Investigation on the kind of *Larix polonica* R a c. wood formed under various photoperiodic conditions

III. Effect of decapitation and ringing on the wood formation and cambial activity

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As shown in an earlier publication (W o d z i c k i 1961a) photoperiodic conditions may influence not only the extension growth of *Larix polonica* seedlings but also the type of wood and activity of cambium. Thick-walled tracheids were formed after 20 short photoperiods, just after the resting bud was formed at the top of shoot. It was demonstrated, however, that the processes bringing about thickening of cell walls of tracheids are not connected with the photoperiodic reaction of shoot apex but dependent on the photoperiodic treatment affecting full grown needles.

Cessation of cambial activity under influence of short photoperiods was observed between 30 and 40 days after the beginning of treatment. Contrary to the observations made on *Robina pseudacacia* (W a r e i n g, R o b e r t s 1956) it may be supposed that the cessation of cambial activity in larch seedlings is connected with the photoperiodic reaction of shoot apex.

The relationship between the activtiy of cambium and the activity of shoot apex was studied by many authors (P r i e s t l e y 1930, P r i e s t l e y, S c o t t 1936, S ö d i n g 1936, M ü n c h 1938, G o u w e n t a k, M a a s 1940, G o u w e n t a k 1941, W a r e i n g 1951 and others). Yet, a clear effect of shoot apex activity on the cambial activity was observed only in the initial stage of the latter. It is not clear yet whether there exists any continuous influence of shoot apex on the cambial activity beyond the period of initiation.

This paper comprises the results of research on larch seedlings with reference to this problem, and to the correlation between the kind of wood formed and the activity of shoot apex.

METHODS

Decapitated seedlings and one-year old ringed plants of *Larix polonica* R a c. were investigated. Prior to, or after decapitation or ringing they were submitted to short photoperiods or continuous illumination. The experiments were carried out in a greenhouse, at the beginning of 1959 with incandescent light, 1300 to 1500 lux at night. Detailed data concerning illumination, temperature and air moisture in the grenhouse have already been described by Ż e l a w s k i (1957) and W o d z i c k i (1961a). Short day treatment (12 hrs. night) was obtained by putting out the light on one side of the greenhouse and drawing the light-proof courtains. Control series of intact plants were exposed to continuous illumination during the whole time of experiment.

For anatomical examination, transversal sections of stems were cut by hand, stained with safranin and light green and than mounted in Canada balsam for permanent preparations. Cell wall thickness and radial diameter of tracheids were measured and the number of new formed tracheids in radial direction was determined. The method of anatomical examination was similar to that used previously (W o d z i c k i 1960, 1961a).

Tops of the plants if necessary were cut off together with four to five growing young needles. Thus after decapitation, fully developed needles remained on the plants and possibly one to three upper needles only had completed their growth. A few days after decapitation an enlarged lateral bud-initials in angles of needles appeared. All these buds were being removed every day at the early stage of development. Thus, one to four buds were removed from each decapitated plant, mostly during the first days after decapitation.

One-year old plants were ringed by removing two strips of bark and phloem 1.5 to 2.0 mm wide around the stem in two places 1 to 1.5 cm distant from each other.

The rings were made at 4 — 6 cm below the top of the previous year shoot.

There was one well developed, lateral shoot between the two rings. After the operation, the rings were covered with lanolin.

RESULTS

1. *Influence of Decapitation*

After 60 days of growth under continuous illumination seedlings were divided into four series. Two series of plants were decapitated. One series of decapitated and one of intact plants remained under continuous illumination. The other two

series were submitted to short photoperiods. After 20 consecutive days, short day treated intact plants were further divided into three series. One of them was decapitated and transferred back to continuous illumination together with one series of intact plants (see diagram fig. 1.).
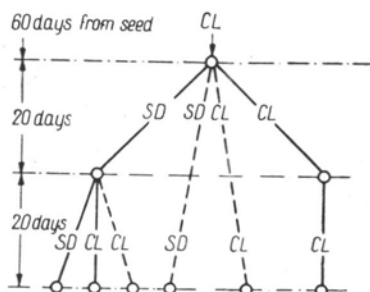

Fig. 1. Diagram of the experiment with decapitated larch seedlings: ————— intact plants; — — — — decapitated plants *CL* — continuous illumination *SD* — short day; —. o.— plants harvested for anatomical examination

Plants were harvested for anatomical examination before the first decapitation, the next time after 20 days (only the control intact plants) and finally after 40 days from all series of plants.

