On the photoperiodic control of extension growth and wood formation in Norway spruce (*Picea abies* (L.) Karst.)

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Investigations on the photoperiodic control of growth and annual ring differentiation of larch and spruce seedlings showed that under short day conditions, extension growth was inhibited and thick-walled tracheids were formed (Żelawski 1956, Żelawski, Wodzicki 1960). In further experiments with larch (Wodzicki 1961a) both appearance of terminal buds and first full differentiated thick-walled tracheids were observed after about 20 short photoperiods. In spite of this correlation, investigation with low intensity light treatment during 12 night hours showed that thick-walled tracheids formation in larch seedlings was probably not dependent on the cessation of extension growth (Żelawski 1957, Molski, Żelawski 1958, Wodzicki 1961a).

Moreover, it was observed in 1-year old larch that if only the top of main shoot was covered (short–day treatment) and all other aerial part of plant subjected to continuous illumination, only the thin-walled tracheids were formed both in plants with lateral shoots decapitated or intact (Wodzicki 1961a). These experiments seem to provide further evidence of the absence of direct connection between photoperiodically controlled processes of extension growth and the thickening of cell walls of tracheids in larch. The conclusion is of great importance for the study of the mechanism of annual ring differentiation in larch and should be further investigated in other conifers.

The above mentioned experiments with only the top of main shoot covered also showed that the photoperiodic reaction bringing about the cessation of extension growth and formation of resting bud in larch was limited only to the shoot under short–day treatment since the lateral shoots under continuous light continued to grow. In this case, photoperiodic stimulus inducing the rest was perceived by young, growing needles or by the shoot apex itself and was not transported to lateral shoots.

The scanty experimental data concerning the locus of photoperiodic perception in relation to dormancy mainly refers to some deciduous

species (W a r e i n g 1954, V a n d e r V e e n 1960) but the problem seems to be very interesting in the light of general discussion on the locus of dormancy in trees.

The present paper reports on some additional results of experiments on Norway spruce with reference to two questions:

a) locus of photoperiodic perception in relation to the rest of shoot apex,

b) influence of the photoperiodically controlled extension growth on the kind of wood formed.

METHODS

Three-year old *Picea abies* (L.) K a r s t. plants potted in W a g n e r's pots were used in the investigation carried out in 1961. Prior to the experimental treatment all plants grew 62 days under continuous illumination and then were subjected to one of the following treatments in a room specially adopted to photoperiodic experiments:

a) continuous illumination

b) short-day (12 hours darkness during the night)

c) continuous illumination and only the top of main shoot covered (the top of shoot under short-day treatment)

d) continuous illumination, top of the main shoot covered and lateral shoots decapitated

e) continuous illumination, lateral shoots decapitated.

The first four combinations consisted each of three plants and the fifth of two plants. The top of main shoots were covered with $40 \times 10 \times 36$ mm boxes made of light-proof photographic paper — black on one side and silver on the other — as in earlier experiments with larch (W o d z i c k i 1961a). During the experimental treatment all the newly appearing buds in two decapitated groups of plants were systematically removed at an early stage of development. After the 30 days of experimental treatment all the plants were subjected to continuous illumination for 20 days and then harvested for anatomical examination.

Continuous illumination, about 4500 lux, was provided by the system of white-light fluorescent "TELAM" tubes. The daily temperatures were nearly constant: mean daily maximum — 23.6°C, mean daily minimum — 22.0. The daily air moisture ranged on the average from 67.7 to 77.0%.

For the sake of comparison, the wood of three comparable spruce plants grown in natural conditions in Experimental Forests in Rogów was also examined.

All plants were killed and preserved in ethyl alcohol. Transversal sections from the basal part of plants were cut by hand. The method

of preparation and staining with safranin and light-green was the same as used in the earlier investigations with larch plants growing in natural conditions (W o d z i c k i 1960). Radial diameter and lumen of tracheids were measured in two transversal sections of each examined plant. Thickness of cell walls was calculated as a difference of radial diameter and lumen of tracheids. * Tracheids were measured in the area of newly formed ring of wood along two radiuses perpendicular to each other. Thus, the wood in each of the first four groups of plants (*a b, c, d*) and of plants grown in natural conditions were characterized by 12 rows of figures and the plants of the last group (*e*) by 8 rows. One of the rows of figures obtained from the measurement of tracheids in plant that were submitted to short-day conditions is set below to illustrate the method:

