Studies on the Formation and Structure of the Compression Wood Cells Induced by Artificial Inclination in Young Trees of *Picea glauca*

I. Time Course of the Compression Wood Formation Following Inclination*

By

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人為的傾斜によるグラウカトウヒ幼齢木の
あて材細胞形成とその構造

I. 傾斜処理に引き続くあて材形成の経時的観察

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Introduction

If a stem or a branch is displaced from its original position, a particular type of wood known as reaction wood will be formed and the displaced organs will recover their original positions through the formation of reaction wood with eccentric

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growth, by expansion in a conifer or by contraction in a hardwood. According to URSPRUNG (1906), eccentric growth of a stem and a branch was already known in the time of MALPIGHI (1628-1694). A recognition of an anomalous type of wood associated with eccentric growth, i. e., reaction wood, dates back at least more than a century and the first anatomical description was, to our knowledge, made by SANIO in 1860. Since the latter decades of the last century, elaborations of many workers have disclosed diverse aspects of the phenomenon, however, many still remain obscure and controversies on main subjects can be found in the literature (see recent reviews, e. g., LOW 1964 a, WESTING 1965, 1968 and WILSON & ARCHER 1977).

Controversies found among the reports on reaction wood would, in part, come from the fact that the most investigations were made on the trees of unknown history grown under forest conditions. At present, reaction wood formation is regarded as a geotropic manifestation*1 of woody plants (WESTING 1965, 1968 and ROBARDS 1969), and therefore, severity of the reaction wood formation would be related primarily to the degree of stem deviation. Since inclined trees, in the course of time, become to recover the vertical position changing their form complicatedly (HARTIG 1901, and LOW 1964 b), a careful analysis of reaction wood in such trees can not be made without any detailed records of their history. Moreover, internal and environmental factors such as growth rate, tree age, duration of leaning of a tree and position in a tree are known to affect the formation of reaction wood and little is known about the influences of other factors such as temperature, soil moisture content, mineral nutrition etc. (see reviews above cited). It seems quite apparent that comparison of results obtained from trees grown in different conditions can not be made without any risk.

Naturally, reaction wood has also been studied by experimental induction. Its history dates back to the last century (e. g., CIESLAR 1896) and many brilliant contributions by earlier workers (HARTIG 1901, EVERT & MASON-JONES 1906, WHITE 1908, BURNS 1920, *etc.*) still have not lost up-to-date values. Experimental induction of reaction wood, as a matter of course, has played an important role to disclose diverse aspects of the problem. However, because each experiment was carried out on the trees of their own nature, it is also difficult to draw comparison of experimental results for the general discussion of the phenomenon. Every aspect of the phenomenon must be interrelated intimately. Therefore, to reaveal the nature of reaction wood formation closely, it was hoped to conduct an extensive research on diverse aspects of the problem using equivalent trees, in which extrinsic factors thought to affect the formation should be excluded as far as possible.

In the present series of studies, the formation and structure of compression wood (a coniferous type of reaction wood) is investigated using young trees of *Picea glauca* chosen from hundreds of trees grown from seeds of the same source and planted in the same ground. To minimize extrinsic factors, trees of the same

*1 See P. 140.

age, equivalent in height and vigour were used in a experiment. As the series of experiments was continued for three years, the trees grew considerably during that period. However, there was wide difference in height of trees in the ground and we chose those of similar height as sample trees as far as possible. Age of trees used is, therefore, different among some experiments.

Experimental induction of reaction wood was done all by bending at or near the base of trees and stems to be examined were tied to stakes with strings to keep the stems straight and to maintain the constant stem deviation throughout the period of inclination. In this way, compressive and tensile force are thought to be eliminated from the stems.

Geotropic stimulus*[2] was given in a variety of ways differing in season or duration or angle of the inclination and several aspects of the formation of compression wood and anatomy of the wood formed in these ways were studied using ordinary light microscopy, ultraviolet microscopy and scanning electron microscopy. Generally, the 1st and 2nd internodes were examined and a general light microscopic observation was made on three portions in each internode to detect possible difference, if any, within and between internodes.

The chief interests in the present series of experiments are the relation between the mode of geotropic stimulation and changes in the structural features of the wood formed, and the perception*[3] of the stimulus by the cells in the cambial and differentiating zone. To begin with, we dealt with alteration from the normal wood formation to the compression wood formation following the inclination of tree, for this kind of experiment was thought not only to give intimate information on the reception*[4] of the stimuli to form compression wood cells, but also important to know the general nature of the sample trees.

Although an increasing number of the cytological studies on compression wood formation has been accumlated for these several decades, histological and cytological changes which would occur in the cambial and differentiating zones following the inclination of trees have little been studied. To our knowledge, two authors devoted only a few lines of their voluminous papers to describe the subject. As early as 1937, Onaka reported that in three-year-old seedlings of *Pinus densiflora* intercellular spaces and red-colored cells with thick cell wall were detected after 2-5 and 5-7 days respectively, and that in June to August such cells would generally appear after about a week. WESTING (1965) also stated that it took an average of 7 days for the first layer of compression wood cells to be fully formed.

As stated above, these observations would give intimate information on the reception of the stimuli to induce the formation of compression wood cells, in other words, this kind of experiment would throw a light on the question where a cell receives the stimuli responsible for characteristic features of a compression wood cell (i. e., rounded outline, thick cell wall, spiral grooves in the secondary wall and excessive lignification). Cells in different developmental stages would percept different kinds of simuli. However, no authors mentioned above

*2,3,4 See P. 140.

stated anything on the problem.

From such a point of view, an important contribution was made by KENNEDY and FARRAR (1965). Seedlings of *Pinus banksiana* and *Larix laricina* were tilted in a variety of ways and after an appropriate period they observed the wood formed, and reached a hypothesis that each stimulus responsible for a characteristic feature was percepted only by the cells in the "susceptible" stage which would be situated at the site immediately before its formation begins.

However, their report was based on only a light microscopic observation, precise information on the structure of the cells was lacking. Recently, FUJITA *et al.* (1979) investigated the transitional zone from normal wood to artificially induced (by inclination) compression wood and *vice versa*, using scanning electron microscopy and a variety of light microscopy. According to FUJITA *et al.*, the hypothesis of KENNEDY and FARRAR (1965) was mostly correct except for the lignification, the susceptible cell to excess lignification was supposed to be the just beginning cell of S 2 thickening. They indicated also that the stimulus for disappearance of the S 3 layer would be percepted at the inner most site, of which KENNEDY and FARRAR did not mention.

However, these investigators did not observed the real changes which would occur in the cambial and differentiating zones following the inclination of the trees. They assumed that the cell number of the differentiating zone and the rate of cell division in the cambial zone before and after the inclination were the same. But, in the cambium on the lower side of inclined stems, the rate of cell division is thought to be higher than in that of vertical ones, judging from the fact that diameter growth on the lower side is generally greater than usual (BURNS 1920, ONAKA 1937 and PILLOW & LUXFORD 1937), and FUKAZAWA (1973) reported that the number of the cells in the course of the secondary wall formation was more numerous on the lower side. It was supposed that the cambial and/or differentiating zones would show rather dynamic alteration following the inclination of trees. We are of the opinion that a morphological observation on the cambial and differentiating zones should be performed prior to building up any hypothesis.

In the present paper, though of a preliminary nature, the time course of the compression wood formation following inclination is reported and some of the features of dynamic conversion from normal wood formation into compression wood formation are revealed.

*1, 2, 3, 4

Reaction wood (compression wood and tension wood) formation is at present, thought to be a manifestation of geotropism in the secondary tissue (WESTING 1965 and ROBARDS 1969). The mechanism of geotropism has been studied mostly in the primary tissues of herbaceous plants such as *Avena, Helianthus, Lupinus* etc. (AUDUS 1969 and JUNIPER 1976). In the primary tissues gravitational stimulus is suscepted in the tips of organs (starch sheath of coleoptile, root cap etc.) and transformed into biochemical information, and the information is transmitted centripetally to the region of response where curvature or extension of organs will occur. On the other hand, in reaction wood formation of the secondary tissue, the stimulus is known to be percepted in or near the region of the response (BURNS 1920, SINNOT 1952 and ONAKA 1937).

However, no detailed studies on the site of susception (the first stage of the perception), the manner and course of transmission of the information etc. have been performed. There would be differences in many aspects of the phenomenon between relatively small and simple primary tissues of herbaceous plants, and complicated secondary tissues of large-sized woody plants. Therefore, in the present paper, the words such as stimulus, perception, reception etc. do not necessarily mean those used in the studies on the geotropism in the primary tissues of herbaceous plants, but are used in the sense of the studies of KENNEDY and FARRAR (1965) and FUJITA *et al.* (1979).