The radial diameter and cell wall thickness of four or six last, fully differentiated tracheids in radial direction along four radiuses (at right angles to one another), were measured. Moreover, along these radiuses, all mature tracheids and living cells in cambial zone were counted.

After 18 to 20 short photoperiods the intact plants formed resting buds. When the plants were subsequently submitted to continuous illumination a visible swelling of the buds was observed. After 40 short days the bud-scales were well lignified and tightly adhered. Intact plants under continuous illumination grew uninterruptedly till the end of the experiment.

The number of tracheids formed after 40 days in decapitated plants was significantly lower than in intact plants, regardless of photoperiodic conditions (Table 1). Cambium of the decapitated plants was dormant. The number of tracheids in these plants increased, but it was not greater than the total number of tracheids and living cells in the cambial zone before decapitation. A fewer number of tracheids has also been observed in intact plants after 20 short photoperiods, however, the absence of differentiating cells in cambial zone (dormant cambium) was observed after 40 short days. The cell wall thickness of tracheids of decapitated plants exposed to continuous illumination was the same as in the control, intact plants. The cell walls of the last two tracheids formed in plants which after decapitation were submitted to short photoperiods, were thicker than of the tracheids formed earlier. They were of the same thickness as in the intact plants under short photoperiods.

Table 1

Influence of decapitation on wood formation in Polish larch seedlings in various photoperiods. Plants grown under continuous illumination before decapitation

(Mean values based on 28 measurements)

Series and period of examination	Number of cells along the radius		Successive tracheids from cambial zone							
	tracheids fully differentiated	tracheids plus living cells in cambial zone **	cell wall thickness (microns)				radial diameter of tracheids (microns)			
			4	3	2	1	4	3	2	1
At the beginning of experiment	7.2	9.7								
During the experiment										
A. Intact plants										
after 20 days of continuous illumination	10.0	12.5								
after 40 days of cont. illum.	13.5	16.0	2.9	2.9	2.9	2.9	9.8	9.8	10.0	9.7
after 20 short photoperiods	8.9	10.4								
after 40 short photoperiods	10.9	10.9	2.9	3.6	4.3	4.4	9.8	9.9	8.9	8.1
B. Decapitated plants										
after 40 days of cont. illum.	9.3	9.3	2.7	3.0	2.9	2.9	9.9	9.6	8.3	8.6
after 40 short photoperiods	9.8	9.8	2.7	3.0	4.1	4.4	9.6	9.2	8.7	8.0
μ.t	0.7*		0.3				0.9			

* Statistical computations by Snedecor's method, t-test at 5 percent level.
** Without cells of cambial initials layer.

Table 2

Influence of decapitation on wood formed in Polish larch seedlings in various photoperiods. Plants treated with 20 short photoperiods before decapitation

(Mean values based on 28 measurements)

Series and period of examination	Number of cells along the radius		Successive tracheids from cambial zone												
	tracheids fully differentiated	tracheids plus living cells in cambial zone	cell wall thickness						radial diameter of tracheids						
			6	5	4	3	2	1	6	5	4	3	2	1
Before short photoperiod treatment	7.2	9.7												
At the end of experiment														
A. Intact plants	11.5	13.0	3.1	3.5	4.3	4.8	4.6	3.9	9.5	9.1	8.7	8.6	7.6	8.4
B. Decapitated plants	10.4	10.4	2.9	.9	3.1	4.2	5.0	4.7	9.8	9.5	9.9	9.6	8.9	8.3
μ.t	0.8		0.4						0.8					

The mean radial diameter of the last two tracheids of decapitated plants under continuous illumination as well as under short photoperiods was lower than in the tracheids formed earlier and in all intact plants exposed to continuous light. A simillar decrease of the radial diameter of the last tracheids was also observed in intact plants under short day conditions.

