# TRACHEID DEVELOPMENT AND WOOD QUALITY IN LARCH SEEDLINGS UNDER CONTROLLED ENVIRONMENT

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Several environmental factors necessary for tree growth undergo rhythmic and sometimes abrupt changes during the course of a year, and even during a day. Since wood cells are susceptible to outside influences during their differentiation, certain fluctuations of environmental conditions invariably leave a permanent imprint on xylem anatomy, and hence significantly influence wood quality. Such features as the width of annual increments, cell length, cell diameter, cell wall thickness, and the development of drought and frost rings are affected by environmental factors to some degree. The effects of environment on xylem differentiation may be either direct or indirect, since xylem differentiation is integrated with other physiological processes in the living tree ( e:g., photosynthesis, respiration, translocation ) which are also subject to environmental influences.

In addition to genetic selection and breeding for desirable wood quality features, the manipulation of environmental factors ( e.g., through irrigation, fertilization, and other silvicultural practices) offers man a limited but nevertheless important tool to influence the anatomy of developing wood cells, and hence wood quality. However, this can only be accomplished successfully if the inter-relationships between wood formation and environment are understood.

The effects of photoperiod on wood formation have been investigated extensively in recent years ( Larson 1960, 1962, 1964; Phillips and Wareing 1958; Nitsch 1963; Wodzicki 1960, 1961, 1964 ). The current consensus is that photoperiodic effects on xylem differentiation are indirect, and are mediated by growth regulating substances. Long photoperiods are associated with intense cambial activity and earlywood differentiation, while short photoperiods favour latewood differentiation and eventual cambial quiescence. Under long days, the synthesis of auxins, gibberellins, and auxin synergists, which are generally regarded as growth promoters, is at a high level, while the synthesis of growth inhibitors is at a low level. The effect of short days on the metabolism of the above substances, on the other hand, appears to be opposite.

The effects of precipitation and the resulting soil and internal moisture conditions on wood formation have also been studied ( Kennedy 1961; Kramer 1962, 1964; Larson 1963; Zahner 1963; Zahner *et al.* 1964; Edlin 1965; Buckingham 1965 ). Two hypotheses were developed to explain the influence of internal water stress on wood formation at the cellular level. According to the first view, water deficit has a direct effect on xylem development, in that a decreased turgor pressure may reduce the enlargement of differentiating xylem cells. The number of cambial divisions may also be reduced. According to the second view ( Larson 1963 ), the effect of drought on xylem development is indirect. Water deficits first reduce the growth of terminal meristems and leaves which results in decreased auxin synthesis. The decreased auxin supply brings about the differentiation of latewood cells. Kramer ( 1964) and Zahner ( 1963 ) both emphasized that both the direct and indirect effects of water deficits were important in xylem development. The water balance of differentiating xylem cells influenced not only their enlargement but also their metabolism. Furthermore, water deficits reduced photosynthesis, and thereby the supply of carbohydrates. Kennedy and Farrar ( 1965 ) observed that drought caused subnormal lignification in tilted seedlings.

Reports about the influence of temperature on wood formation are relatively few. The available studies nevertheless suggest that temperature plays a very important role in wood formation. Richardson and Dinwoodie ( 1960) found an inverse relationship between cell wall thickness and night temperatures. Tracheid length and lumen diameter, on the other hand, increased with increasing temperatures, either day or night. They suggested that cell wall thickening was a function of net assimilation rate, which apparently dropped with increasing night temperatures.

Many of the aforementioned results were derived from experiments with seedlings because seedlings are easily obtained and subjected to various treatments. Most conclusions concerning basic physiological processes have general validity; however, many investigators caution against broad generalizations and unreserved interpretation of results for forest-grown trees.

This study examines certain effects of two different photoperiods on the initiation of cambial activity and subsequent xylem development in inactive and actively growing eastern larch *( Larix laricina* ( DuRoi ) K. Koch ) seedlings; explores some influences of mild, intermediate, and severe drought conditions on xylem development; and

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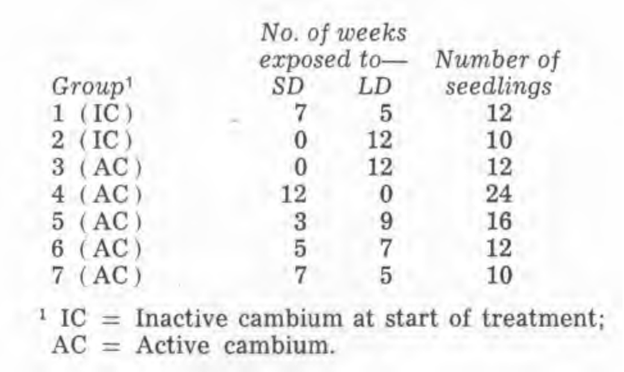
evaluates certain effects of synthetic IAA and TIBA on xylem differentiation under short and long photoperiods, respectively.