Materials and Methods

Young trees of *Picea glauca* grown in The Laboratory of Forest Tree Breeding in Nayoro, College Experiment Forests, Hokkaido University, ca. 1.7 m high were bent at the basal part of the tree to be inclined at 45 degrees and tied to woody stakes with strings in early July 1977 (Photos 1 and 2). No compression or tension is expected to have been exerted on the stems to be examined. The 1st and the 2nd internodes were harvested 0, 2, 4, 6, 8, 10, 15, 20, 25 and 26 days after the inclination, one tree on each, and other two trees which had already been inclined at 45 degrees in mid June were also sampled at the beginning of the experiment. In early August 1977 an additional experiment was carried out using equivalent trees grown on the same stand, and after 0, 2, 5, 6, 7 and 21 days similar portions of the trees were harvested, two trees on each. The trees sampled after 25 and 26 days in July were regarded as inclined controls in this experiment. Each internode was divided into three portions, i. e., distal, middle and proximal portion and materials including both the lower and upper sides of the leaning stem were severed from each portion.

For an ordinary light microscopic observation, materials were fixed either phosphate buffered 10% acrolein at pH 7.2 or chromium-acetic acid solution or Zirkle's reduced chromium solution (ZIRKLE 1928), the latter giving the most excellent result. After washing in running water, the materials were dehydrated in n-butanol series and embedded in paraffin. After softening in water (BALL 1941), sections of 15 microns were cut on a sliding microtome and fixed with a Ullrich's adhesive (JOHANSEN 1940) on slide glasses and stained with a gentian violet — orange G, an iron haematoxylin — orange G combination and tannic acid — iron chloride.

Materials to be examined under an ultraviolet (UV) microscope were excised from the middle portions of the first internodes and fixed in FAA and cut into small pieces containing only the lower side of the tilted stem. After dehydrated in ethanol series, the specimens were embedded in Spurr's low viscosity resin mixture and sectioned on an ultramicrotome (LKB Ultrotome III). Sections of 0.5 micron were fixed on quartz slides and mounted in glycerin with quartz cover slips. Photographs were taken under an UV-microscope (Carl Zeiss, Type MPM-01) at a wavelength of 280 millimicrons using ordinary commercial films.

Results and Discussion

a) *Observation on the vertical and inclined controls*

Cambial and differentiating zones of vertical and inclined trees, harvested at the beginning of the experiment in July, are shown in Photos 3 and 4. In the present study, the course of lignification was estimated on the preparations stained with gentian violet. In this kind of study safranine O or T has generally been used, while JACKSON (1926) applied crystal violet which has almost the same nature with gentian violet, for a histological use. According to JACKSON, crystal violet gave satisfactory results to differentiate weakly lignified tissues from non-lignified ones, though for the finer structural details of the lignified elements, the violet was not so precise as safranine. In this study, gentian violet was used as a lignin stain, simply because it gives sharper monochromatic photographs than safranine does.

Lignification begins in or near the middle lamella of the cell corner and proceeds tangentially and then radially in both normal wood (Photo 3) and compression wood (Photo 4). Slight irradiation of gentian violet into the secondary wall seems an artifact, because such a phenomenon was not found in UV-photographs and has not been reported in other studies (KUTSCHA and SCHWARZMANN 1975, IMAGAWA 1976 and FUJITA *et al.* 1978 a). The lignification of the secondary wall seems to occur with some delay after that of the middle lamella. In this respect a contradiction has been observed in the literature. IMAGAWA (1976) showed using UV-microscopy and UV-photometry that in vertically grown *Larix leptolepis* lignification of the secondary wall occurred gradually and continuously following that of the middle lamella, while FUJITA *et al.* (1978 a) reported that it occurred abruptly on the lower side of inclined *Cryptomeria japonica* seedlings with a short interval of time after the middle lamella was lignified. There might be a difference in the course of lignification between normal wood and compression wood, and/or among species. However, the photographs by IMAGAWA (1976) indicate that after the lignification of the middle lamella, bulk of the secondary wall remains unlignified up to "cell 15" in his Fig. 10. Since to investigate the detailed course of lignification is not the subject of the present study, it can be assumed that there are two major phases of lignification; the first one is the lignification of the middle lamella and the second is that of the secondary wall. This would seem conspicuous in compression wood because of its high concentration of lignin.

In Photo 4, many particles or droplets of unknown nature, strongly stained with gentian violet, appear in the cytoplasm of the differentiating cells. These particles or droplets were seen in all acrolein fixed specimens of compression wood, including very slight one (Photo 6) and completely restricted in these materials. Never were they observed in the normal wood specimens. The particles are about 1–5 microns in diameter and variable in form. In Photo 5, cells at the bottom are in the early stage of the secondary wall formation and at the top lignification of the secondary wall begins. The particles are confined between these two

developmental phases. Neither did they appear in cambial cells nor in the cells where the lignification of the secondary wall was in progress. Starch grains have similar dimensions and are also stained with gentian violet. However, despite the fact that starch grains showed birefringence between crossed nicols, the particles did not. Starch grains can be fixed in any other fixatives. Hence, they are thought not to be starch grains. Since such a kind of particle has not been reported in the literature (FUJITA *et al.* 1978 b and TIMELL 1979), there is little possibility that the particles are really one of the organelles or formed under a biological process. As well known, acrolein can be easily polymerized and bound with amino acids (SMITH 1962). And cytoplasm of differentiating compression wood tracheids is thought to be rich in phenylalanine, an aromatic amino acid, as a lignin precursor (FUJITA and HARADA 1979). Therefore, it is highly plausible that these particles were produced by polymerization of acrolein under a high concentration of phenylalanine, though further studies are needed.

b) *Anatomical observation on the time course*

Two series of experiments were performed, namely the experiments in July and in August.

The experiment in July was undertaken to observe changes in the form and the number of cells in the cambial and differentiating zones, which would occur during the period of the transition from the normal wood formation to the compression wood formation. Furthermore, the experiment was continued thereafter with a longer interval of sampling. Samples were harvested 2, 4, 6, 8, 10, 15, 20, 25 and 26 days after the inclination, and the materials for the ordinary light microscopy sampled after 2, 4 and 6 days were fixed in buffered acrolein and the others were fixed in chromium-acetic acid solution. On the upper (opposite) side of the inclined stems, little appreciable change in anatomical features was obtained, therefore, descriptions will be restricted on the lower side in the July experiment.

Two days after the inclination (Photo 7), none of the characteristics of compression wood cells was observed in the cambial and differentiating zones, except for the above mentioned unknown particles. The particles appeared in all the portions (the portion denotes a sampling position in the 1st and 2nd internodes), although they were distributed sparsely and were fairly small.

The rounded outline of the differentiating cells in a cross section was first found after 4 days (Photo 8) in all the portions. Intercellular spaces also appeared in these specimens but not in the most proximal portion. These two characteristics were more distinct in the distal portions. Excessive lignification of the seemingly normal S 2 layer and formation of the slightly thicker wall began in the distal two portions. The particles were bigger and more numerous than those of the 2-day specimens.

After 6 days (Photo 9), intercellular spaces were found in all the portions and the middle lamella around intercellular spaces became lignified and thick-walled cells under intensive lignification were observed in the 1st internode. In the most distal portion, one or two rows of cells having slightly thicker walls seemed to be matured.

Heavily lignified cells having slightly thicker walls were found in all the portions after 8 days (Photo 10). The typical compression wood cells having unlignified S 2 layer and intercellular spaces appeared in all the portions, especially in the distal two portions the S 2 layer of such cells became lignified. The 8-day tree showed some deviation in the progress of the compression wood formation among portions, and this might be caused by the exsistence of compression wood before the experiment. The difference in the initiation and the completion of lignification among radial files was also observed in the most proximal portion, and this may be related to the formation of traumatic resin canals (WERKER and FAHN 1969).

After 10 days (Photo 11) the S 2 layer of the cells having intercellular spaces became lignified in the 1st internode and in the most distal portion a few rows of the typical compression wood cells seemed to be matured. In this tree, the progress of the compression wood formation was somewhat retarded in the 2nd internode, and in the most proximal portion the progress was found to be in earlier stage than the comparable portion of the 8-day sample.

After 15 days (Photo 12), ca. 15 rows of mature typical compression wood cells were found in all the portions. The appearance of the cambial and differentating zones was seemingly not different from that of the 10-day samples and the inclined controls harvested at the beginning of the experiment. The materials sampled 20 (Photo 13), 25 (Photo 14) and 26 days after the inclination also gave similar images.

In the experiment in July, the rounded outline in a cross section and intercellular spaces appeared so suddenly that the detailed course of their emergence could not be confirmed, therefore, another supplemental experiment had to be carried out in August to observe early morphological changes. In this series two trees were sampled on each day and as the materials were not fixed in acrolein, the above mentioned particles could not be observed.

At the beginning of the experiment, the number of the cells in each developmental stage in vertical controls seemed somewhat greater than that of July. Samples were harvested 2, 5, 6, 7 and 21 days after the inclination as stated before.