It is noteworthy that an essential increase of cell wall thickness in intact plants under short day conditions was ascertained in the third tracheid counting from the cambial zone. A decrease of the radial diameter was first observed in the second tracheid.

Fewer tracheids and the absence of differentiating cells in the cambial zone was observed when the plants were decapitated after 20 short photoperiods (Table 2). Thickwalled tracheids with a smaller radial diameter than in the control plants were also formed.

The cell wall thickness of the last tracheid in intact plants which after 20 short photoperiods were returned to continuous illumination, was smaller than that of earlier formed. The cell wall thickness of last tracheid in decapitated plants remained the same as of the preceding tracheids.

The results show that the removal of the shoot apex together with growing young needles caused the cessation of cambial activity regardless of photoperiodic conditions. The numerical increase of tracheids after decapitation may be due to the completion of the differentiation process in earlier formed cells in cambial zone. Short photoperiods may also induce the cessation of cambial activity and the formation of thick--walled tracheids. These results substantiate earlier observations (Wodzicki 1961a), that the influence of daylength on thick-walled tracheid formation did not depend on the photoperiodic reaction of the shoot apex, and further suggest that the process of radial growth of cells in cambial zone was connected with activity of shoot apex.

2. Influence of stem ringing

In order to verify the results obtained with seedlings, further experiments were carried out with one-year old plants by the ringing of stems. This method made it possible to observe the formation of tracheids above the ring influenced by the shoot apex, and under the ring with the growing lateral shoots being below the examined section. Thus, the plant was simultaneously a proper control in itself, which is of great importance considering the variability of the tracheids number in the investigated plants.

The plants grew 82 days under continuous illumination except for one series consisting of 14 plants which during the last 20 days of this period were exposed to short photoperiods. Seven short photoperiod-treated plants and seven plants under continuous illumination were then double-ringed in the above mentioned manner. During the next 20 days all plants were exposed to continuous illumination and then harvested for anatomical examination.

There were, on the average, 14 lateral shoots on each individual plant; usually, either the fifth or sixth or seventh shoot (as from the top of the plant) was situated between the rings (fig. 2). All apical and lateral shoots of the plants under continuous illumination were still growing.

Fig. 2. Double-ringed stem of one-year old larch plant 20 days after the beginning of experiment

Plants exposed to short photoperiods formed resting buds. These buds at the shoots below the ring began to grow at the end of the following period of continuous light treatment, but those above the upper ring only substantially swelled.

The mean number of tracheids running in the radial direction (from the cambial zone to the late wood of previous year) was determined on 20 symetrically situated radiuses in each transversal section of stem in order to eliminate the side effects of irregularites of the stem on the result of experiment.

The natural change in the number of tracheids along the stem was determined by the examination of intact plants grown under continuous illumination at distances of 1 cm, 3.5 cm, 5.2 — 5.5 cm below the base of the new formed main shoot and at 0.5 cm below the cotyledonary node (fig. 3). On the basis of these data it was established that the number of tracheids in the upper part of stem increased basipetally, on the average, 0.5 to 0.6 per 1 cm (Table 3).

The ringed plants were examined at the following height of stem: 1 cm below the base of the new formed main shoot, 1 mm, 1 cm, and 2 cm above the upper ring, 2 mm below the upper and 2 mm below the lower