## Materials and Methods

Two-year-old nursery transplants of 132 eastern larch seedlings 40 to 60 cm tall and 5 to 8 mm in diameter at stem base were studied. The seedlings were transplanted into individual 500 ml containers, using Perlite rooting medium. The rooting medium was subrrigated with complete nutrient solution three times daily. The investigation was carried out in three phases.

### Photoperiodic Treatments

First, the effects of two photoperiods ( short days and long days) on the initiation of cambial activity and on subsequent xylem differentiation were studied in 96 seedlings. These seedlings were sub-divided into seven groups and exposed to either short days ( SD ), long days ( LD ), or both, for 12 weeks:



| Group[1] | No. of weeks exposed to— SD | LD | Number of seedlings |
|---|---|---|---|
| 1 ( IC ) | 7 | 5 | 12 |
| 2 ( IC ) | 0 | 12 | 10 |
| 3 ( AC ) | 0 | 12 | 12 |
| 4 ( AC ) | 12 | 0 | 24 |
| 5 ( AC ) | 3 | 9 | 16 |
| 6 ( AC ) | 5 | 7 | 12 |
| 7 ( AC ) | 7 | 5 | 10 |

[1] IC = Inactive cambium at start of treatment; AC = Active cambium.

The short photoperiods were provided in a growth chamber regulated for 10-hour day length, 1,500 ft-c light intensity, and temperatures of 25° C day and 15° C night. Long photoperiods were provided in a greenhouse, where sunlight was supplemented with artificial illumination to obtain a 16-hour day length. Temperatures in the greenhouse ranged from 25° to 29° C during the day, and from 15° to 19° C during the night.

The cambia of seedlings in Groups 1 and 2 were inactive ( IC ) at the commencement of photoperiodic treatment. These seedlings had their winter chilling requirements met outdoors. However, the seedlings in Groups 3 to 7 had been actively growing ( AC ) and forming earlywood prior to treatment due to long-day exposures. Thus it was necessary to demarcate the commencement of treatment in these seedlings. All seedlings in Groups 3 to 7 were tilted for 3 days at 60° from the vertical, then put upright for 6 days, and again tilted for 3. This method had been employed by Kennedy and Farrar ( 1965) to produce two compression-wood marker arcs.

During the 12-week photoperiodic treatment the height growth of seedlings was determined at weekly intervals. At the same time the condition of apices, the appearance of needles, and the setting of resting terminal buds were observed.

The sampling schedule is outlined in table 1. From each seedling three stem pieces, approximately 2 cm long, were excised at 2, 10 and 20 cm from the stem base ( lower, middle, and upper stem, respectively ), and aspirated in FAA solution. Transverse sections were cut on a sliding microtome and stained by the safranin-fast green technique. All sections were examined microscopically for the pattern of xylem differentiation that accompanied the photoperiodic treatments. The radial and tangential diameters, and tangential double-wall thicknesses of all tracheids ( matured after the commencement of treatment ) were measured in five typical radial files. These measurements were taken only on sections from the middle stem of the 16 seedlings sampled at the end of 12 weeks. The radial files measured were selected on the basis of maximum tangential diameters to assure that tracheids in the files were cut close to their midlength. The values of tracheid diameters and wall thickness were used to calculate three indices. The cell enlargement index ( CEI ) was defined as the ratio between the radial ( r ) and tangential (t) diameters of the cell ( r/t ). The wall thickness index ( WTI) was defined as the ratio between the tangential double-wall thickness ( 2w ) and the tangential diameter ( t ) of a tracheid ( 2w/t ). The specific gravity index ( SGI ) was defined as the ratio between the tangential double-wall thickness ( 2w ) and the radial diameter ( r ) of a tracheid. Since tangential tracheid diameters vary but little from early- to latewood, the r/t and 2w/t ratios directly express the degree of radial enlargement and wall thickening, respectively. A CEI of 0.90 may be used as an arbitrary boundary between early- and latewood rather than Mork's index, which has been criticized by tree physiologists because it confounds wall thickness and radial lumen diameter, two cell features which may vary independently of one another.

### Drought Treatments

Twenty actively growing, 2-year-old eastern larch seedlings were divided into four groups, with five seedlings in each group, and exposed to different watering conditions for 3 weeks. All seedlings were tilted prior to treatment, in a manner described previously, to induce two compression-wood marker arcs. One group was exposed to "mild" drought ( 200 ml water every 5 days ), another to "intermediate" drought ( 100 ml water every 5 days ), and another to complete drought ( no water ). The controls received normal watering by subirrigation. After a 3-week-long drought exposure, normal watering was resumed for all