Nothing different from the vertical controls was observed in the 2-day materials. After 5 days, the cells initiating the secondary thickening showed slight rounding-off of the outline, especially in the distal portions. Intercellular spaces were found in the 1st internodes after 6 days. The rounded outline became more apparent in all the portions. After 7 days, intercellular spaces were found in all the portions, and excessive cell wall thickening and heavy lignification were observed in the 1st internode of a sample tree but not of the other.

Twenty-one days after the inclination, many typical compression wood cells matured, however, the amount of these cells was considerably reduced compared with the 20-day materials in July and similar to that of the inclined controls which had been inclined in mid June and harvested after 21 days in early July.

As already mentioned, almost no anatomical changes were observed on the upper (opposite) side of the inclined stems in July. However, latewood-like cells,

narrow in radial direction having thicker wall, were found in all the portions of the 21-day materials in August (Photos 15 and 16). Such cells also appeared in the materials harvested in July, although the occurrence was only occasional. These cells on the upper side were thought to have been formed shortly after the inclination. There would be a transient deficiency in the substance to stimulate wood formation (LARSON 1964) or a temporal increase in growth inhibitor level (WODZICKI 1964) caused by inclination at that time. This would be suggested also by the fact that the occurrence was inclined to the later season.

In the 21-day materials in August, clusters of the cells which show abnormality in lignification were observed in the later part (cambial side) of the transitional zone from normal wood to compression wood (Photos 17 and 18). The clusters of the cells were not stained with iron haematoxylin, which means that the cells were lignified scantly as compression wood cells, and lined up tangentially. Such clusters were also occasionally observed in similar positions of the materials for other series of investigations and showed the same staining properties and arrangement. They can not be the ending parts of resin canals, because only a small number of resin canals could be observed in the specimens, compared with the fact that many clusters were found throughout the internodes. The formation of these clusters would be related to the disordered cell differentiation observed in the 8-day materials in July. The phenomenon has not been investigated by UV-microscopy.

The morphological changes presented above are summerized in Tables 1 and 2. In the tables, portions are numbered in the proximal direction and the portions I to III belong to the first internode and the portions IV to VI to the second. After the inclination the unknown particles appeared in the first place, followed by the rounding-off of the outline and the formation of intercellular spaces in succession. Next to these features the formation of the thick cell wall and the heavy lignification of the S 2 layer occurred almost simultaneously. The results agree with those of ONAKA (1937), except for the particles of which he did not mention. However, this sequence of the changes may be of a superficial nature and there would be other essential changes brought about by inclination, not

Table 1. Morphological changes following the inclination in July

Time after inclination (day)	Unknown particles	Roundness in a cross section	Intercellular spaces	Excessive thickening of cell wall	Heavy lignification of S 2	Lignification of middle lamella around intercellular spaces	Maturation of slight compression wood cells
2	I-VI	—	—	—	—	—	—
4	I-VI	I-VI	I-V	I-II	I-II	—	—
6	I-VI	I-VI	I-VI	I-VI	I-VI	I-III	I
8		I-VI	I-VI	I-VI	I-VI	I-VI	I-VI
10		I-VI	I-VI	I-VI	I-VI	I-VI	I-VI

Portions are numbered in the proximal direction, and the portions I to III belong to the 1st internode and the portions IV to VI to the 2nd. As the materials harvested 8 and 10 days after the inclination were fixed in chromium acetic acid, no particles could be observed.

Table 2. Morphological changes following the inclination in August

Time after inclination (day)	Roundness in a cross section	Intercellular spaces	Excessive thickening of cell wall	Heavy lignification of S2	Lignification of middle lamella around intercellular spaces	Maturation of slight compression wood cells
2a	—	—	—	—	—	—
2b	—	—	—	—	—	—
5a	I-VI	—	—	—	—	—
5b	I-VI	—	—	—	—	—
6a	I-VI	I-VI	—	—	—	—
6b	I-VI	I-III	—	—	—	—
7a	I-VI	I-VI	—	—	—	—
7b	I-VI	I-VI	I-III	I-III	I, III	—

Portions are numbered in the proximal direction as in Table 1. In the August experiment two trees were harvested on each day, and this is shown in the table with letters a and b.

detected by the methods used in the present study, including physiological ones.

It is apparent from Tables 1 and 2 that the more distal the portion is, the more the progress of compression wood formation advances, though this tendency is not strict and there were some cases where the progress advanced more in the proximal portion than in the distal one. A similar phenomenon was reported by KENNEDY and FARRAR (1965) between the hypocotyl and the mid-stem of the 6-month-old seedlings of *Pinus banksiana*. Younger tissues are thought generally more sensitive to stimuli than older ones.

Another fact apparent from the tables is that the transition from the normal wood formation to the compression wood formation proceeded twice as fast in July as in August. This difference in the rate is also suggested from the evidence that the amount of compression wood formed for 20 days in July was almost twice as much as that formed during a similar period (21 days) in June and in August.

c) *Changes in the cell number of the cambial and differentiating zone and the rate of cell division*

Cell number of the cambial and differentiating zone was measured to obtain the information on its change following the inclination. Measurements were carried out on both the lower and upper sides of all six portions of materials harvested in July. The zones were divided into three developmental phases for convenience; Phase A denotes the cambial zone showing no birefringence between crossed nicols; Phase B contains the cells with birefringence, having unlignified middle lamella; and Phase C is composed of the cells with lignified middle lamella, having unlignified secondary wall. No measurement was made for the duration of lignification of the secondary wall, because completion of the lignification could not be well detected by the present methods. Each value represents a mean of five radial files. Xylem diameter (lower side to opposite side) was also measured with a projector.

No relation could be found between the cell number of the cambial zone (Phase A) of the lower side and the duration of the inclination, and mean values of ca. 14 and 20 cells were obtained for the 1st and 2nd internode respectively (Figs. 1 and 2). KUTSCHA *et al.* (1975) reported that in *Abies balsamea* normal

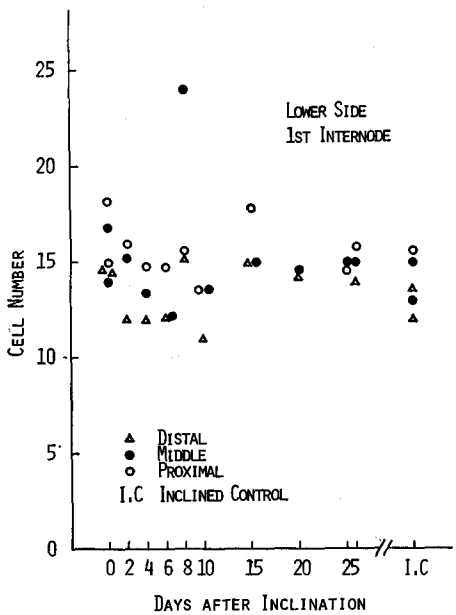

Fig. 1. Change in cell number of Phase A (cambial zone) on the lower side of the 1st internode.

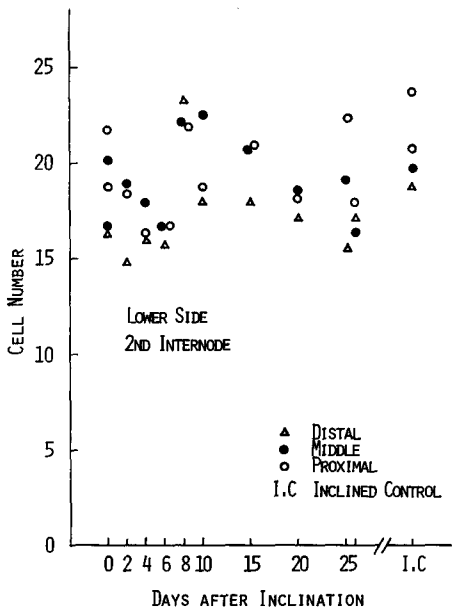

Fig. 2. Change in cell number of Phase A (cambial zone) on the lower side of the 2nd internode.

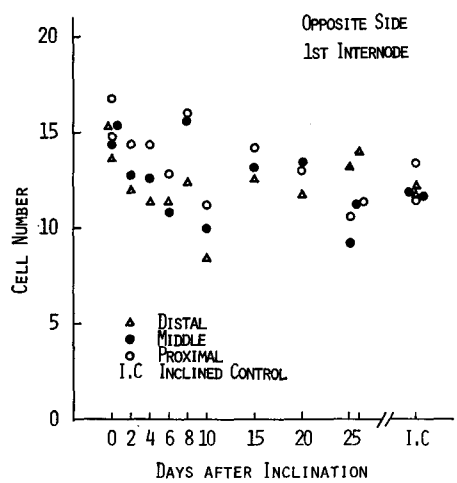

Fig. 3. Change in cell number of Phase A (cambial zone) on the opposite side of the 1st internode.