ring. It was established that the increase of tracheids in these plants per 1 cm downwards the stem was not greater than 0.7 in the following interval: 1 cm below the base of new formed main shoot — 1 cm above the upper ring (Table 3). In the interval 1 cm — 1 mm above the ring, there was an average increase of 5 tracheids down the stem. It may be inferred, therefore, that the significant direct influence of ringing on the numerical increase of tracheids did not extend further than 1 cm above
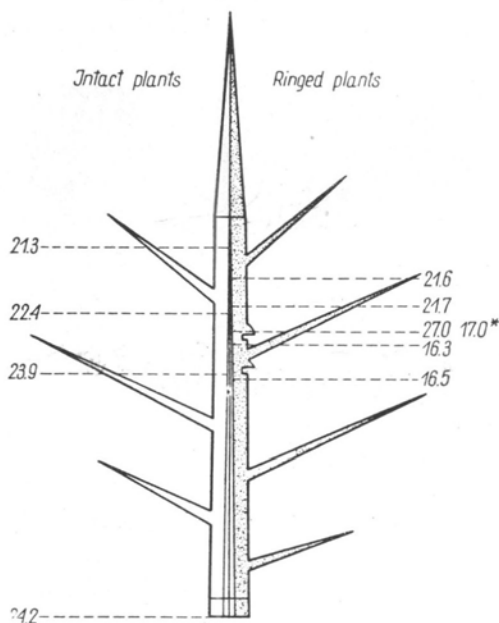

Fig. 3. Number of tracheids at different levels of the stem of intact and ringed plants. (Mean values from seven plants)

  * Number of tracheids between the previous year late wood and a circular belt of wide resin canals.

the ring. In order to make certain that the examined section above the ring was situated beyond the swelling caused by the proximity of the ring, the number of tracheids in the sections below rings was compared with the number at a height of 2 cm above the upper ring.

The results are specified in Table 4 and in fig. 3. There were on the average five tracheids less under both the rings than above the upper ring. A circular belt of wide resin canals (fig. 4 and 7) was observed in the section 1 mm above the ring (cutting through the swelling of stem). The number of tracheids between previous year late wood and resin canals was nearly the same as in the sections under the rings (Table 4).

Plate I
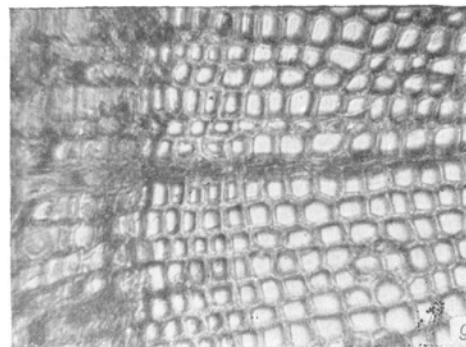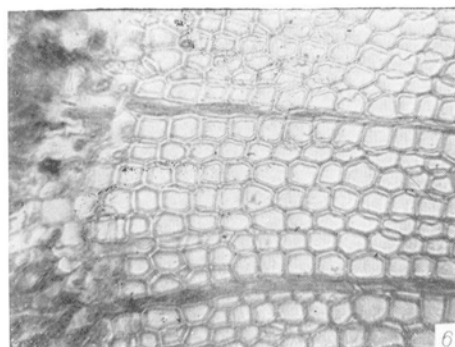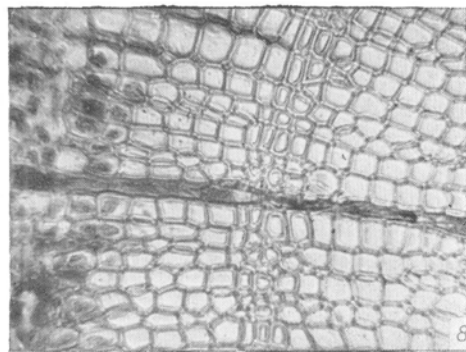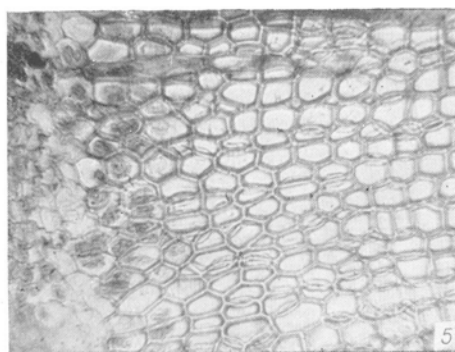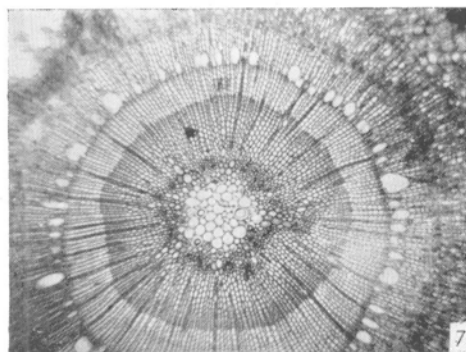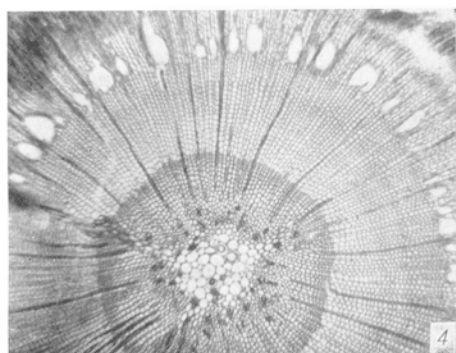
Transversal sections of the stem of one-year old larch plants (Fig. 5, 6, 8, 9, in the same scale)

