled tracheids occurred. This fact was subsequently demonstrated on spruce seedlings (Żelawski, Wodzicki 1960). It is well known that under short day conditions in many species of wody plants extension growth ceases and resting buds are formed (Wareing 1948, 1956, Nitsch 1957). This fact found also its confirmation in experiments with larch seedlings (Żelawski 1956). It was suggested earlier (Priestley, Scott 1936) that late wood formation is connected with cessation of extension growth in woody plants. Nevertheless it has been clearly shown by Molski and Żelawski (1958) that thick-walled tracheids were also formed during continuous growth of larch seedlings under uninterrupted illumination obtained by using additional low intensity (10 lux) light during night hours in greenhouse. Thus, it might be supposed that cell wall thickening (affected by light conditions) was not

directly connected with the photoperiodic reaction of the shoot apex and extension growth of the plant. The literature dealing with extension growth and wood formation relatioship in the light of studies on photoperiodic reaction of woody species is reviewed in detail in another paper (in press).

Early and late wood in conifers differs generally by radial diameter and cell wall thickness of tracheids. The present investigations were undertaken to examine the sequence of changes in wood structure during the vegetation season in larch seedlings growing in natural conditions. Changes of radial diameter and of cell wall thickness of tracheids were investigated and extension growth of shoots was observed.

MATERIAL AND METHODS

For the investigations in 1957, 3-years-old plants of *Larix decidua* Mill. were taken grown on an experimental plot near the Agricultural College S.G.G.W. in Warsaw. Plants were harvested at monthly intervals from May till November and twice in winter on December 23, 1957 and February 10, 1958. Each time 5 plants were taken for anatomical examination and about 5 cm pieces of the basal part of stems were fixed in 90 per cent ethyl alcohol. Transversal sections were cut with a sliding microtome, stained with safranin and light green and mounted in Canada balsam as permanent preparations. The method already described by Wight (1933) has later been used by Wareing.

For the investigations in 1958, 2-years-old plants of *Larix polonica* Rac. were used, grown in the nursey of S.G.G.W. Experimental Forests in Rogów *. Plants were harvested at 1 and 2 week intervals from August to December 1958 and once on January 24, 1959. Each time, for anatomical examination 20 plants were taken and placed in ethyl alcohol. The method of preparation was the same as in the previous year with *Larix decidua* plants, except that transversal sections from the basal part of stems were cut by hand.

Measurements of tracheids in each plant were carried out on two sections from the same basal level of the stem. Radial diameter (between two neighbouring tangential middle lamellae) and radial lumen were measured only in the tracheids lying along two lines perpendicular to each other and joinig the pith and cambial zone (thus the measured tracheids were situated along two perpendicular radiuses of the trans-

* Seeds for the plant material were collected from the same trees as these used later in greenhouse experiments.

versal section of the stem). The thickness of cell walls was calculated from these two values, therefore the cell wall thickness of tracheids is given as the thickness of two tangential cell walls of each of the measured tracheids.

The wood formation rate was determined by counting all the tracheids along the examined part of the radius from the cambial zone to late wood already formed in the previous year. Simultaneously with measurements of mature elements of wood, some observations of cells in the cambial zone were carried out which will be described later.

RESULTS

Larix decidua Mill.

114 tracheids were formed in the studied annual wood ring in radial direction during the vegetation season (Table 1). The minimal monthly increment of tracheids was 12 and maximal 28. Measurements of diameter and lumen of tracheids were carried out on the 10 last formed tracheids along each radius. This was done in order not to measure a second time the tracheids which were characteristic for the previous period. For determination of the size of early wood tracheids, in 3 samples 10 tracheids were measured formed as the first wood cells in spring (from late wood of previous year in radial direction). Late wood was characterized by measurements of the 10 last formed tracheids in 3 samples, after the cambial activity had ceased.

Table 1

Number of tracheids in radial direction in stems of European larch seedlings during the third vegetation season 1957 (Averages from 30 measurements)

Samples	Number of tracheids	Increment
May 2. 1957.	0	
		22
June 2. 1957.	22	
		18
July 2. 1957.	40	
		18
August 2. 1957.	58	
		12
September 2. 1957.	70	
		28
October 2. 1957.	98	
		16
November 4. 1957.	114	

From Table 2 it may be seen that the diameter of early wood tracheids was larger only at the beginning of the season and then gradually decreased. The diameter of tracheids of late wood decreased significantly at the very end of wood ring formation.

Table 2

European larch seedlings. Radial diameter of 10 successive tracheids of early and late wood in microns

Successive tracheids from previous year late wood	Early wood				Successive tracheids from cambium	Late wood			
	Samples			Average		Samples			Average
	I	II	III			I	II	III	
1	24.9	18.6	22.8	22.1	10	18.9	17.3	18.8	18.4
2	28.0	22.4	25.3	25.3	9	19.2	17.5	19.1	18.6
3	27.7	22.8	26.3	25.6	8	19.2	17.6	19.2	18.7
4	26.1	23.6	27.6	25.8	7	19.2	17.2	18.3	18.3
5	27.2	25.5	25.8	26.1	6	17.7	15.4	17.3	16.8
6	28.2	24.2	25.8	26.1	5	17.1	16.5	17.3	17.0
7	29.0	26.1	25.9	27.0	4	17.4	15.0	16.1	16.2
8	27.4	26.5	26.1	26.7	3	15.9	14.7	15.3	15.3
9	26.9	25.6	25.6	26.1	2	15.3	13.7	13.6	14.2
10	25.9	26.0	23.8	25.2	1	11.9	11.7	11.2	11.6
	F_e 1.2<F_t 1.64*			μ.t 2.1		F_e 0.49<F_t1.64			μ.t 1.1
Average based on 200 measurements	27.1	24.1	25.5	25.6	Average based on 200 measurements	17.2	15.1	16.6	16.5
	μ.t 1.1					μ.t 0.6			

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

Cell wall thickness did not change significantly among 10 radially consecutive tracheids, neither in the region of early wood nor in that of late wood (Table 3). Only the cell wall thicknesses of the first two tracheids in early wood and of the last one of late wood were lower than the others.