*Table 1. — Sampling schedule for the seedlings*

| Group | Sampling time (weeks after commencement of treatment) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | Number of seedlings sampled | | | | | | | | | | | |
| 1 | - | - | 2 | - | 2 | - | 2 | - | 2 | - | - | 4 |
| 2 | - | - | 2 | - | 2 | - | 2 | - | 2 | - | - | 2 |
| 3 | 2 | - | 2 | - | 2 | - | 2 | - | 2 | - | - | 2 |
| 4 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 5 | - | - | - | 2 | 2 | 2 | 2 | 2 | 2 | 2 | - | 2 |
| 6 | - | - | - | - | - | 2 | 2 | 2 | 2 | 2 | - | 2 |
| 7 | - | - | - | - | - | - | - | 2 | 2 | 2 | 2 | 2 |

seedlings, and they were grown for an additional 5 weeks. During the entire 8 weeks the seedlings were in a greenhouse under long ( 16-hour ) days. At the end of 8 weeks three stem pieces were excised from each seedling, sectioned, stained, and evaluated microscopically the same way as the samples from the photoperiodic experiments. The external responses of seedlings were also observed.

### Treatments With IAA and TIBA

Sixteen actively-growing, 2-year-old eastern larch seedlings were divided into four groups, with four seedlings in each. Two groups ( 8 seedlings ) were exposed to short days ( 10-hour ) for 3 weeks to induce latewood formation, while the other two groups were tilted in the earlier described manner to induce two compression-wood marker arcs. One group ( 4 ) of the SD seedlings was treated with IAA, and one group of the LD seedlings was treated with TIBA in the following way. The dead outer bark was removed on a 2-cm portion of the stem of each seedling at a distance 10 cm from the stem base. Three shallow longitudinal blazes were cut into the inner phloem, each at 120° angle from the other, and extending to, but not beyond, the cambium. Immediately after the blazes were cut, the exposed surfaces were sprayed with distilled water. Then a single paper strip ( 3 sq cm ), containing 50 micrograms of IAA or TIBA ( 50 micro-liters of 1000 ppm solution ), was moistened with distilled water and placed over the inner phloem surface. The outer surface and edges were covered with lanolin, which was further covered with a dark masking tape. Controls of both SD and LD groups were also treated but the paper strip did not contain any compound. The SD seedlings remained in the growth chamber, while the LD seedlings were kept in the greenhouse for 3 weeks following treatments. At the end of 3 weeks, three stem pieces 2 cm in length were excised from each seedling, one immediately below the blaze, a second and third at 2 and 4 cm respectively below the blaze. The stem pieces were sectioned, stained, and examined microscopically, as described previously.