Fig. 4—6 — Plants under continuous illumination

Fig. 7—9 — Plants under short photoperiods before ringing

Fig. 4, 7 — Sections 1 mm above the upper ring

Fig. 5, 8 — Sections 2 cm above the upper ring

Fig. 6, 9 — Sections 2 mm below the lower ring

Table 3

Downward increment of tracheids in the upper part of stem of plants grown under continuous illumination. (Mean values counted per 1 cm of length of the stem from 7 plants)

Intact plants		Ringed plants	
interval:		interval:	
1 to 3.5 cm	1 to 5.5 cm	1 cm below the base of new formed main shoot to 1 cm above the upper ring	1 mm to 1 cm above upper ring
below the base of new formed main shoot			
0.5	0.6	0.7	5.0

$\mu \cdot t$ 0.5

Table 4

Polish larch plants grown under continuous illumination. Number of tracheids in radial direction at different level of stem of the ringed plants (Mean values from 20 radiuses)

Plants	Number of tracheids at the level:			Difference between number of tracheids above and below		Number of tracheids at the level 1 mm above the ring	
	2 cm above the ring	2 mm below the upper ring	2 mm below the lower ring	upper ring	lower ring	from cambial zone to the previous year wood	from the wide resin canals to the previous year wood
1	20.0	17.6	19.9	2.4	0.1	26.1	19.1
2	19.7	16.1	17.2	3.6	2.5	22.4	17.6
3	26.1	18.0	17.3	8.1	8.8	29.8	17.8
4	18.5	12.0	11.4	6.5	7.1	22.8	12.9
5	25.6	21.6	20.7	4.0	4.9	30.4	21.9
6	15.8	11.3	10.5	4.5	5.3	21.7	11.2
7	25.7	17.5	18.6	8.2	7.1	35.1	18.9
Mean	21.6	16.3	16.5	5.3	5.1	26.9	17.0

The cell wall thickness of tracheids above and below the rings of plants under continuous illumination was the same (fig. 5. and 6). Plants which were submitted to 20 short photoperiods before the ringing, formed thick-walled tracheids above and beneath the ring (fig. 8 and 9), but new thin-walled tracheids were formed only above the ring. The layer of thick-walled tracheids was situated just below the wide resin canals, (fig. 7).

The results give ground for regarding the severed connection with the upper part of stem through cambium and phloem as the cause of

cessation of cambial cell division, regardless of photoperiodic conditions. This was also confirmed by a comparison of the mean number of tracheids beneath the rings and the mean number of tracheids between previous year late wood and the circular belt of wide resin canals. This last number is a reliable indication of how many tracheids were formed along each radius just before of ringing.

As in the experiments with decapitated seedlings the influence of photoperiods on the thickening of cell walls was observed. No effect of the ringing on cell wall thickness of tracheids was found.