From the comparison of the mean diameters of tracheids which were studied in three samples it may be seen that they differ significantly between each other in early as well as in late wood. No such differences could be demonstrated between mean cell wall thicknesses of tracheids of individual samples either in the region of early or late wood (Table 3). However, mean values of diameter, lumen and cell wall thickness of early and late wood tracheids differ much more significantly between themselves (Table 4).

The results in Table 5 and Fig. 1 show changes in the type of wood that was formed during the season. Since the samples were taken at the beginning of each month, the measured tracheids represent the wood formed in the previous one.

Significant increase of cell wall thickness began not earlier than in September (sample Oct. 2). This gradual rise produced a doubled cell

wall thickness of tracheids at the season's end. The diameter of tracheids first slowly decreased in spring and then stabilized. Only the last tracheids of the annual ring of wood were obviously flattened.

Table 3

European larch seedlings. Cell wall thickness of 10 successive tracheids of early and late wood in microns

Early wood					Late wood				
Successive tracheids from previous year late wood	Samples I	II	III	Average	Successive tracheids from cambium	Samples I	II	III	Average
1	3.4	3.4	3.5	3.4	10	7.9	7.7	7.6	7.8
2	3.3	3.3	3.4	3.3	9	8.0	7.8	7.9	7.9
3	3.5	3.7	3.4	3.6	8	7.9	8.0	8.0	7.9
4	3.9	3.6	3.6	3.7	7	8.1	8.0	7.8	8.0
5	3.8	3.8	3.3	3.7	6	8.3	8.1	7.7	8.1
6	3.8	3.8	3.5	3.7	5	7.8	7.9	8.0	7.9
7	3.9	3.9	4.0	3.9	4	7.9	8.0	8.0	7.9
8	3.9	3.8	3.8	3.8	3	8.1	8.1	7.9	8.1
9	4.0	4.0	3.7	3.9	2	8.2	7.7	7.6	7.8
10	3.7	3.9	3.8	3.8	1	7.0	7.2	6.8	7.0
	F_e 0.65 < F_t 1.64			μ.t 0.3		F_e 1.38 < F_t 1.64			μ.t 0.5
Average based on 200 measurements	3.8	3.7	3.6	3.7	Average based on 200 measurements	7.9	7.9	7.7	7.9
	F_e 1.15 < F_t 3.02					F_e 1.7 < F_t 3.02			

Table 4

European larch seedlings. Radial diameter, cell wall thickness andlumen of early and late wood in third year of vegetation 1957 (each average based on 600 measurements) microns

	Early wood	Late wood	μ.t
Radial diameter	25.6	16.5	0.6
Cell wall thickness	3.7	7.8	0.1
Lumen	21.9	8.7	0.5

Table 5

European larch seedlings. Radial diameter and cell wall thickness of 10 last formed tracheids in radial direction in each individual samples during the third vegetation season 1957

Successive tracheids from cambial zone or first 10 tracheids of early wood	Samples													
	First tracheids of early wood		June 2		July 2		Aug. 2		Sept. 2		Oct. 2		Nov. 4	
	t*	d**	t	d	t	d	t	d	t	d	t	d	t	d
10	3.4	24.9	4.0	26.1	4.3	22.3	4.6	20.4	4.3	22.5	4.8	23.7	7.9	18.9
9	3.3	28.0	4.0	25.2	4.1	20.3	4.9	20.4	4.2	23.2	4.9	23.0	8.0	19.2
8	3.5	27.7	4.0	25.8	4.4	22.4	4.5	20.5	4.2	21.6	5.2	22.0	7.9	19.2
7	3.9	26.1	4.1	25.1	4.2	21.9	4.7	21.6	4.2	21.3	5.5	21.4	8.1	19.2
6	3.8	27.2	4.0	24.5	4.5	22.0	4.5	22.0	4.5	23.2	5.4	21.0	8.3	17.7
5	3.8	28.2	3.9	23.0	4.6	19.6	4.2	22.9	4.3	22.0	5.7	19.1	7.8	17.1
4	3.9	29.0	4.1	22.8	4.5	18.5	4.4	21.6	4.2	21.4	5.7	19.6	7.9	17.4
3	3.9	27.4	4.0	22.3	4.7	19.3	4.1	23.4	4.4	21.9	6.2	20.6	8.1	15.9
2	4.0	26.9	4.0	22.2	5.0	19.4	4.3	22.8	4.4	21.6	6.4	19.8	8.2	15.3
1	3.7	25.9	4.0	23.4	4.9	18.8	4.5	22.9	4.5	22.5	6.6	19.9	7.0	11.9
μ.t	for cell wall thickness 0.6								for radial diameter 2.9					
Correlation coefficient	+0.27		+0.18		+0.06		—0.08		+0.12		—0.13		+0.37	
Correlation coefficient for whole season — 0.28														
Average based on 200 measurements μ.t	3.8	27.1	4.0	24.0	4.5	20.5	4.5	21.8	4.3	22.1	5.7	21.0	7.9	17.2
For cell wall thickness					0.2									
For radial diameter of tracheids					0.9									

* t — cell wall thickness of tracheids in microns.
** d — radial diameter of tracheids in microns.