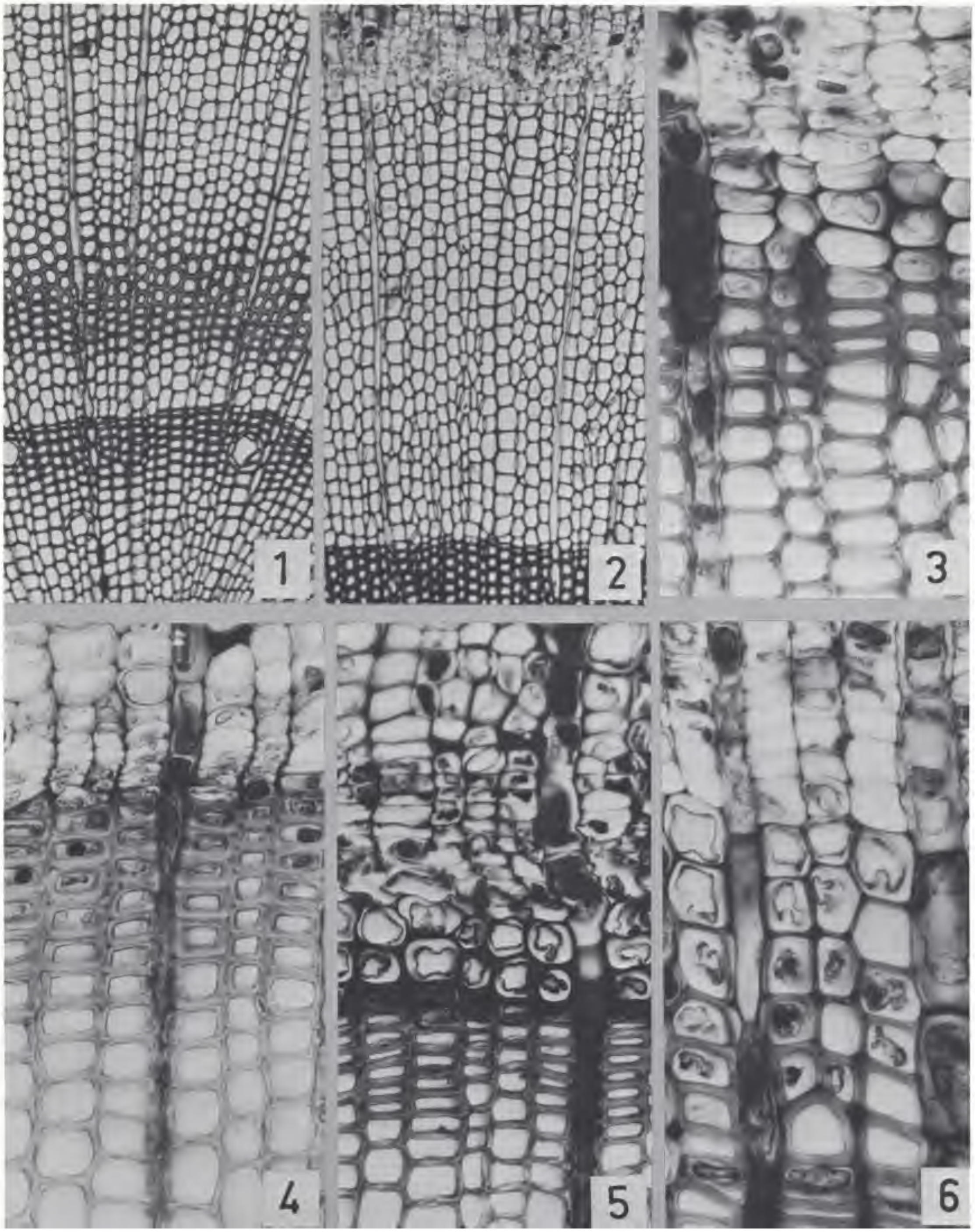
## Results and Discussion

### Photoperiodic Treatments

Growth activity in the buds and cambium of the seedlings in Groups 1 and 2 occurred under both short and long days. The buds of seedlings in Group 1 ( initial SD) began swelling around the twelfth day, whereas those in Group 2 ( LD ) began around the ninth day. The growth of the new needles on the short shoots was nearly completed by the end of the third week in both groups; this coincided with the commencement of long-shoot extension and cell division in the cambial zone. However, by the end of the fifth week the SD seedlings were forming a terminal bud, and their average shoot growth ( 4.6 cm ) was only half that of LD seedlings for the same period. The LD seedlings continued unabated shoot extension growth during the entire 12 weeks.

Swelling of the cambial zone occurred in both Groups 1 and 2 by the third week, indicating that this phase of cambial activity is not a photoperiod-dependent phenomenon, but rather correlated with temperature. Cell division in the cambial zone commenced around the end of the third week, coincidentally with rapid shoot extension, indicating a correlation and dependence of cell division in the cambial zone on endogenous auxins originating in active apical meristems.

The first-matured tracheids had CEI greater than 0.90 ( earlywood ) in the seedlings of both Groups 1 and 2 ( figs. 1 and 2 ). The average CEI of the first 3-4 cells per radial file was 1.09 in both groups ( fig. 7 ). However, the SD seedlings ( Group 1) formed a narrow band of latewood cells ( CEI less than 0.90 ), coincidental to the cessation of shoot extension ( figs. 1 and 7 ). The formation of 3-4 earlywood tracheids per file under short days may seem surprising, but it took place during the short period of shoot extension growth when endogenous auxins were available in sufficient amounts to facilitate earlywood differentiation. The effects of short days only became apparent after the development of the photoreceptive organs ( leaves ).



FIGURES 1 to 6. — The pattern of xylem differentiation and tracheid anatomy in larch seedlings under different photoperiods (IC — inactive cambium, AC — active cambium, at commencement of treatment.

(1) Group 1, IC, 7 weeks SD plus 5 weeks LD, lower stem.
(2) Group 2, IC, 9 weeks LD, lower stem.
(3) Group 4, AC, 3 weeks SD, middle stem.
(4) Group 4, AC, 4 weeks SD, lower stem.
(5) Group 5, AC, 3 weeks SD plus 1 week LD, lower stem.
(6) Group 5, AC, 3 weeks SD plus 2 weeks LD, lower stem.