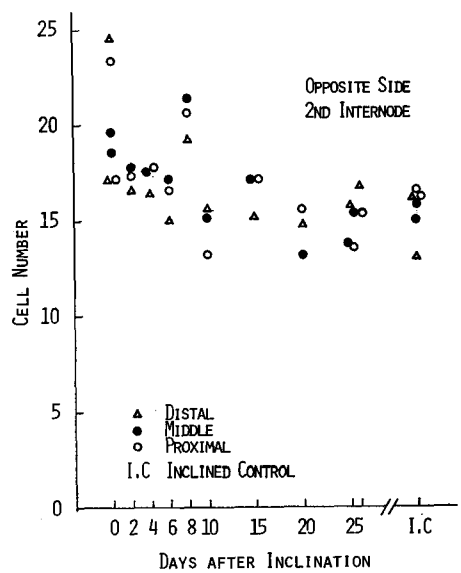

Fig. 4. Change in cell number of Phase A (cambial zone) on the opposite side of the 2nd internode.

wood reached a maximum cambial width of 15 cells on June 7, while in compression wood cambial zone reached a maximum width of 16 cells on may 30, although their normal wood specimens were obtained from a large dominant tree, while that of compression wood were taken from smaller and more shaded trees, moreover, mostly of branch wood. On the contrary, the values for Phase A of the upper side decreased by 10 day after the inclination (Figs. 3 and 4). In a previous paper (YUMOTO and ISHIDA 1979), we found using equivalent trees grown on the same stand with the present work that current xylem increments on the lower side were almost constant irrespective of the degree of inclination, while on the upper side a good negative correlation was obtained between the current increment and the degree of inclination. There might be a positive correlation between the amount of xylem increment and the width of the cambial zone. However, as will be mentioned later, the rate of cell division is thought to be higher in compression wood than in normal wood, therefore, whether or not the number of cells in cambial zone reflects the rate of cell division still remains a moot question. Figs. 1 and 2 show also that the number of cells in the cambial zone did not change during

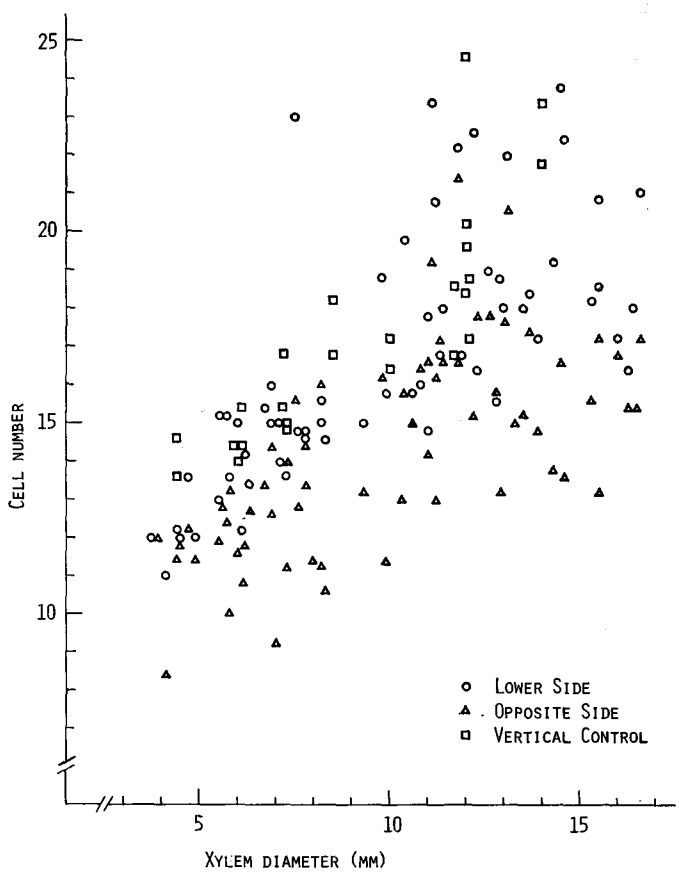

Fig. 5. Relation between cell number of Phase A and xylem diameter (1st and 2nd internodes).

the experimental period, because the inclined controls, sampled at the beginning of the experiment, and the 25- and 26-day materials in July give almost the same values. By the way, a positive correlation was found between the cell number of the cambial zone and the stem diameter (Fig. 5). Hence, attention should be called to this relation in experiments using seedlings or young trees. In the present study, the reflection of the increase in diameter on the width of the cambial zone was negligible.

The cell number for Phase B did not show any correlation with the duration

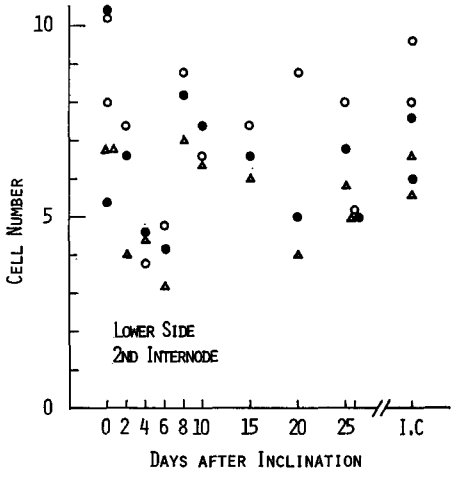

Fig. 6. Change in cell number of Phase B on the lower side of the 2nd internode.

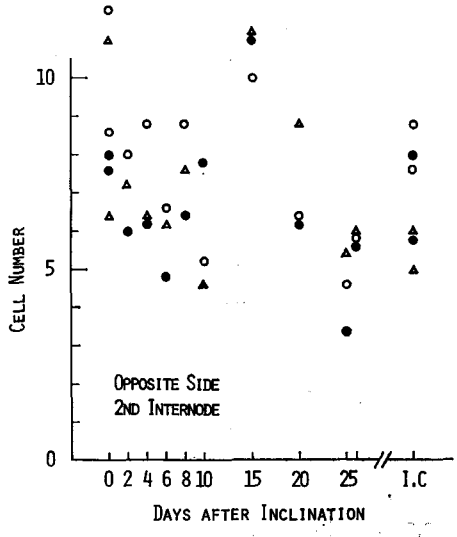

Fig. 7. Change in cell number of Phase B on the opposite side of the 2nd internode.

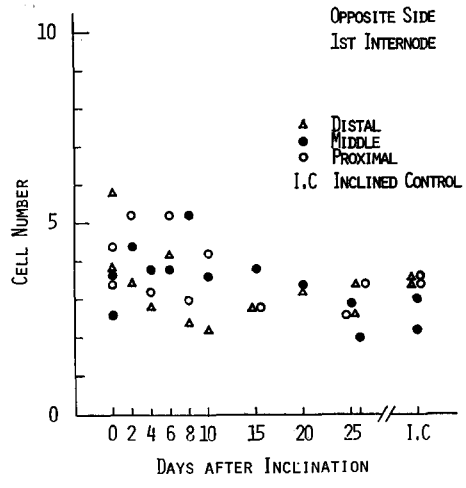

Fig. 8. Change in cell number of Phase C on the opposite side of the 1st internode.

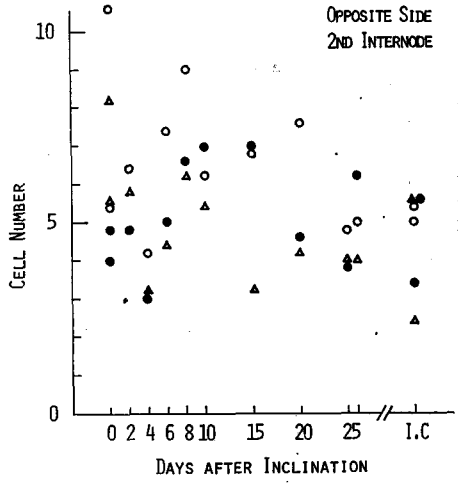

Fig. 9. Change in cell number of Phase C on the opposite side of the 2nd internode.

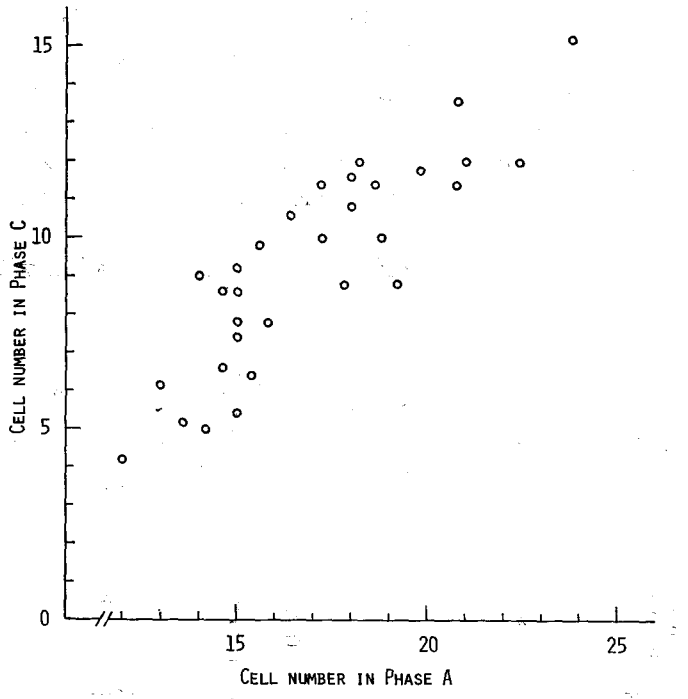

Fig. 10. Relation between cell number of Phase A and that of Phase C. Data from the inclined controls and the trees harvested after 15, 20, 25 and 26 days are shown in this figure.