The correlation coefficient for the radial diameter and cell wall thickness of tracheids was quite low in all the samples. The increment of cell wall thickness took place somewhat earlier than the decrease in diameter of tracheids.

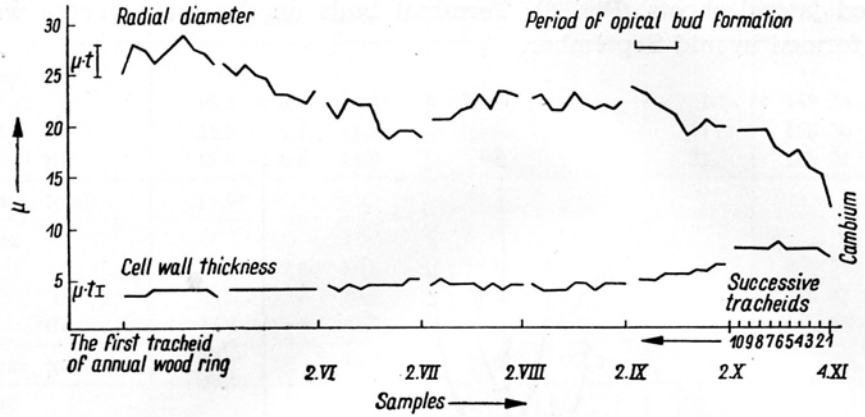


Fig. 1. European larch seedlings. Radial diameter and cell wall thickness of tracheids during the vegetation season 1957

It is interesting, that in samples taken in July and August a certain increase of cell wall thickness and also some decrease of diameter in part of the measured tracheids was observed. In all later studied samples two distinct parallel layers of tracheids were observed with diminished lumen (Fig. 2). This irregularity of wood ring formation may

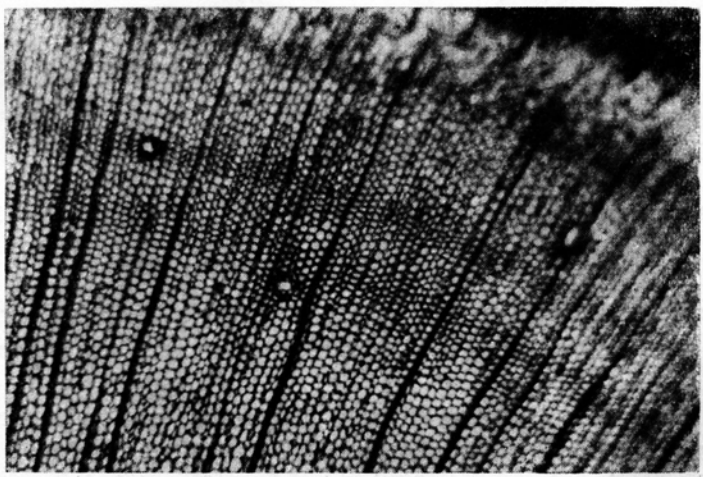


Fig. 2. European larch seedlings. Transversial section of stem at basal level. Two layers of tracheids with smaller lumen are visible

be connected with two periods of drought in the end of May and second decade of June, since other climatic factors did not differ significantly during this time (Table 6).

Resting buds at the end of the lowest lateral shoots had already formed on August and up to September they appeared on ever higher placed lateral shoots (Fig. 3). Terminal buds on the main shoots were last formed in mid September.

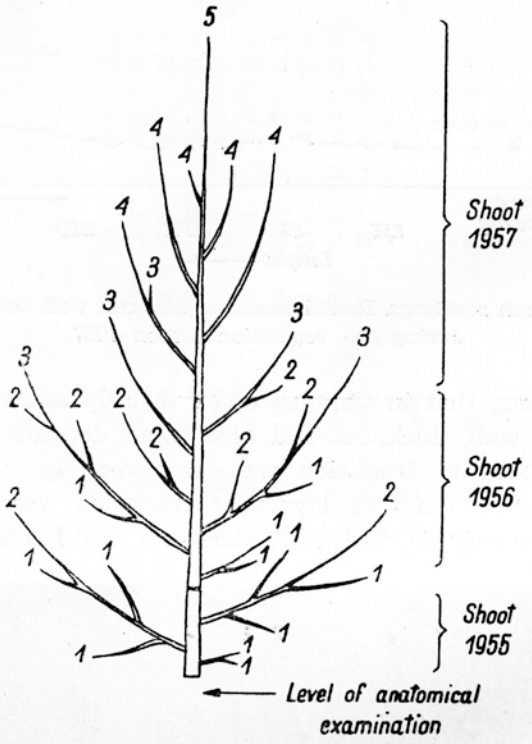


Fig. 3. Relative time of resting bud formation: *1* — earliest; *5* — latest

Simultaneously with measurements of mature tracheids some observations in the cambial zone (on the side of wood formation) were carried out.

Three layers of cells were distinguished in the cambial zone:

1. Cambium layer (*C*) — flattened, thin walled cambium cells and neighbouring cells where no visible changes of radial diameter (Fig. 4) could as yet be detected.