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          21** 21  24  18  19  17  11  15  20  20  22  25  27
cambial zone                                         previous year late wood
          8*** 8   8   8   6   6   6   5   4   3   4   4   4
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(the values are given in micrometer units; one micrometer unit = 0.7 microns)

Wood that had formed during the first period of growth under uniform conditions of uninterrupted illumination was characterized in all groups by the radial diameter and cell-wall thickness of the third, fourth and fifth tracheids counting from the previous year late wood. In plants under short-day treatment, thick-walled tracheids occured in the outer part of newly formed wood. In order to characterize the wood in this zone, the dimensions of the last three tracheids were taken into account. Simultaneously, in all other groups of plants, the mean dimensions of the last three tracheids were considered as characteristic for the wood formed under various experimental treatment.

The early wood of plants from natural conditions was characterized by the radial diameter and cell-wall thickness of the third, fourth, fifth and sixth tracheids as from the boundary of previous year annual ring of wood in radial direction. Late wood was represented by the size of third, fourth, fifth and sixth tracheids as from the cambium after the annual ring formation was completed.

The method of characterizing the wood formed under various experimental conditions on the basis of the average sizes of a few selected tracheids of each zone was applied and tested in earlier experiments with larch and proved most convenient for this kind of investigation (W o d z i c k i 1961a).

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* Cell-wall thickness of each tracheid represents the total thickness of two tangential cell-walls.

** Radial diameter of tracheids.

*** Cell-wall thickness of tracheids.

RESULTS

Extension growth of plants under continuous illumination was continuous except for one short period of cessation of growth which occured at different times in most plants of groups $a, c,$ and e. This inhibition was manifested by the formation of a few light-green, scale-like needles at the top of lateral or main shoots but no resting-buds were formed and, in all cases, the growth was resumed within 2 to 7 days. It is noteworthy, that this temporary depression of growth in some plants did not occur at the same time in different shoots. Such a pattern of intermittent growth was also observed earlier in larch under continuous illumination (Żelawski 1956) and in some other woody species (the literature reviewed by Wareing 1956, Nitsch 1957) and it did not influence much the results of present investigations.

Five of the plants with the top of main shoot covered formed the resting bud after 22—25 days and only one after 29 days. At the very beginning of the period of keeping the top of shoot under cover, the last plant (of group c) had just interrupted its growth, as described above, and in spite of the cover, the main shoot began to grow a few days later. Finally, the growth of this plant stopped and the resting-bud formed but with some delay as compared with the other plants. This observation gives ground for assuming that the reaction of that plant as being similar as of other plants in groups c and d in which the top of main shoot was covered.

Short-day treated plants (group b) formed the resting-buds at the top of main shoot at different times than at the top of the lateral shoots. The buds at the top of lateral shoots situated lower down began to form after 10 to 12 short photoperiods and at the leaders after 21 to 23 short days.

As mentioned above, all the plants were submitted to continuous illumination again for 20 days after the period of experimental treatment. During that time the newly formed initial buds in angles of needles of decapitated plants were not removed and they grew out in the new shoots. Resting-buds at the top of lateral shoots in plants that had been submitted to short photoperiods (group b) began to develop but the buds at top of main shoot of these plants as well as those only with the top of main shoot covered (group c and group d) did not develop within that time.

Anatomical examination showed that only plants subjected to short photoperiods formed thick-walled tracheids differing significantly from cell-wall thickness of all other groups of plants (Table 1). Neither the

Table 1

Cell wall thickness of tracheids formed under various experimental treatment
(in microns)

Experimental treatment	Wood formed at the beginning of experiment	Wood formed under various experimental treatment	$\mu \cdot t_x$
a) Continuous illumination	2.8	3.6	0.4
b) Short day	2.7	5.6	0.4
c) Continuous illumination, only the top of main shoot covered	2.8	3.4	0.3
d) Continuous illumination, the top of main shoot covered and lateral shoots decapitated	2.8	3.3	0.5
e) Continuous illumination, lateral shoots decapitated	2.6	3.4	0.4
$\mu \cdot t_x$	Fe 0.77 F_t 3.44	0.4—0.5	

Statistical computations by Snedecor's method, t-test at 1 percent level.