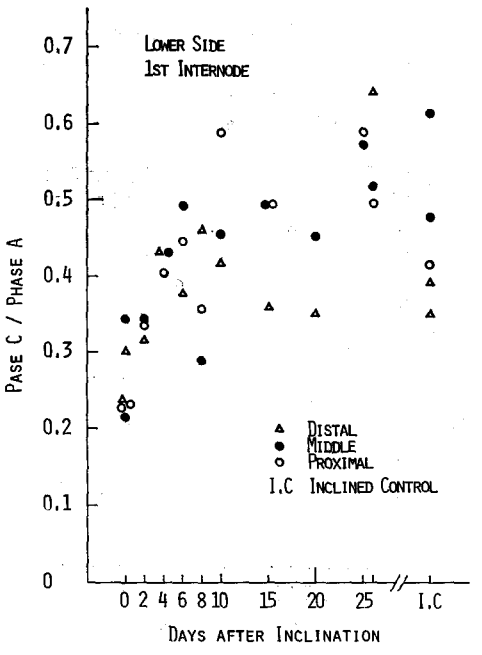

Fig. 11. Change in cell number of Phase C in proportion to that of Phase A; lower side of the 1st internode.

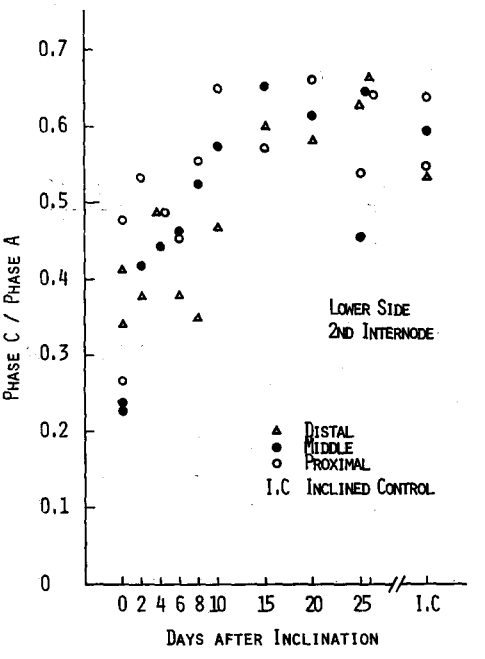

Fig. 12. Change in cell number of Phase C in proportion to that of Phase A; lawer side of the 2nd internode.

of the inclination on both sides and the values of 5 and 7 cells were obtained for the 1st and the 2nd internode respectively. Since the values varied considerably, the cell number of Phase B might not have any physiological significance.

On the other hand, values for Phase C on the lower side increased by 10 days after the inclination, that of the upper side decreasing slightly (Fig. 8) or remaining relatively constant (Fig. 9). A close correlation was obtained between the values for Phase A and those of Phase C in compression wood specimens (Fig. 10). Therefore, it seems to be more adequate to give the value in proportion to that of Phase A (Figs. 11 and 12). KENNEDY and FARRAR (1965) supposed in their hypothesis that the width of the differentiating zone would remain constant, but in fact, the width did change. The reason for the change is not clear. This might simply come from the increase in the wall thickness of compression wood cells. The number of the cells in Phase C is thought to be determined by the relation between the rate of cell division and that of the differentiation (lignification). The increase might occur simply because the former exceeds the latter on the lower side of inclined stems.

As noted above, duration of the secondary wall lignification was not investigated in the present study. However, a greater number of cells under lignification of the

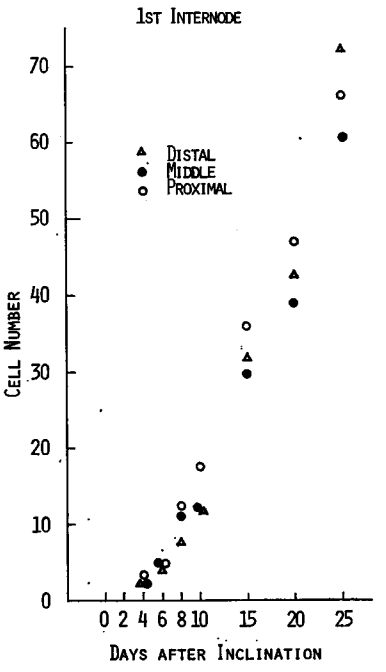

Fig. 13. Number of the typical compression wood cells formed after inclination in the 1st internode.

Cells with intercellular spaces and the secondary wall were counted irrespective of maturity.

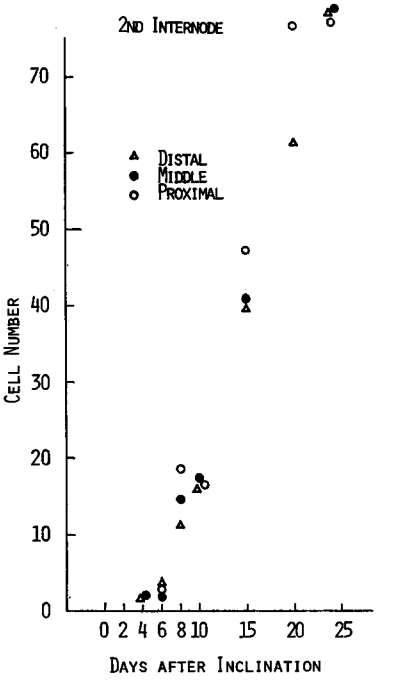

Fig. 14. Number of the typical compression wood cells formed after inclination in the 2nd internode.

Cells with intercellular spaces and the secondary wall were counted irrespective of maturity.

secondary wall were found in compression wood than in normal wood. This can be well understood from the fact that compression wood cells have thicker wall and are higher in lignin concentration than normal wood cells, and that the rate of cell division is rapid in compression wood.

To estimate the rate of cell division in the cambial zone of compression wood, typical compression wood cells formed after the inclination were counted. From Figs. 13 and 14 the values of ca. 3 and 4 cells per day were obtained for the 1st and 2nd internode respectively. Figs. 13 and 14 also indicate that the rate of cell division in the cambial zone of compression wood was nearly constant throughout in July. The rate in vertical controls could not be determined in this manner, however, judging from the counting on the trees (vertical controls in the August experiment), with the date marking by inclination (45 degrees, duration of 4 and 8 days), the rate of ca. 2.0 cells per day for the 1st internode and ca. 2.5 cells for the 2nd seemed to be most probable.

To estimate the change in the rate, mitotic figures in the cambial zone were counted on radial sections (12 sections of 1 cm long in axial direction on each portion) from another set of specimens embedded in celloidin. However, the values varied markedly and no trend was indicated. The deviation may be caused by the formation of resin canals (WERKER and FAHN 1969) and/or by the diurnal periodicity of cell division (LYNDON 1976).

d) *Reconstruction of the standard course*

From the evidences presented above, though deviations were observed to some extent, the changes in the anatomical features and the number of the cells could be represented diagrammatically. As shown in Tables 1 and 2, the progress of the compression wood formation is more accelerated in distal portions, therefore, the course should be represented on each portion, if possible. However, such a detailed study could not be carried out because of a small number of sample trees, hence the course was thought in terms of internodes.

Tables 3 and 4 show the values for Phases A, B, C (the values for Phase C are given in proportion to those given for Phase A) and the rate of cell division in the 1st and 2nd internode respectively. Since the change in the rate of cell division was not caught in the present study, the values were decided arbitrarily with consideration for the change in the values for Phase C. The number of the cell in Phase C is thought to be determined by the rate of cell division and that of differentiation. As the cell number of Phase C sharply increased after the inclination, the rate of cell division, at least, must have been accelerated at the same time, even though the change in the rate of cell differentiation was not known.

Some fluctuation in the progress of compression wood formation among trees was observed as noted above. We have an impression that the trees harvested after 4 and 8 days would be accelerated and the 10-day tree would be slightly retarded, especially in the 2nd internode. Therefore, the 6-day materials were taken as a standard in the present study.