Table 6

Meteorological data for the southern part of Warsaw city during the vegetation season 1957 (after PIHM*)

Decade	Temperature of air °C averages max.	min.	mean	Rainfall mm	sky overcast	day	Length of day (from sunrise to sunset)
May							
I	10.1	3.5	6.5	38.6		1	14h 54 min.
II	21.9	9.7	15.8	0.6		11	15h 30 ,,
III	15.6	6.8	11.0	2.5		21	16h 01 ,,
mean, total	15.9	6.7	11.2	41.7	6.0		
June							
I	22.3	12.5	17.4	18.8		1	16h 24 ,,
II	26.2	13.0	19.8	0.1		11	16h 42 ,,
III	23.8	12.9	17.8	9.3		21	16h 48 ,,
mean, total	24.4	12.8	18.3	27.9	4.7		
July							
I	28.2	15.4	21.3	19.2		1	16h 42 ,,
II	24.3	16.0	19.7	39.5		11	16h 24 ,,
III	21.2	14.3	18.6	28.8		21	16h 03 ,,
mean, total	24.5	15.0	19.2	87.5	6.4		
August							
I	23.3	13.1	17.6	28.3		1	15h 31 ,,
II	24.3	14.6	18.6	27.9		11	14h 57 ,,
III	18.6	10.1	13.7	37.0		21	14h 24 ,,
mean, total	21.9	12.6	16.5	93.2	5.7		
September							
I	21.1	11.1	15.3	5.4		1	13h 47 ,,
II	16.0	8.6	11.5	23.1		11	12h 56 ,,
III	12.9	6.3	9.0	37.4		21	12h 17 ,,
mean, total	16.7	8.7	12.0	65.9	6.7		
October							
I	12.7	4.1	8.0	5.2		1	11h 37 ,,
II	14.7	6.4	10.0	1.1		11	10h 57 ,,
III	12.6	5.8	8.9	2.8		21	10h 18 ,,
mean, total	13.3	5.4	9.0	9.1	6.7		
November							
I	13.9	6.7	9.8	0.6		1	9h 36 ,,
II	3.9	—5.7	1.2	0.0		11	9h 00 ,,
III	5.2	—3.6	1.9	25.4		21	8h 29 ,,
mean, total	7.7	0.9	4.3	26.0	7.8		

* State Hydro-Meteorological Institute.

2. Layer of radial diameter growth (*G*) — thin walled cells with wide lumen, in which visible thickening or lingnification of cell walls could not be detected.

3. Differentiation* layer (*D*) — full grown cells, visible thickening and partial lignification of cell walls. Presence of protoplasm still observed in these cells.

Results of observations in the cambial zone are presented in Table 7:

1. At the beginning of wood ring formation (May 2, Fig. 5) there was a preponderance of cambial cells in the whole cambial zone.