Table 2

Radial diameter of tracheids formed under various experimental treatment
(in microns)

Experimental treatment	Wood formed at the beginning of experiment	Wood formed under various experimental treatment
a) Continuous illumination	11.6	13.3
b) Short day	12.0	13.0
c) Continuous illumination, only the top of main shoot covered	11.4	12.7
d) Continuous illumination, the top of main shoot covered and lateral shoots decapitated	11.5	11.8
e) Continuous illumination, the lateral shoots decapitated	12,0	13,8
$\mu \cdot t$		1.4—1.6

covering of the top of main shoot, nor decapitation of lateral shoots did induce the formation of thick-walled tracheids. The differences between cell-wall thickness of tracheids of plants in the above conditions and of intact plants throughout under continuous illumination were not significant.

The cell-wall thickness of tracheids formed at the beginning of experiment in those groups (c, d, e) of plants was smaller than that of last formed but the differences were of the same significance as in intact control plants under continuous illumination (group a).

The examination of wood showed the absence of essential differences between the mean radial diameter of tracheids in all groups of plants (Table 2).

The radial diameter of tracheids formed both at the beginning of experiment and under various experimental treatments corresponded to the radial diameter of tracheids of late wood in natural conditions, (Table 3).

Table 3

Cell wall thickness and radial diameter of early and late wood tracheids of plants grown under natural conditions
(in microns)

	Early wood	Late wood	$\mu \cdot t$
Cell-wall thickness	3.0	6.9	0.4
Radial diameter	18.5	12.6	1.5

In the earlier experiments with larch (W o d z i c k i 1961a), however, it was showed that the decapitation, if only of the lateral shoots, caused the decrease of radial diameter of tracheids. This reduction of radial diameter was not associated with any increase of thickness of cell walls of tracheids. For this reason, an additional experiment was made. Three spruce plants, similar to those described above, all the time subjected to continuous light conditions, were completly decapitated. Newly formed initial buds on the shoots of these plants were being removed during the following 20 days. After this period, the appearing buds were allowed to grow again for the next 30 days and they formed new shoots.

The anatomical examination of wood revealed that in all cases, a few layers of tracheids with greatly reduced radial diameter were formed as compared with analogical tracheids of intact plants under continuous illumination (Fig. 1). In this region of wood, it was observed, that 1 to 3 layers of tracheids preserved their protoplasmatic content and the cell
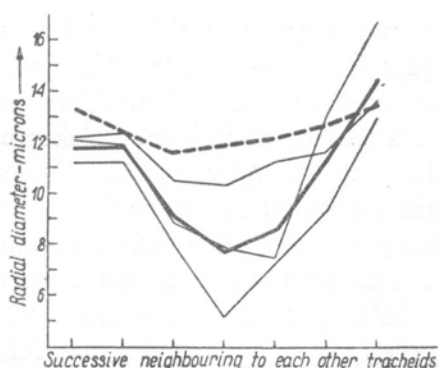
Fig. 1. Effect of complete decapitation of plants on the radial diameter of tracheids.

Continuous lines — successive tracheids in the zone of reduced radial diameter in decapitated plants; dotted line — tracheids in intact plants; heavy lines — denote the mean values of three plants; light lines — the mean values of individual plants
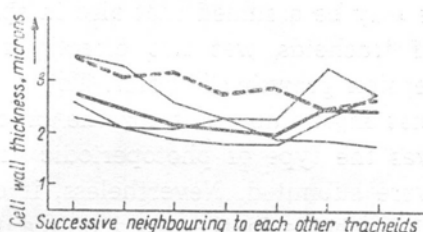
Fig. 2. Effect of complete decapitation of plants on the cell-wall thickness of tracheids.

Continuous lines — successive tracheids in the zone of reduced radial diameter in decapitated plants; dotted line — tracheids in intact plants; heavy lines — denote the mean values of three plants; light lines — the mean values of individual plants

walls of tracheids was somewhat thinner than in intact plants (Fig. 2 and Fig. 3 c, d). The walls of the former were also less stained with safranin, probably owing to the lower degree of lignification.