DISCUSSION

The experiments have proved that the cessation of cambial activity may be induced by decapitation of seedlings or the ringing of older plants as well as short photoperiods after the formation of resting bud. These facts lead to the conclusion that the influence of height growth on cambial activity extends beyond the stage of initiation at the beginnig of the vegetation season (in young Polish larch plants) and continues when the cambium is still active. Therefore, it may be assumed that cessation of the division of cambial cells in the autumn might be also due to the completion of primary meristem activity.

The possible influence of shoot apex activity on cambial activity has already been noted by Priestley and Scott (1936). These authors suggest that in trees in which the extension growth is completed early in summer further activity of shoot apex (under the bud scales *) may affect the activity of cambium.

It is possible that in some deciduous trees activity of cambium may be affected also by the reaction of full grown leaves to photoperiodic conditions, irrespective of the extension growth (investigation on *Robinia pseudacacia* carried out by Wareing and Roberts, 1956). This possibility has not been confirmed, however, in the case of *Larix polonica*. Wareing and Roberts suggested that the leaves under long photoperiods produce more auxins affecting cambial activity. On the basis of many investigations (reviewed by Wareing 1951, 1958, Wodzicki 1961b) it has been assumed that the influence of developing buds on the initiation of cambial cell division depends on the supply of the growth substances to the cambium. It is also known that a growing shoot apex and growing young leaves are a rich source of auxins which are basipetally transported (Went, Thimann 1937). Decapitation or separation by a ring of these parts of plant body caused the cessation of

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* This activity leads to formation of next year shoot inititials in bud.

cambial activity. The cessation occured in spite of the presence of growing lateral shoots under the ring beneath the examined place on the stem. It may be inferred from these facts that the cessation of cell division was due to the cutting off the supply of growth substances. Consequently, these substances produced by active primary meristems, and growing leaves would be required for the s t i m u l a t i o n of cell division in cambium during the whole period of vegetatin.

This supposition should not necessary be considered contradictory to S ö d i n g' s (1952) hypothesis which postulates the possibility of auxin formation in the cambium itself. According to this hypothesis, basipetelly transported growth substances stimulate only the growth of the cambial cells laying just below the shoot apex. These cambial cells would produce a new quantity of growth regulators stimulating other cambial cells laying just below. In this way the cambial activity could be observed for a longer period of time than the activity of shoot apex although in the last instance former is dependent on the latter.

Taking into account even the possibility of the existance of such a mechanism of stimulation of cambial activity as postulated by S ö d i n g, it may be presumed that the rapid cessation of cell division in cambium, observed in decapitated larch seedlings was due to the short distance between the top of shoot and the examined level on the stem.

The experiments also provide some new data concerning the growth and differentiation of cells in the cambial zone. It was found that the thickening of cell walls might be induced by short day treatment regardless of decapitation or ringing. These operations did not cause any thick-walled tracheid formation when plants grew under continuous illumination. The results suggest that the thickening of cell walls in cambial zone did not depend on the extension growth of larch seedlings. This conclusion is in accordance with the data given by M o l s k i and Ż e l a w s k i (1958) that the cell wall thickness of tracheids is not related to the photoperiodic reaction of the shoot apex of *Larix decidua*. It also substantiates the results of other experiments (W o d z i c k i 1961a) which revealed that the thickening of cell walls in the cambial zone depends on the photoperiodic treatment of full grown needles.

As shown by earlier experiments, thick-walled tracheid formation in greenhouse was observed not earlier than after 20 short photoperiods, after the resting bud has alreedy been formed. In natural conditions, thick- walled tracheids were also formed after the resting bud formation (W o d z i c k i 1960).

All these facts lead to the supposition that thickwalled tracheid formation in larch growing under natural conditions (connected with late wood formation) is controlled by photoperiodic conditions at the end of

the vegetation season, regardless of photoperiodically controlled cessation of extension growth.

A correlation between the thickness of cell walls of tracheids and the width of the differentiation layer of the cambial zone was observed in natural conditions (experiments cited above). The thickness of cell walls was greater when the differentiation layer was wider at the end of the vegetation season. The enlargement of the differentiation layer immediately preceded the appearance of thick-walled tracheids. As this change of width of the differentiation layer required some time, it seems probable that the delay in the formation of thick-walled tracheids under the influence of short photoperiods, observed in greenhouse, was also connected with the incidence of similar changes in the cambial zone. The nature of these changes is not known yet, but possibly there is a relationship between the length of life of differentiating cells in the cambial zone and the thickness of cell wall of tracheids.