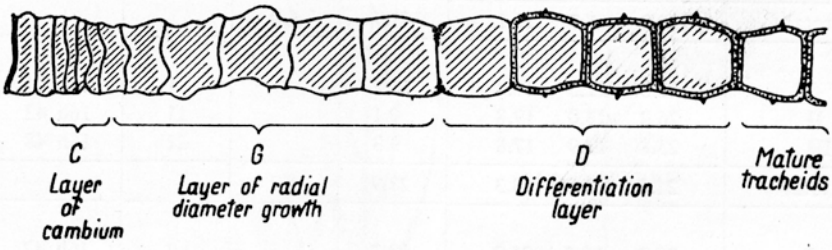


Fig. 4. Cambial zone

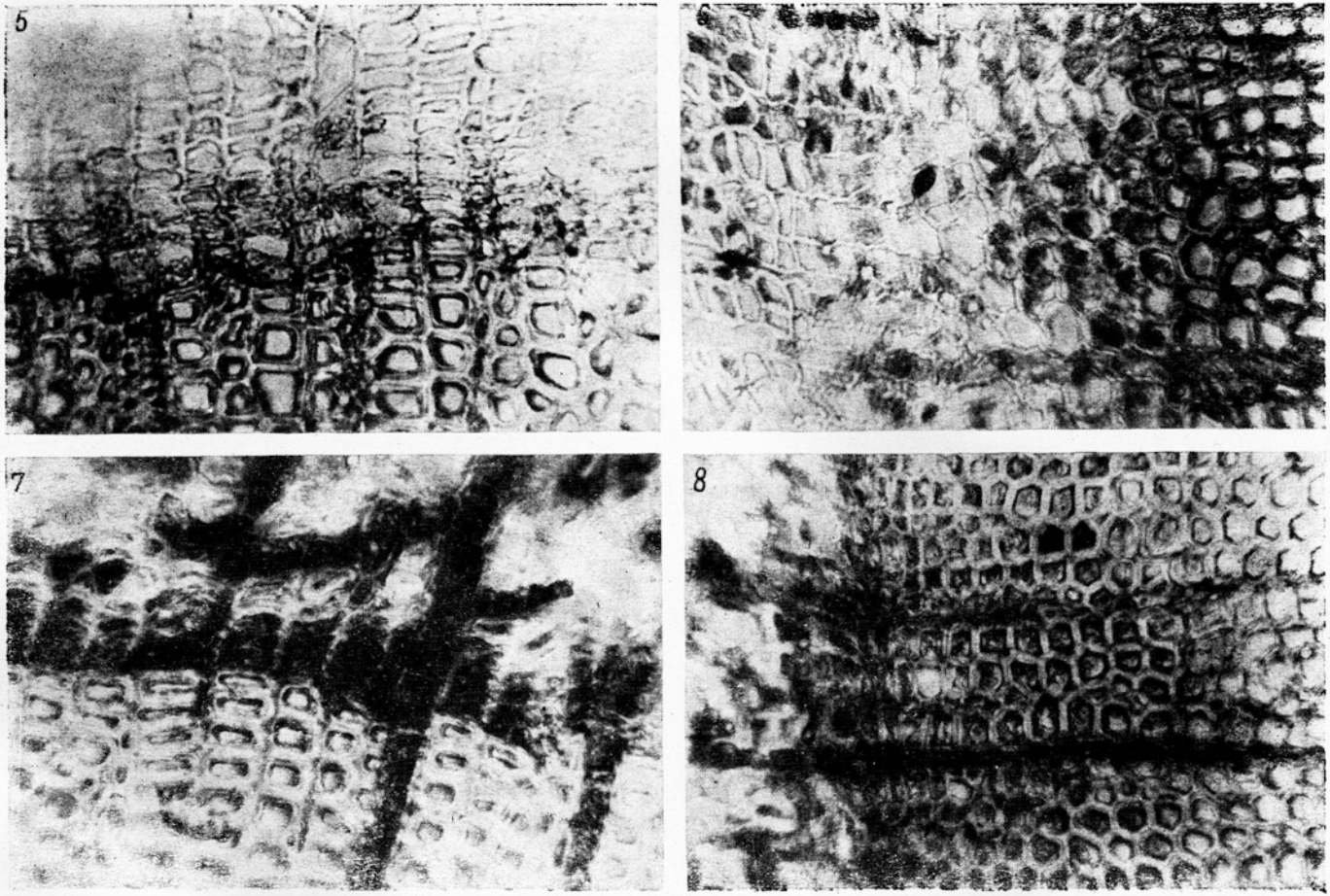
Table 7

European larch seedlings. Number of cells in particular layers of cambial zone during the vegetation season 1957

Samples	Number of cells (averages from 5 plants)			
	C	G	D	total
May 2. 1957.	7.3±0.3	3.3±0.5	0.4±0.2	11.0±0.7
June 2. 1957.	3.9±0.2	6.0±0.3	3.6±0.1	13.5±0.4
July 2. 1957.	3.7±0.2	4.9±0.3	3.4±0.2	12.0±0.5
August 2. 1957.	3.2±0.2	5.5±0.4	3.6±0.2	12.2±0.6
September 2. 1957.	3.0±0.1	6.2±0.6	4.8±0.4	14.0±1.0
October 2. 1957.	2.5±0.2	3.0±0.4	10.8±1.0	16.3±1.1
November 4. 1957.	5.3±0.2	0.0	0.0	5.3±0.2
December 23. 1957.	5.0±0.2	0.0	0.0	5.0±0.2

2. The total number of living cells in the cambial zone seems to be approximately constant during the summer months. Thus, it seems probable that the rate of cambial divisions in this period is almost proportional to the increment of fully differentiated tracheids. Simul-

* The term „differentiation" is mostly used in the present paper to denote processes bringing about cell wall thickening.



European larch seedlings. Transversial sections of the cambial zone in different time of vegetation season 1957

Fig. 5. May 2; Fig. 6. June 2; Fig. 7. November 4; Fig. 8. October 2

taneously, the mutual ratio of individual layers (distinguished above) proved to be similar during summer months. The situation in the cambial zone in June may be seen on Fig. 6.

At the end of the season (Oct. 2, Fig. 8) significant increase of the number of cells in the whole cambial zone, generally due to a nearly threefold increment of cell number in the differentiation layer, was observed. The number of cells in the radial diameter growth layer simultaneously decreased considerably.

4. In the first days of November (Fig. 7) the cambial cells adherring closely to the mature tracheids of summer wood could only be distinguished. Radial walls of the cambial cells were thickened and the general pattern of the cambium was similar to that observed during winter dormancy.

Table 8

European larch seedlings. Number of cells in the cambial zone and increment of tracheids during vegetation season 1957 (averages from 5 plants)

Samples	Period	Number of cells in cambial zone	Difference in cell number of cambial zone	Increment of tracheids	$\frac{3}{4+5}$
1	2	3	4	5	6
May 2		11.0			
	May 2 — June 2		+2.5	22	$\frac{13.5}{24.5}=0.6$
June 2		13.5			
	June 2 — July 2		—1.5	18	$\frac{12.0}{16.5}=0.7$
July 2		12.0			
	July 2 — Aug. 2		+0.3	18	$\frac{12.3}{18.3}=0.7$
Aug. 2		12.3			
	Aug. 2 — Sept. 2		+1.7	28	$\frac{14.0}{29.7}=0.5$
Sept. 2		14.0			
	Sept. 2 — Oct. 2		+2.3	12	$\frac{16.3}{14.3}=1.1$
Oct. 2		16.3			
	Oct. 2 — Nov. 4		—11.0	16	$\frac{5.3}{5.0}=1.1$
Nov. 4		5.3			

On basis of observations on the width of the cambial zone and of the number of cells formed in monthly intervals an attempt was undertaken to compare the length of cell life from the moment of division to the end of full differentiation. The visible lack of protoplasm in cells nearest to the cambial zone was adopted as criterion of cessation of the differentiation process. The ratio of the cell number in the cambial zone

to the total number of tracheids formed during the studied period plus the difference in the number of living cells, may be treated as a kind of indicator of the length of cell life in the cambial zone, since it is believed that it indicates, what part of the examined period, each cell spent in the cambial zone.