The theoretical time courses of the compression wood formation are recon-

Table 3. Changes in the number of cells in the cambial and differentiating zone and the rate of cell division on the lower side of the 1st internode in July

Time after inclination (day)	Phase A (cell)	Phase B (cell)	Phase C / Phase A	Phase C (cell)	Rate of cell division (cell/day)
0			0.3	4	2.0
2			0.35	5	2.5
4			0.4	6	2.5
6	14	5	0.45	6	3.0
8			0.475	6	3.0
10			0.5	7	3.0
15			0.5	7	3.0

Table 4. Changes in the number of cells in the cambial and differentiating zone and the rate of cell division on the lower side of the 2nd internode in July

Time after inclination (day)	Phase A (cell)	Phase B (cell)	Phase C / Phase A	Phase C (cell)	Rate of cell division (cell/day)
0			0.35	7	2.5
2			0.4	8	3.0
4			0.45	9	3.5
6	20	7	0.5	10	3.5
8			0.525	11	4.0
10			0.55	11	4.0
15			0.6	12	4.0

Tables 3 and 4. The cambial and differentiating zone were divided into three developmental phases for convenience; Phase A denotes the cambial zone showing no birefringence between crossed nicols; Phase B contains the cells with birefringence leaving the middle lamella unlignified; Phase C is composed of the cells with the lignified middle lamella leaving the secondary wall unlignified. No measurement was made for the duration of lignification of the secondary wall because of technical difficulties. The values for Phase C/Phase A were determined from Figs. 11 (1st internode) and 12 (2nd internode), and those of the rate of cell division were decided arbitrarily in due consideration of the change of the values of Phase C. The values of Phase C were given by multiplication of the values of Phase C/Phase A by that of Phase A.

structed in Figs. 15 and 16. Cells near the cambial initials are not marked with letters, because cell division occurs not only in the cambial initial but also in the xylem mother cells. From these figures it is apparent that the first cell having intercellular spaces (cell "B") was a xylem mother cell when the tree was inclined. The number of cells situated in the transitional zone between normal wood and the typical compression wood containing intercellular spaces was measured on the trees harvested after 15, 20 and 26 days, and averages of 11 cells for the 1st internode and 13 cells for the 2nd were obtained. Therefore, the first cell (cell "A")

showing the least appreciable features (i. e., slightly thicker wall and faint excessive lignification) of compression wood cells in the 1st internode was the first cell in the Phase B, and in the 2nd the cell was situated in the Phase A near the Phase B at the commencement of the experiment. This difference between internodes would be related to the fact that the progress of the compression wood formation was more advanced in the 1st internode than in the 2nd, though the difference might be simply within a limit of experimental errors.

Concerning to the perception of the stimili responsible for characteristic features of a compression wood cell, KENNEDY and FARRAR (1965) proposed a hypothesis that each stimulus is percepted only by the cells in the immediately earlier developmental stage than its formation begins. However, the hypothesis seems to have

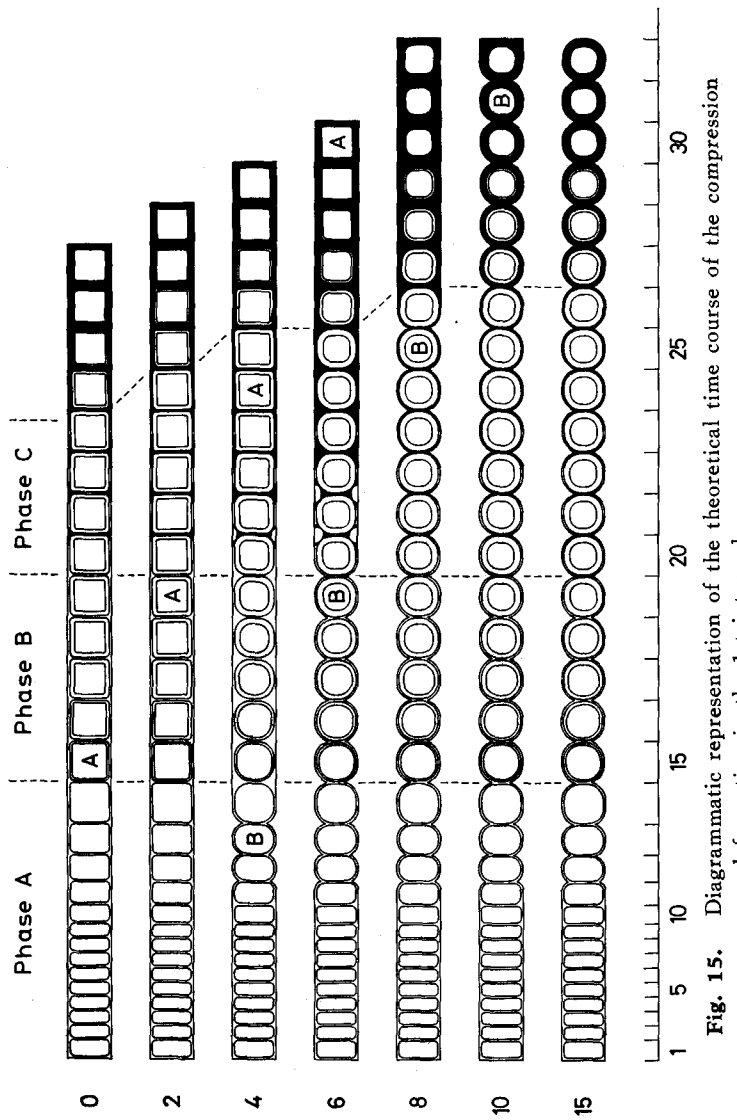

Fig. 15. Diagrammatic representation of the theoretical time course of the compression wood formation in the 1st internode.

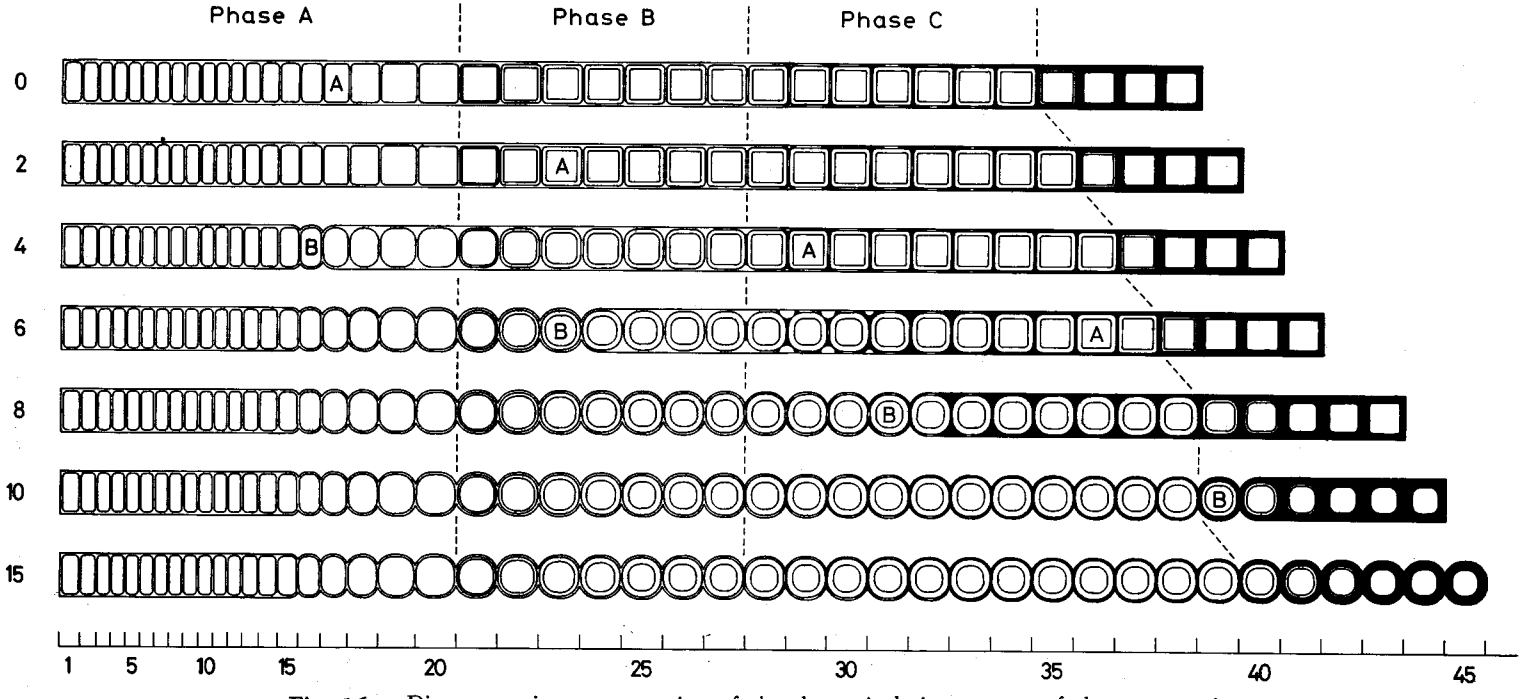

Fig. 16. Diagrammatic representation of the theoretical time course of the compression wood formation in the 2nd internode.