DISCUSSION

The experiments confirmed the results of previous investigation on the one-year old larch plants. It was demonstrated that the shoot apex of the main shoot may be induced to dormancy with short photoperiods exerting an effect on the young growing needles or the shoot apex itself. Besides, the rest-inducing stimulus arising under short–day treatment was not transferred to other shoots growing under continuous illumination. Thus, the results provide an additional evidence that the individual shoots may be largely independent from each other in respect of extension growth and onset of dormancy. It is noteworthy, that the photoperiodic reaction of shoot apex occured in spruce, as in the earlier experiments with larch, although in each case there were different light and especially different temperature conditions. The experiments with larch were conducted under incandescent light in greenhouse where the diurnal amplitude of temperatures was considerable. As in the case of larch, it was demonstrated that short photoperiods caused the formation of thick-walled tracheids. Neither the cessation of height growth (as

result of placing the top of main shoot under cover combined with re-
moving of all other growing points in plant) nor the temporary complete
decapitation did induce the thick-walled tracheids formation. Therefore,
it may be assumed that also in spruce, the process of cell-wall thickening
of tracheids was not directly related to the termination of the ex-
tension growth of shoots. The experiments provide an indirect evidence
that most important for the process bringing about cell-wall thickening
was the type of photoperiodic treatment to which full grown needles
were submited. Nevertheless, it cannot be discounted that a few layers
of tracheids in the wood of plants completly decapitated were not fully
differentiated (the tracheids which preserved the protoplasm). The walls
of these cells were somewhat thinner and probably the degree of their
lignification was lower than those of the control plants. A similar response
to decapitation was also observed earlier in larch seedlings (W o d z i c k i
unpublished data) and in the study of wood formed after ring barking
in other woody species (literature recently reviewed by W a r d r o p,
B l a n d 1959). These disturbances of the normal wood differentiation
may also, to some extent, be compared to the formation of large resin
ducts after removing a strip of bark and phloem round the stem of 1-year
old larch (W o d z i c k i 1961b) and probably should be regarded as
connected with the mechanical damage rather than with the extension
growth inhibition.

This problem requires, however, a further study, especially taking
into account the results of experiments in which the influence of growth
substances on differentiation and lignification of conducting elements
of wood was evident (J a c o b s 1952, W a r e i n g 1958 and others).

The radial diameter of tracheids formed both at the beginning of
experiment and under the various experimental conditions (except for
complete decapitation) corresponds to the radial diameter of tracheids of
late wood. This means, that the radial diameter of tracheids formed
under continuous illumination was smaller than the radial diameter of
early wood tracheids.

Probably, this can be partially explained by taking into account the
fact that the experimental plants were transplanted into pots shortly
before they were transferred to continuous illumination, while the plants
in natural conditions had been growing for two years at the same site.