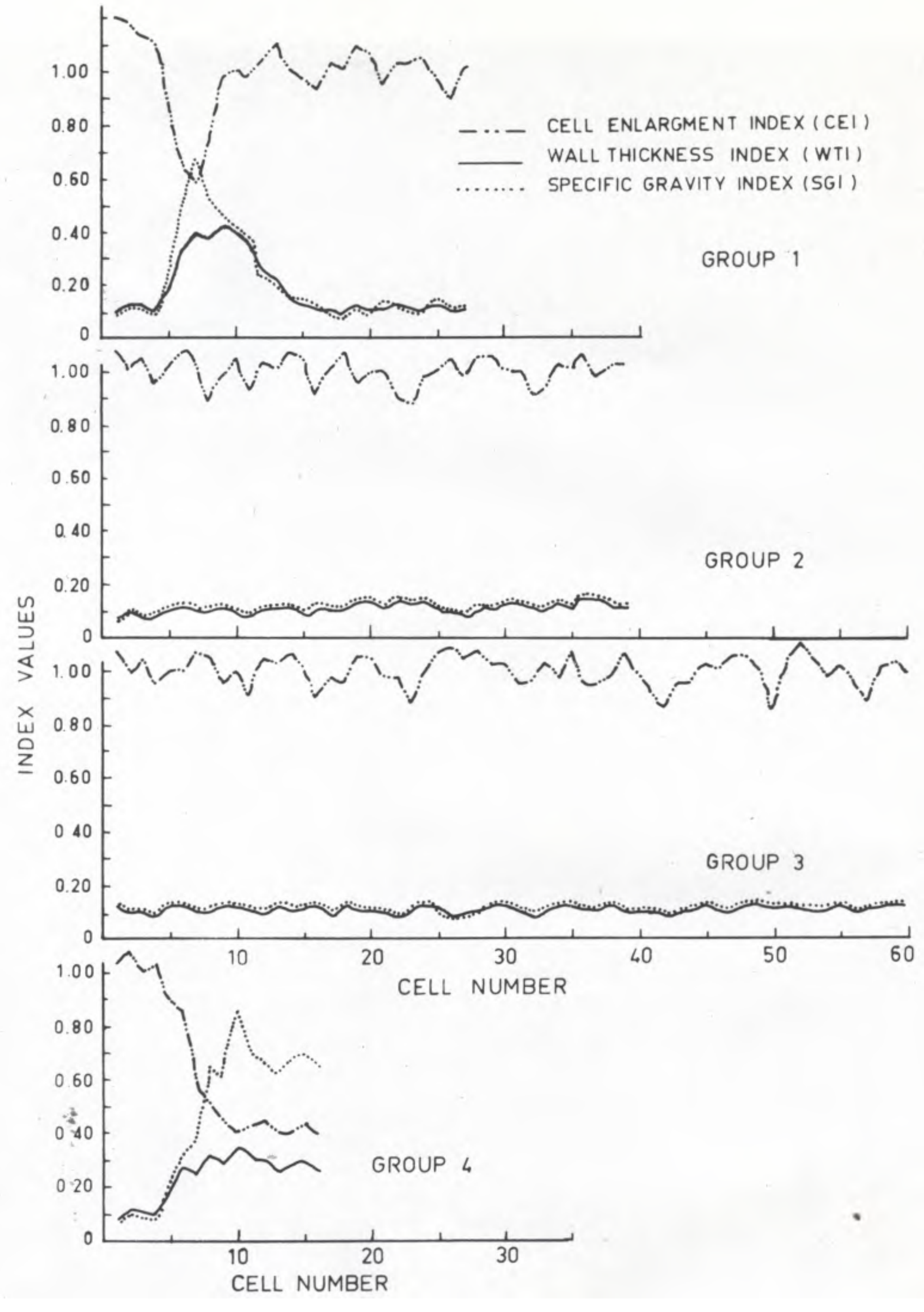


FIGURE 7. — The variation of CEI, WTI, and SGI in the middle stem of seedlings in Groups 1, 2, 3, and 4.

The narrow latewood band ( 3-4 tracheids per file ) in SD seedlings was followed by a band of compression-wood like tracheids ( 4-5 per file ), which apparently formed after the seedlings were transferred to long days at the end of 7 weeks ( fig. 1 ). The formation of this compression wood band was an interesting physiological development. We offer the following explanation. The SD treatment lowered endogenous auxin levels in the seedlings, which was fairly abruptly increased after the seedlings were transferred to long days. Thus the relative increase of auxin facilitated the development of compression wood. Compression wood development ceased to continue because the cambium and differentiating cells became "accustomed" to the change.

The actively growing seedlings of Groups 3 to 7 also showed some interesting responses to the photoperiodic treatments. The LD control seedlings ( Group 3) continued height growth during the entire 12 weeks. The seedlings in the other groups, which were exposed to various periods of SD treatment, showed reduced extension growth after the second week, and were forming resting terminal buds by the end of the third week of short photoperiod.

The seedlings in Groups 5, 6, and 7 were transferred to long days at the end of the third, fifth, and seventh Weeks, respectively. The inactive buds in Group 5 began flushing within the first 2 weeks of LD treatment, whereas those in Group 6 began during the third and in Group 7 during the fourth week of LD treatment. The seedlings in Groups 5 and 6 kept their old foliage; however, those in Group 7 lost most of their needles prior to transfer.

The periodic samplings of two seedlings during the treatment, and of two seedlings at the conclusion of treatment ( table 1) allowed the assessment of the progress and possible changes in xylem differentiation. In Group 3, earlywood differentiation continued during the entire 12 weeks. There were 73 fully mature tracheids per file in these seedlings, and only minor variations occurred in CEI, WTI, and SGI of tracheids in the radial files ( fig. 7 ). In Group 4 ( SD controls ), there were only 16 mature tracheids per file at the end of 12 weeks; 10 of these had CEI less than 0.90. Short days caused a reduction in the rate of cell division by the end of the first week, and cell division almost ceased by the third week. The CEI of enlarging tracheids was also reduced between the first and third weeks, while WTI and SGI were increased during the same period ( fig. 7 ). Between the fourth and fifth weeks of SD treatment the cambium became quiescent ( fig. 4 ).