Figs. 15 and 16. The numbers of the cells in Phase A, B and C were given in Tables 3 and 4, and the numbers of the cells formed during the increase of the rate of cell division were calculated on the assumption that the rate had increased linearly by 6 and 8 days after the inclination in the 1st and 2nd internode respectively. The course of the surface growth, formation of the secondary wall and lignification, and wall thickness are arbitrarily illustrated. The degree of the lignification is not represented. The cells showing the least appreciable features of compression wood cells are marked with letter "A" and the first cells having intercellular spaces marked with letter "B".

Ca. 11 (1st internode) and 13 (2nd internode) cells were counted for the number of the transitional cells situated between normal wood and typical compression wood on the sections stained with iron haematoxylin (see text), however, smaller values than these seemed suitable from the anatomical observation on the time course (Photo 7–14). Therefore, 9 and 11 cells are illustrated as the transitional cells in the figures, although cells are marked with letters based on the counting mentioned above. Such a contradiction would imply the need of further studies.

some important problems. For example, it can be thought that some of the stimili are percepted fairly later than the time of the tilting treatment, and the perception occurs in an earlier developmental stage than that they believed. In the present investigation, the first cell having slightly thicker wall (cell "A") was found to have been situated near the earliest stage of the secondary wall formation at the beginning of the experiment (see Figs. 15 and 16). Assuming that the normal secondary wall formation could not be disturbed by inclination after its commencement, such a time lag or lags could not exist, or if any, with due consideration for experimental errors, the lag would remain within only a small extent in this case. On the other hand, this is not the case with the stimuli for heavy lignification and intercellular space formation, because the first cell showing the least excessive lignification, which is the same cell with that having slightly thicker wall (cell "A"), was found in the far earlier developmental stage at the beginning of the inclination, and a similar relation was obtained in the case of intercellular space formation as shown in Figs. 15 and 16. There must be some kinds of lags. This seems quite plausible because of relatively long presentation time for the induction of compression wood (ONAKA 1937 and KENNEDY and FARRAR 1965).

The rounded outline of compression wood cells has been thought to be established during the phase of surface growth, accompanying the formation of intercellular spaces (WARDROP and DAVIES 1964 and CASPERSON and ZINSSER 1965). However, the shape of cells can be also modified through the secondary wall formation, apparent in the case of the transitional cells (Figs. 15 and 16).

In the transitional zone, 11 and 13 cells were counted for the 1st and 2nd internode respectively. The difference in the value between the internodes is apparently smaller than that of the cell numbers in the cambial and differentiating zones. If the hypothesis proposed by KENNEDY and FARRAR is the case, the difference in the cell number of the cambial and/or differentiating zone between internodes should be reflected in that in the transitional zone.

Another important problem found in the hypothesis is a complete lack of the consideration on the degree of the development of compression wood cells. In the transitional zone, the first cell adjoining the normal wood seems to have slightly thicker wall and shows faint excessive lignification, and with increasing distance to the cambial side these features become more conspicuous, shifting to the typical compression wood cells. Apparently, the cells in the transitional zone show more or less gradual increase in the degree of compression wood cells as reported by FUJITA *et al.* (1979). Any hypothesis should explain the change in the degree of compression wood cells found in the transitional zone.

Conclusions

From these considerations, it is apparent that the transition from normal wood to compression wood can not be explained simply by the hypothesis of KENNEDY and FARRAR. They assumed that the width of differentiating zone and the rate of cell division before and after the inclination were the same, and that perception

occurred after inclination without any kinds of delay. However, as revealed by the present investigation, the width of the zone between the initiation of lignification of the middle lamella and that of the secondary wall showed gradual increase by ca. 10 days after the inclination, and the first row of the cells showing the least appreciable excessive lignification and that having intercellular spaces were found to have been situated, at the commencement of the inclination, in far earlier stages than those to be expected by the hypothesis. Furthermore, the theory can not explain the gradual increase in the severity of compression wood found in the transitional zone from normal wood to typical compression wood.

It is also apparent that detailed information on the cell wall structure of the transitional zone and other series of experiments are needed to disclose the nature of the perception of the stimuli. And it would be instructive for finding a key to clarify the subject to speculate on the relation between geotropic phenomenon of the primary tissues of herbaceous plants and the present problem. Such aspects of studies will be presented in following papers.

Acknowledgements

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要　　約

北海道大学農学部付属演習林名寄林木育種試験場に植えられている樹高約1.7 mのグラウカトウヒ (*Picea gluca*) を根元から曲げて45°に傾斜させ，それに引き続く，形成層帯，及び分化帯における細胞の形態的，数量的変化を日を追って観察した。

実験は2度行い，7月の実験では傾斜処理の0, 2, 4, 6, 8, 10, 15, 20, 25, 26日後に，また8月では0, 2, 5, 6, 7, 21日後に，1年生及び2年生節間のそれぞれ3カ所（先端部，中央部，基部）から傾斜の下側，上側の双方を含む試料を取った。試料は固定，脱水，パラフィン包埋の後，15 μ厚の木口面切片とし，ゲンチアンバイオレット—オレンジG，鉄ヘマトキシリン—オレンジG等で染色し検鏡した。また一部の試料は細切後，樹脂包埋し，紫外線 (UV) 顕微鏡で観察を行った。

得られた定性的，定量的結果は以下の通りである。

1) アクロレインを用いて固定した傾斜木試料では，その分化中のあて材細胞に，ゲンチアンバイオレットで強く染色される粒状物が見出された。この粒状物は2次壁形成の開始から，その木化の開始までの段階にある細胞の細胞質中にのみ見られ，他の分化段階にある細胞，正常材細胞ではまったく認められなかった。これは分化中のあて材細胞中に多量に蓄積されていると考えられるフェニルアラニンの存在下で，アクロレインが重合を起こしたものと推測される。

2) 傾斜処理後，樹幹の下側では，まず上記の粒状物が観察され，次に細胞の丸身，細胞間隙，細胞壁の異常肥厚と2次壁の強い木化の順で，分化中の細胞の形態に変化が現われた。これらの変化はいずれも樹木の先端に近い方でやや早く認められ，また7月では8月の約2倍の速度で進行した (Tables 1, 2 参照)。

3) 傾斜樹幹の上側にはあまり目立った形態的変化が認められなかったが，8月の実験では傾斜処理後一時的に形成されたと思われる晩材様の，壁が厚く半径方向に扁平な細胞が数列観察された。

4) 7月の試料については，形成層及びその派生細胞を便宜的な3つの分化段階 (Phase

A: クロスニコル間で複屈折を示さない，Phase B: 複屈折を示すが細胞間層の木化は始まっていない，Phase C: 細胞間層の木化は開始されているが2次壁の木化は始まっていない）に分け，その数を測定した（5半径列の平均）。また，木部直径（偏心のある場合は長径）についても測定を行った。

その結果，傾斜処理後樹幹の下側では，Phase C の値が約10日後まで増大し，傾斜前の約2倍となったが，Phase A, Phase B の値には変化が認められなかった。一方，樹幹の上側では Phase A の値が約10日後まで減少を続けたのに対し，Phase B の値は変化なく，また Phase C では一定あるいは多少の減少を示した。

5) Phase A と Phase C の値の間には正の相関関係が見出され，またこれにやや劣るが，木部直径と Phase A との間にも同様の関係が認められた。苗木や若木を用いての定量的研究を行う際には，これらの関係に注意する必要があろう。

6) 傾斜処理後に形成されたあて材細胞数の増加から，傾斜樹幹下側における細胞分裂の速度を，また，一時的に傾斜させることにより date marking した垂直木から，正常材における分裂速度を算出した。その値は垂直なものよりも傾斜樹幹の下側で大きく，また第2節間では第1節間よりも大きな値が得られた。傾斜処理後の分裂速度の変化を求める為に，形成層帯における分裂像数を柾目切片上で測定したが，バラツキが大きく変化のパターンを知ることは出来なかった。

7) 以上の形態的変化，各 Phase における細胞数の変化，及び細胞分裂速度の変化（Phase C の値の変化からの推定による）から，傾斜処理後に形成層とその派生細胞に現われた変化を論理的に再構成した。また，正常材から細胞間隙を含む典型的あて材までの移行部の細胞数を測定した。これから，光顕レベルで最初にあての特徴を示す細胞（木化の程度がやや強く，壁も多少厚い），また最も内側の細胞間隙を有する細胞は，傾斜設定時にそれぞれ，2次壁形成開始前後，木部母細胞帯にあったと推定された。

以上から形成層帯，及び分化帯における，あて材形成刺激の感受について考察した。

Explanation of photographs

Photo 1. General appearance of the experiment; a day after the inclination. Photographed on July 4, 1977.

Photo 2. A sample tree; 5 days after the inclination. Photographed on July 8, 1977. The tree is also seen in the above photo.