Another possibility which does not exclude the first, is that the
process of radial diameter growth of cells in cambial zone was more
affected by the provided temperature conditions which were found less
favourable for growth than the periodic changes of temperature during
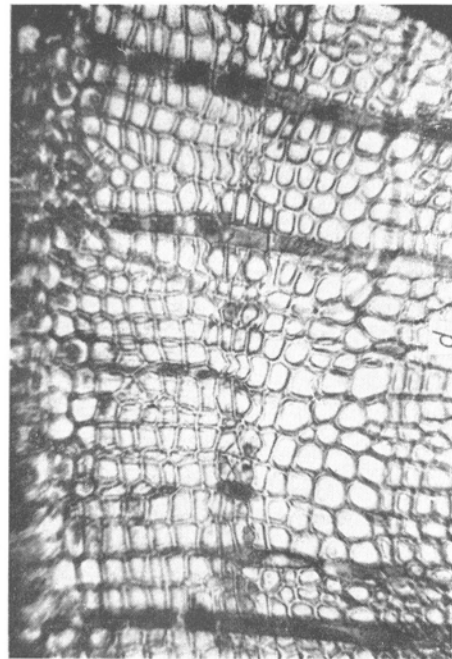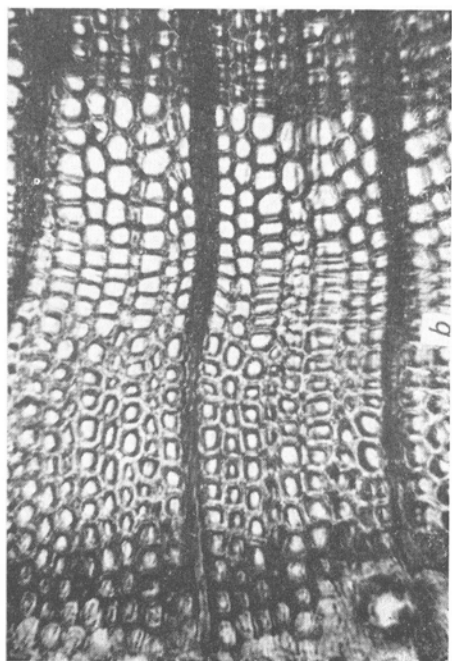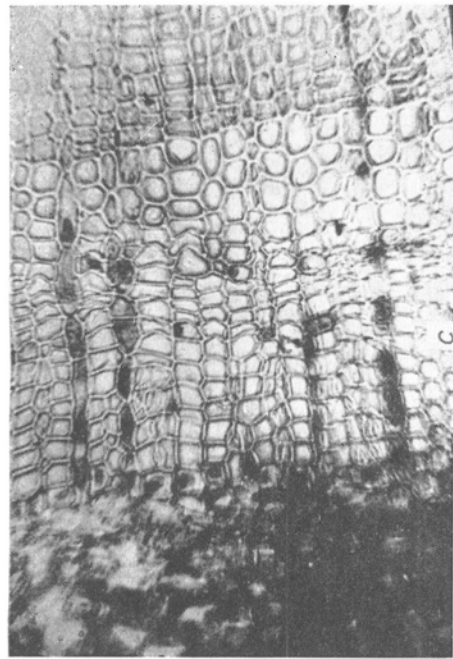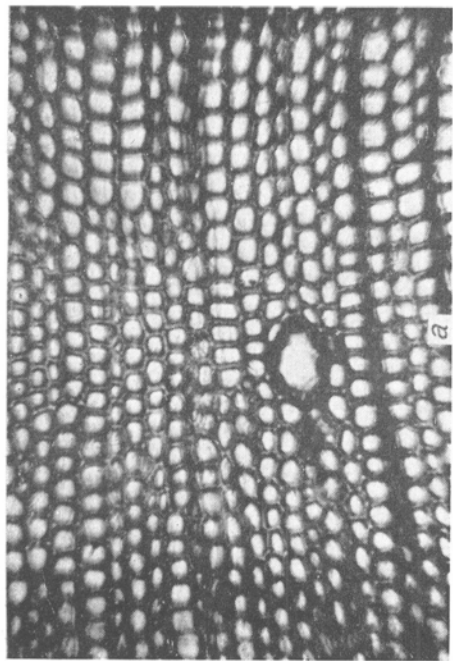the day (K r a m e r 1958).

Fig. 3. *a* — Wood formed under continuous illumination; intact plants, *b* — Wood formed under short day conditions; *c, d* — Wood formed under continuous illumination; decapitated plants

Although, the question cannot be sufficantly clarified on the basis of the present investigation the experiment with completly decapitated plants showed that the process of radial diameter growth of tracheids may be supressed by the removal of all growing apexes. It may be inferred from this observation that there is a dependence of radial diameter growth of tracheids upon the extension growth of shoots as sugested in the earlier experiments with larch.

SUMMARY

Some aspects of the influence of short-day conditions on the height growth and wood formation of 3-year old spruce (*Picea abies* (L.) Karst.) plants were studied. Whole plants or only the top of main shoot were subjected to 12-hours photoperiods. It was shown, as in earlier experiments with larch, that the apex of main shoot may be induced to dormancy separately by placing under cover the apical part of shoot only, during extension growth of all the lateral shoots. Therefore, the type of photoperiodic conditions to which young growing needles or the growth apex itself were submitted was the most important factor affecting extension growth regardless of the photoperiodic treatment to which were subjected other aerial parts of the plant.

The anatomical examination of wood showed that only when the whole plant was influenced by short-day conditions the thick-walled tracheids were formed. Neither the covering of the top of main shoot (even when all lateral shoots were decapitated) nor the full decapitation induced thick-walled tracheids formation. The decapitation of all growing shoots in plants under continuous illumination, however, caused the reduction of radial diameter of tracheids and disturbed their normal differentiation. The results are discussed.

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