All seedlings in Groups 5, 6, and 7 also formed a band of latewood, since they were all exposed to at least 3 weeks of SD treatment. However, there were differences in the response of these three groups to long days. The seedlings in Group 5, which received only 3 weeks of SD treatment, continued cambial division and xylem differentiation within the first week of LD treatment ( fig. 5.) and thereafter at a relatively rapid pace ( fig. 6 ). The seedlings in Group 6 recommenced cambial division and xylem differentiation during the second week of LD treatment ( fig. 9 ), while those of Group 7 recommenced during the third week. At the end of 12 weeks, there were 61, 44, and 35 fully mature tracheids per file in Groups 5, 6, and 7, respectively. The variation in CEI, WTI, and SGI of mature tracheids in these latter three groups is shown in figure 8. The CEI of the first 4-5 tracheids per file which matured under long days showed a gradual increase in Groups 5 and 6 ( fig. 10 ), and an abrupt increase in Group 7 ( fig. 11). Also, the WTI and SGI showed a gradual decrease in Groups 5 and 6, but an abrupt decrease in Group 7. These differences were probably due to the presence of old needles in Groups 5 and 6, and their absence in Group 7.

The foregoing results confirmed that photoperiod plays a decisive role in the regulation of cambial activity and subsequent xylem differentiation. Short days alone were sufficient to bring about the differentiation of tracheids with low CEI ( latewood ). Larson ( 1962, 1964) and Wodzicki ( 1961, 1964) made similar observations for coniferous seedlings. The effects of photoperiod on xylem differentiation are believed to be mediated by endogenous growth-regulating substances.

## Drought Treatments

Wilting of different magnitudes accompanied the various drought treatments. The seedlings under complete drought were affected the most; three out of four died before the completion of treatment. The seedlings under both "mild" and "intermediate" drought wilted in between the 5-day watering intervals, and lost 40 to 70 percent of their foliage by the end of the drought exposure. Three of the five seedlings under "mild" drought and all five under "intermediate" drought formed resting terminal buds by the end of drought treatment. The controls continued height growth throughout the entire period of treatment.

Drought also interfered with cell division in the cambial zone and all phases of xylem differentiation. All three drought treatments were severe enough to "check" several tracheids in the various phases of differentiation ( i.e., to cause the death of tracheids prematurely ). Thus there were 2-3 tracheids per file with subnormal lignification; as many as 5-6 tracheids were checked in wall thickening; and 4-8 tracheids were checked in the-phase of enlargement. This pattern indicates the direct effect of drought on tracheid development. A similar scheme was observed by Kennedy and Farrar ( 1965) in jack pine *(Pinus banksiana* Lamb.) seedlings.

Drought also interrupted the growth of apical meristems and needles, which in turn reduced endogenous auxin levels and facilitated the differentiation of a relatively wide band of latewood tracheids ( fig. 12 ). This development prevailed for some time after the resumption of watering, and illustrated the indirect effects of drought on xylem development. Larson ( 1963) proposed that drought directly influenced the growth of the terminal meristems, and only indirectly the tracheid diameter through the intermediate action of auxin. Kramer ( 1964) and Zahner ( 1963) emphasized that both the direct and indirect effects of