The experiments with decapitated and ringed larch plants growing under continuous illumination have also shown that these operations caused a decrease of the radial diameter of tracheids. This fact confirms an earlier assumption that the radial growth of cells after their division in cambium, may be affected by the shoot apex.

The existence of the shoot apex influence upon the radial growth of young cells in the cambial zone, the absence of an influence of shoot apex on the thickening of cell walls, the possible formation of thin-walled tracheids with diminished radial diameters and the absence of a clear marked correlation between the cell wall thickness and the radial diameter of tracheids (W o d z i c k i 1960) — all these facts lead to the assumption that there is no direct dependence between the radial growth and the thickening of cell walls in the cambial zone. Nevertheless, the two processes may be affected by the same photoperiodic factor. Owing to this fact, the research on the processes leading to early and late wood formation is rather difficult.

Although the above mentioned physiological processes may be only discussed indirectly on the basis of the present experiments, the results cannot be explained by any known hypothesis concerning early and late wood formation (O p p e n h e i m e r 1945), W e r e i n g 1958). According-ing to O p p e n h e i m e r's hypothesis, late wood is probably formed under conditions of a limited supply of auxins and a large supply of products of assimilation to the cambium. It may be presumed that such conditions occured both in experiments with decapitated and ringed plants growing under continuous illumination as well as in earlier experiments with only the top of the shoot covered (W o d z i c k i 1961a). None of the plants used in the experiments formed thick-walled tracheids,

although there was a decrease of the radial diameters. This absence of thick-walled tracheids in such conditions cannot be sufficiently explained also by the auxin hypothesis of W a r e i n g (1958).

The fact that the cell wall thickness of tracheids below the upper ring was affected only by photoperiodic conditions regardless of the presence of a well developed lateral shoot between the rings, may possibly point to the absence of direct dependence between the supply of assimilation products and of thick-walled tracheid formation. Preasumably the outflow of assimilates from this shoot to other parts of plants was cut off or considerably limited by two rings (above and below the shoot within the distance of a few milimeters). Therefore, cambium in the sector of the stem neighbouring on this lateral shoot may possibly be supplied better in the products of assimilation. According to O p p e n h e i m e r's and earlier, P r i e s t l e y's (1930) hypothesis, in such conditions late wood (consequently, thick-walled tracheids too) would be formed, but this was not found to be in the case with ringed larch growing under continuous illumination. This argumentation may be accepted with some reservations only, becouse the influence of the ringing on the distribution of products of photosynthesis in the examined part of stem is not known. All these facts, however, point to the necessity of further research on the processes bringing about the annual wood ring differentiation.

In the case of larch seedlings it seems that the radial diameter of tracheids and the duration of cambial activity are related to the activity of primary meristem, and thereby are affected also by photoperiods. The cell wall thickness of tracheids, although affected by photoperiods too, does not depend on the extension growth of the shoot. Finally, it should be recalled that the appearance of thick-walled tracheids also under conditions of water deficit (W o d z i c k i 1960), shows that the role of external factors in this process may be more complex.

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SUMMARY

The influence of extension growth on the cambial activity and wood formation in seedlings and one-year old plants of *Larix polonica* R a c. was studied.

The investigations were conducted with decapitated seedlings and ringed plants. Cambial activity in all the decapitated plants ceased, irrespective of photoperiodic conditions. The cessation of cambial activity was also observed 2 mm below a ring made round the stem although under the examined section of the stem, there were growing lateral shoots. Thick-walled tracheids with smaller radial diameter were

formed as a result of short photoperiod treatment regardless of decapitation or ringing. On the other hand decapitation or ringing did not induce formation of thick-walled tracheids in plants under continuous illumination.

The results of experiments and some data concerning previous investigation of the problem were discussed.

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