The dates in Table 8 show that towards the end of the vegetation season cell life was longer. It has been previously pointed out that the differentiation layer in this period was wider. Thus it is probable that the major part of the life of cells in the cambial zone in autumn, falls in the period of thickening and lignification of the cell walls.

Larix polonica R a c.

Further investigations were carried out with seedlings of *Larix polonica* R a c., only at the end of the vegetation season. Owing to the shorter period of studies, more plants could be taken under observation and a greater precision of results was achieved.

For determining the kind of wood that was formed, the 4 last tracheids in radial direction were measured. In this way, mean values of cell wall thickness and radial diameter of tracheids were calculated

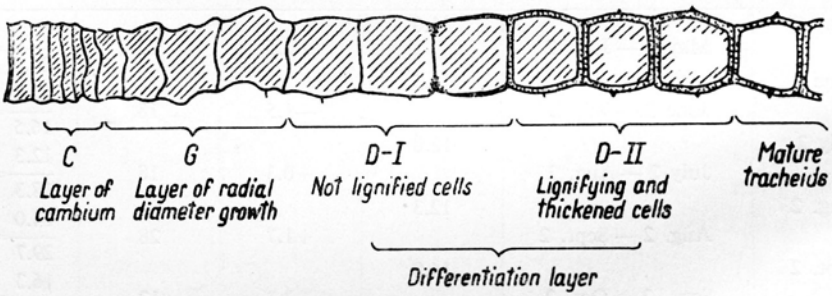


Fig. 9. Cambial zone

on the basis of 320 measurements in each sample. Samples were taken more frequently and measurements in some cases might have partly regarded tracheids that had already been formed in the previous period. Simultaneously, the 4 first tracheids of early wood in radial direction were measured at all sections of all samples, for control and comparison.

As before, fully differentiated tracheids and cells in the cambial zone (in radial direction) were counted. On the basis of more detailed

Table 9

Polish larch seedlings. Number of cells and characterization of wood elements in the last part of the vegetation season 1958

Samples	Cambial zone (number of cells)										Number of mature tracheids	Total: mature tracheides+ (G)+(D)	Tracheids		
	Number of examined radiuses	Layer		Total (C)+ (G)	Number of examined radiuses	Layer of differentiation (D)			Total layers (G)+ (D)	Entire cambial zone			cell wall thicknesses		diameter
		Cambium (C)	Rad. diam. growth (G)			D—I	D—II	D—I+ D—II					Wood actually formed	Early wood	Wood actually formed
4.VIII.1958	46	3.7	4.0	7.7	80	2.2	2.0	4.2	8.2	11.9	16.9	25.1	3.3	3.2	13.6
1.IX. 1958	48	3.7	3.8	7.5	80	2.7	2.9	5.6	9.4	13.1	26.0	35.4	3.6	3.3	14.2
29.IX. 1958	58	4.1	3.6	7.7	80	3.3	3.9	7.2	10.8	14.9	31.6	42.2	4.1	3.3	14.9
13.X. 1958	65	4.4	2.5	6.9	80	3.0	4.4	7.4	9.9	14.3	36.7	46.6	4.2	3.3	14.7
20.X. 1958	65	4.5	1.9	6.4	80	3.1	4.4	7.5	9.4	13.9	38.6	48.0	4.2	3.3	16.3
27.X. 1958	76	5.3	1.6	6.9	80	2.7	6.1	8.8	10.4	15.7	44.1	54.5	4.5	3.2	15.1
3.XI. 1958	80	4.4	0.5	4.9	80	2.3	5.7	8.0	8.5	12.9	48.3	56.8	4.6	3.3	14.7
10.XI. 1958	80	4.5	0.4	4.9	80	0.4	4.7	5.1	5.5	10.0	49.4	54.9	5.2	3.4	14.2
24.XI. 1958	80	5.1	0.2	5.3	80	0.3	1.8	2.1	2.3	7.4	53.8	56.1	4.8	3.5	13.7
1.XII. 1958	80	4.9	0.3	5.2	80	0.2	1.3	1.5	1.8	6.7	56.4	58.2	4.9	3.3	14.1
24.I. 1959	80	4.6	0.2	4.8	80	0.0	0.1	0.1	0.3	4.9	55.3	55.6	5.0	3.5	12.8
		μ.t 0.3—0.4					μ.t 0.4	μ.t 0.5					μ.t 0.1	3.35 mean value of 3520 measurements	

* In each plant 4 perpendicular radiuses were examined, except those of the first samples where some parts of the cambial zone were destroyed by preparation (when the shoot is growing actively the cambial zone is still very delicate).

observations, certain modifications were introduced in the division of the cambial zone established in 1957. A layer of cambium (*C*) was distinguished, a layer of radial diameter growth (*G*), as previously, and moreover, the layer of differentiation was divided into two parts: the unlignified, thin-walled cells (*D-I*) and lignifying cells with visible thickening of cell walls (*D-II*) (Fig. 9).

Cells in the layer of radial diameter growth could be easily distinguished from the next layer of differentiation, due to their very thin and soft walls which were nearly always creased by preparation. There exists a distinct boundary in the cambial zone where the cells adjoining the radial diameter growth layer are stiff walled, though these walls are not thickened yet. It may thus be supposed that these are the cells which just ended the radial diameter growth *.