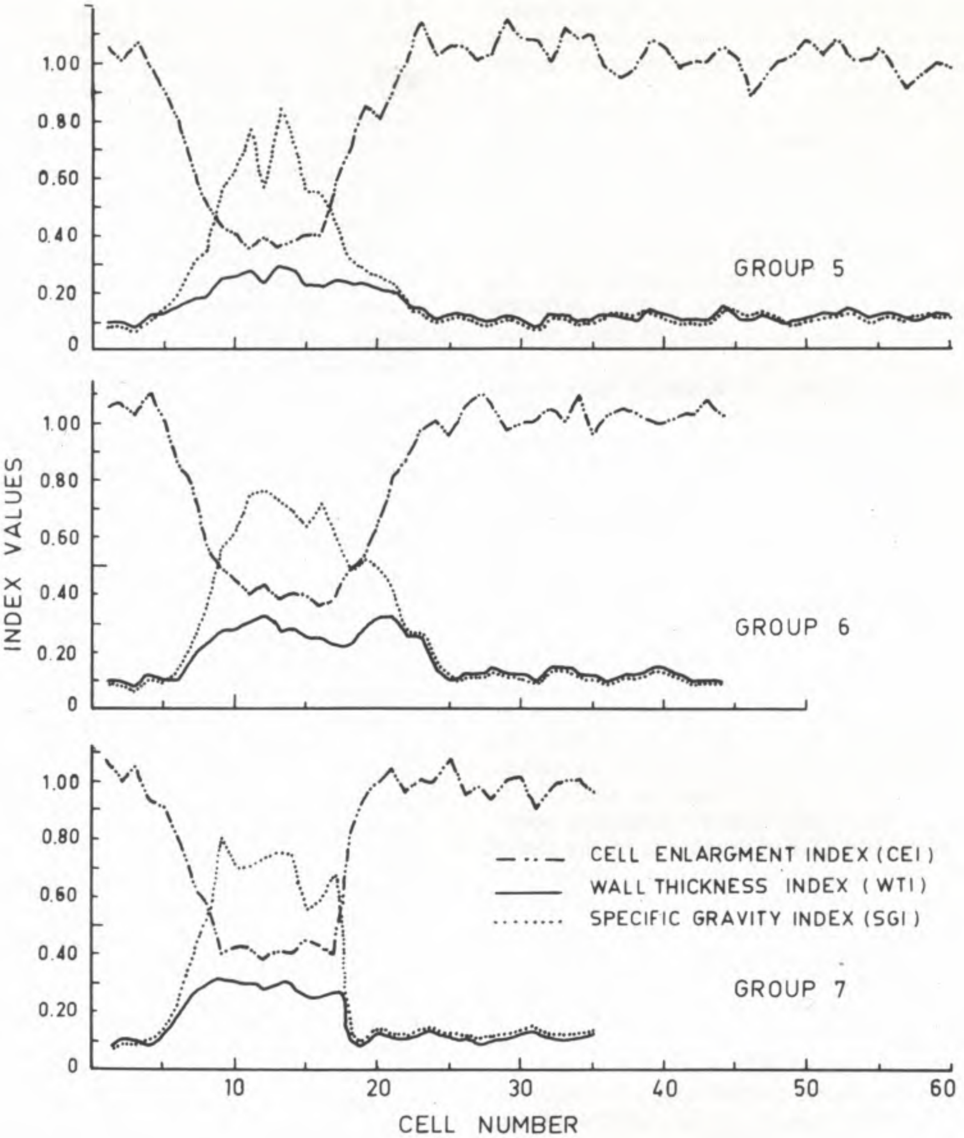


FIGURE 8. — The variation of CEI, WTI, and SGI in the middle stem of seedlings in Groups 5, 6, and 7.

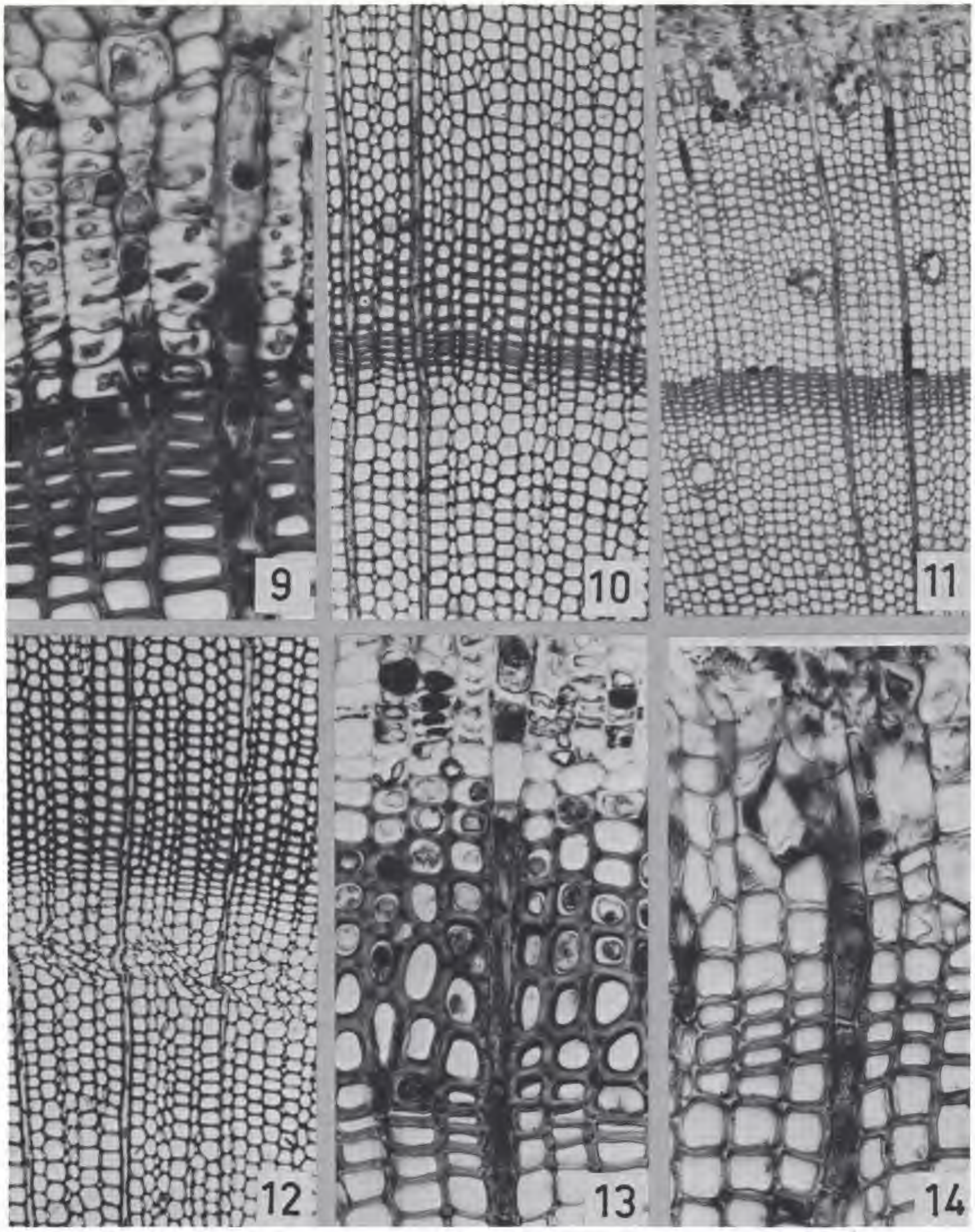
water deficits were important in xylem development.

## Treatments With IAA and TIBA

The 3-week exposure to short days, prior to IAA application, facilitated a reduction in CEI and an increase in WTI. In fact, the control seedlings became quiescent by the fourth week. However, the IAA-treated SD seedlings resumed a limited number of cell divisions and continued xylem differentiation ( fig. 13 ). The CEI of newly differentiated tracheids showed considerable increase ( greater than 0.90) and their WTI remained fairly high ( about 0.25 ). The newly differentiated tracheids had slightly excessive lignification ( characteristic of reaction wood ). The growth-stimulating effect of IAA was strongest immediately below the site of application; it was less at 2 cm below, and no apparent effect was present at 4 cm below the blaze.

These results indicated that the SD treatment lowered the level of endogenous auxins sufficiently, first, to cause latewood differentiation and eventually cambial quiescence. However, synthetic IAA could successfully be substituted to reverse this trend temporarily.

The treatment of actively growing LD seedlings with the inhibitor TIBA significantly reduced the enlargement ( CEI ) of 4-5 tracheids per radial file ( fig. 14 ), while LD controls continued forming



FIGURES 9 to 14. — The pattern of xylem differentiation and tracheid anatomy in larch seedlings under different photoperiods, drought exposure, and treatment with synthetic IAA and TIBA.

(9) Group 6, AC, 5 weeks SD plus 2 weeks LD, lower stem.

(10) Group 6, AC, 5 weeks SD plus 7 weeks LD, lower stem.

(11) Group 7, AC, 7 weeks SD plus 5 weeks LD, lower stem.

(12) The effect of "mild" drought on tracheid anatomy. The "direct" effects of drought are seen in the band of thin-walled, collapsed tracheids, immediately followed by thin-walled tracheids with narrow radial diameters. The "indirect" effects of drought are seen in the following zone of thick-walled tracheids with narrow radial diameters, which formed following drought while the seedling had resting terminal buds.

(13) The effect of IAA treatment on xylem differentiation and tracheid anatomy in an SD larch seedling.

(14) The effect of TIBA treatment on xylem differentiation and tracheid anatomy in an LD larch seedling.

earlywood. It is probable that TIBA, an auxin antagonist, interfered with auxin action during the enlargement phase of tracheid differentiation. Larson ( 1964) was also able to induce the formation of narrow-diameter tracheids in young red pine growing under long photoperiods.

## Summary and Conclusions

Results of this experiment are in agreement with the concept that certain anatomical and hence wood quality characteristics of mature tracheids are determined during differentiation. Photoperiod, water availability, and treatments with synthetic IAA and TIBA all affected the degree of radial enlargement, wall thickness, and hence specific gravity of mature tracheids. Short photoperiods, water deficits, and treatment with TIBA favoured the differentiation of tracheids with low cell enlargement index ( i.e., CEI less than 0.90 or latewood ), while long photoperiods, adequate water supply, and treatment with IAA favoured the differentiation of tracheids with high cell enlargement index ( i.e., CEI greater than 0.90 or earlywood ).

The results fitted the theory of limiting factors, i.e., a factor which falls below an optimal threshold will set the pace for physiological events which affect the differentiation of tracheids. Thus, short days alone were sufficient to bring about latewood differentiation, as were water deficits and treatment with TIBA. These observations may have some practical significance. Therefore, in any treatment of forest stands which aims to affect tree growth and wood quality ( e.g., irrigation, fertilization, thinning ), all environmental conditions should be assessed before treatment is made. The treatment may be wasted or will fail to produce the expected results if one single important environmental factor ( e.g., photoperiod ) is below a growth-limiting threshold.

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