Investigations were carried on from August 4 till the end of the season. The first buds on main shoots appeared somewhere about September 15, at the end of September all seedlings had formed resting buds but the colour of bud scales changed until the middle of October and higher parts of the main shoots remained not fully lignified for the next 3-4 weeks.

Results of measurements are shown in Table 9. It is seen that during the part of the vegetation season under consideration and during winter rest, the number of cells in the cambium layer was generally the same (4-5 cells). In the radial diameter growth layer, however, since mid October (13—20.X.) the number of cells diminished and at the beginning of November they practically disappeared. Thus, the cambial zone at this time consisted only of a cambium layer and a layer of tracheid differentiation (Fig. 10). The number of cells in the differentiation layer gradually increased from the beginning of September. Maximal width of this layer was reached in October and then gradually decreased. This increment of the number of cells in the differentiation layer was generally due to a more than twofold increment of cells whose walls were thickening and lignifying. The total width of the cambial zone was also greater at this time, but simultaneosly a decrease of the number of cells in the radial diameter growth layer was observed so this total increment was small.

The number of fully differentiated tracheids increased in radial direction approximately at a uniform rate until the end of the studied

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* The cells of the differentiation layer could be distinguished from fully differentiated tracheids due to the lack of protoplasm in the latter. The staining method used in these examinations proved very useful for these observations.

part of the vegetation season. However, the total increase of fully differentiated tracheids and cells in the cambial zone (without the cambium layer), was visibly arrested at the end of October (Fig. 11). This period may be considered as the time of cessation of cambial

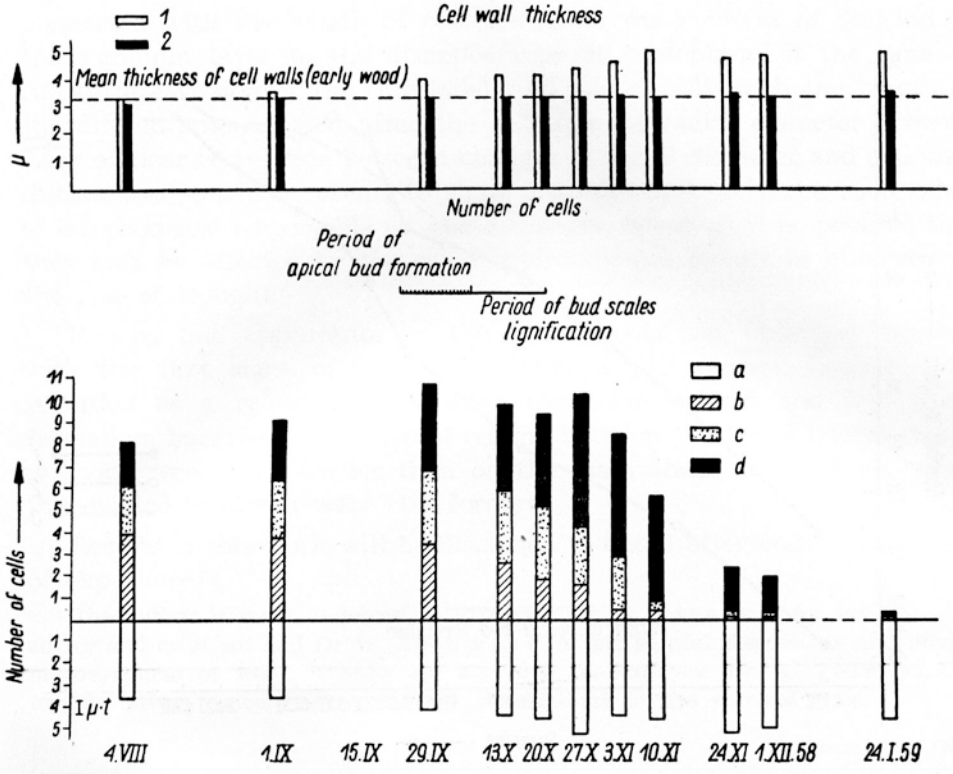

Fig. 10. Polish larch seeedlings. Changes of the cell number in cambial zone and increase of the cell wall thickness in the end of vegetation season 1958; *1* — wood actually formed; *2* — early wood; *a* — (C) layer of cambium; *b* — (G) layer of radial diameter growth; *c* — (D—I) and *d* — (D—II) layer of differentiation

activity (cambial cells division). Therefore the increment of mature tracheids observed later might only be connected with gradual protoplasm dissappearance in the earlier formed cells.

Cessation of differentiation of the last layer cells in the cambial zone on the side of wood formation was observed at the beginnig of December. Thus, it may be supposed that the period of life of these last

cells in the annual ring (from the time of division until full differentiation of the tracheid) lasted about one month or some more.

No thick-walled tracheids were observed on August 4. A small increase of cell wall thickness was noted on September 1, but still it was not significantly higher than in tracheids of spring wood (Fig. 10). During the next few weeks the cell wall thickness of newly formed

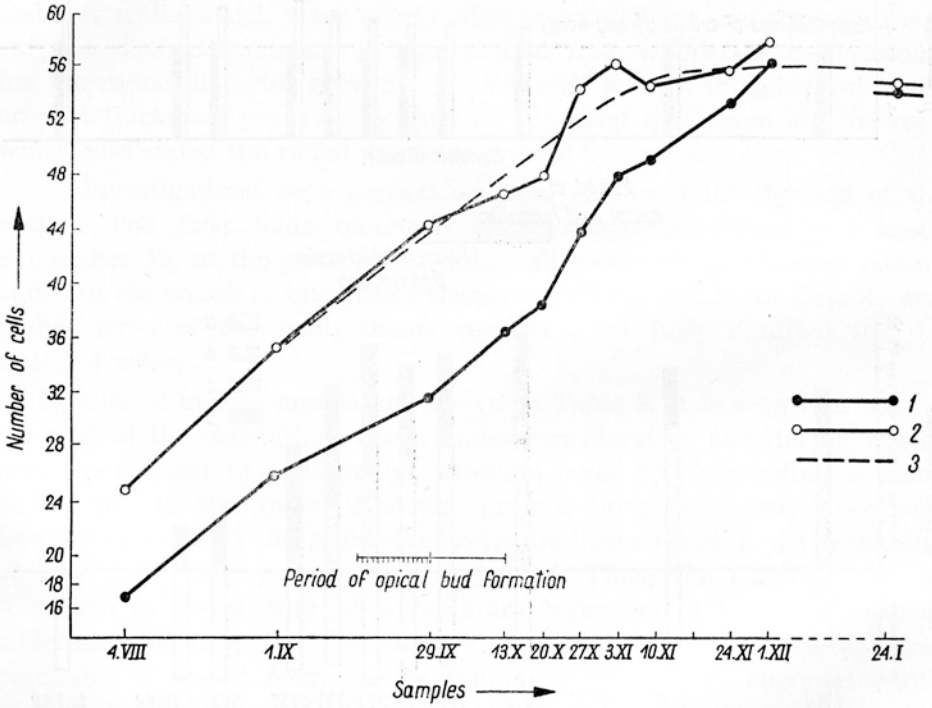

Fig. 11. Polish larch seedlings. Increase of total number of tracheids and cells of cambial zone in the end of vegetation season 1958: *1* — mature tracheids; *2* — mature tracheids plus cells in cambial zone (without the layer of cambium); *3* — mean

tracheids gradually but visibly rose till November and finally was stabilized. Thus, a clear correlation between the width of the tracheidal differentiation layer of the cambial zone and cell wall thickness of tracheids was observed as in the previous year.

Radial diameter of tracheids during the investigated part of the season was generally constant and only the last few tracheids were visibly flattened.

SUMMARY

On basis of studies on wood ring differentiation in 2- and 3-years-old larch grown in natural conditions it was observed that cell wall thickness of tracheids is correlated with the width of the tracheid differentiation layer of the cambial zone. It may be supposed that this process is connected with the length of cell life (from the moment of division in the cambium layer to the disappearance of protoplasm at the time of full differentiation of the tracheids), and particularly with the length of the diferentiation period after the cessation of radial diameter growth. Lack of clear correlation between changes of radial diameter and cell wall thickness of tracheids seems to show a greater independence each other of the processes responsible for these changes, however, it is, possible that they may be affected by the same environmental factors as observed in the case of drought.

Resting bud appearance on the main shoots was observed together with the first signs of late wood formation, it cannot, howewer, be regarded as a relationship between extension growth and late wood formation, because appearance of resting buds on the lower lateral shoots was observed much earlier than on the main shoot at the time, when thin-walled tracheids were still forming.

Results of this work will be discussed in detail after ending the series of experiments.

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Department of Plant Physiology,
Agricultural College SGGW
Warsaw

REFERENCES

Molski B., Żelawski W., 1958, Wstępne badania anatomiczne procesu kształtowania się drewna późnego w słoju rocznym u siewek modrzewia *(Larix europaea* D. C.) w związku z warunkami długości oświetlenia dzienego. Acta Soc. Bot. Pol. 27 (1): 83—102.

Nitsch J. P., 1957, Photoperiodism in woody plants, Proc. Am. Horst. Sci. 70: 526—544.

Priestley J. H., Scott L. I., 1936 A note upon summer wood production in the tree, Proc. Leeds Phil. and Lit. Soc. Sci. Sec. 3: 235—248.

Wareing P. F., 1948, Photoperiodism in woody species, Forestry 22 (2): 211—221.

Wareing P. F., 1951, Growth studies in woody species. III Further photoperiodic effect in *Pinus silvestris*, Physiologia Plantarum 4 (1): 546—561.

Wareing P. F., 1956, Photoperiodism in woody plants, Ann. Rev. of Plant Physiology 7: 191—214.

Wareing P. F., Roberts D. L., 1956, Photoperiodic control of cambial activity in *Robinia pseudacacia* L. The New Phytologist 55: 356—366.

Wight W., 1933 Radial growth of the xylem and starch reserves of *Pinus silvestris*, a preliminary survey, The New Phyt. 32: 77—96.

Wodzicki T., 1961, Związek między wzrostem na wysokość i tworzeniem się drewna w świetle badań nad reakcją fotoperiodyczną drzew, Wiadomości Botaniczne (in press).

Żelawski W., 1956, Badania rocznej rytmiki rozwojowej rośliny drzewiastej ze szczególnym uwzględnieniem reakcji fotoperiodycznej siewek modrzewia europejskiego, Acta Soc. Bot. Pol. 25 (2): 245—274.

Żelawski W., 1957, Dalsze badania reakcji fotoperiodycznej siewek modrzewia (*Larix europaea* D. C.), Acta Soc. Bot. Pol. 26 (1): 80—103.

Żelawski W., Wodzicki T., 1960, Różnicowanie się słoja drewna u siewek *Picea excelsa* Lk. w związku z rytmiką dziennego oświetlenia, Folia Forestalia Pol. 2, ser. A 113—121.