Photo 3. Cambial and differentiating zone of a vertical control harvested at the beginning of the experiment in July; the middle portion of the 1st internode; fixed in buffered acrolein and stained with a gentian violet — orange G combination.

Photo 4. Cambial and differentiating zone of an inclined control which had been inclined for 21 days before harvest. Note; particles of unknown nature in the cytoplasm strongly stained with gentian violet (arrows); the middle portion of the 1st internode; fixed in buffered acrolein.

Photo 5. An enlargement of Photo 4. Cells at the botton are in the course of the secondary wall formation and at the top lignification of the secondary wall begins. The particles (arrows) are restricted between these two developmental phases.

Photo 6. The particles (arrows) found in the differentiating zone of slight compression wood.

Photos 7–14. Changes in the cambial and differentiating zone on the lower side following the inclination in July. Sections were all stained with a gentian violet — orange G combination. Photos 7–9 and Photos 10–14 were taken from the specimens fixed in buffered acrolein and chromium — acetic acid solution respectively. The middle portion of the 1st internode.

Photo 7. Two days after the inclination. Note; nothing different from the vertical control except for the particles (arrows).

Photo 8. Four days after the inclination. Rounded outline in a cross section, intercellular spaces, excessive thickening of the cell wall and heavy lignification are all evident.

Photo 9. Six days after the inclination. Lignification of the middle lamella around intercellular spaces occurs.

Photo 10. Eight days after the inclination. A few rows of slight compression wood cells seem to have matured. For the section was fixed in chromium — acetic acid solution, the particles found in above photos are not seen.

Photo 11. Ten days after the inclination. The S 2 layer of the typical compression wood cells having intercellular spaces becomes lignified.

Photo 12. Fifteen days after the inclination. The appearance of the cambial and differentiating zone is seemingly not different from that of the 10-day material and the inclined control shown above.

Photo 13. Twenty days after the inclination.

Photo 14. Twenty-five days after the inclination.

Photo 15. Latewood-like cells formed on the upper side of a 21-day tree in August. The cells are radially narrow and have thicker cell wall, followed by the cells wider in radial direction; fixed in Zirkle's reduced chromium solution and stained with tannic acid — iron chloride.

Photo 16. An enlargement of Photo 15.

Photo 17. Clusters of the cells showing lesser degree of lignification as compression wood cells formed in a 21-day material in August. The clusters are found in the outer part of the transitional zone from normal wood to compression wood and are arranged tangentially; stained with an iron heamatoxylin — orange G combination.

Photo 18. An enlargement of Photo 17.


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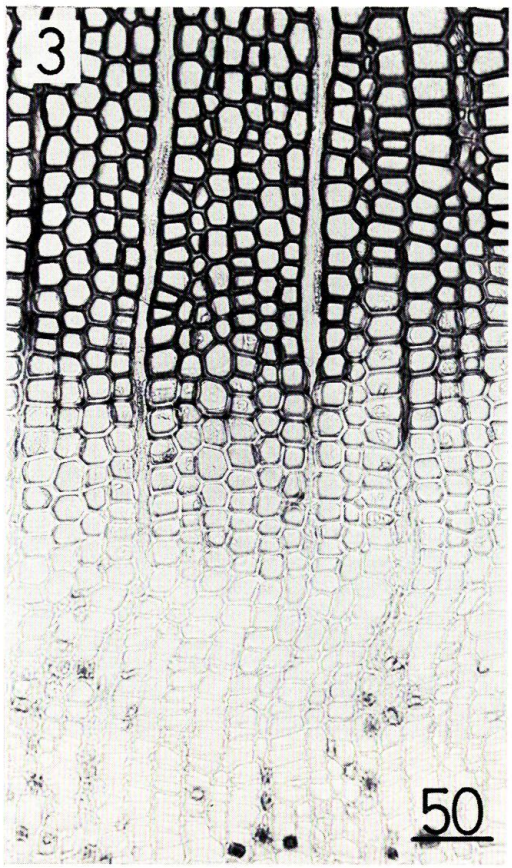
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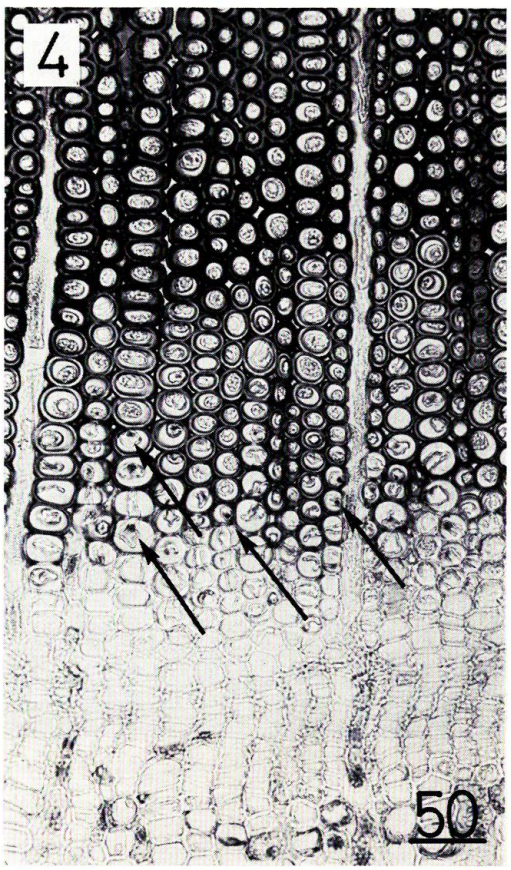
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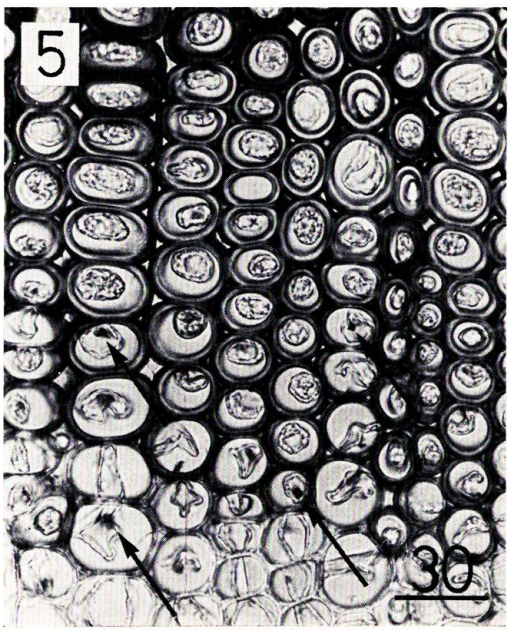
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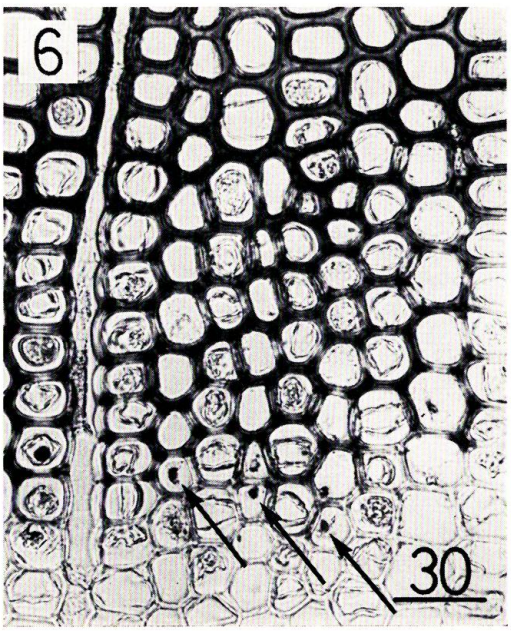
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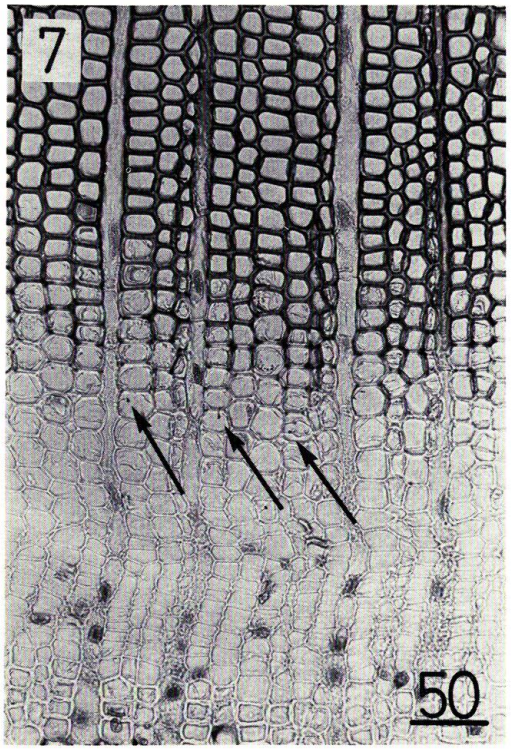
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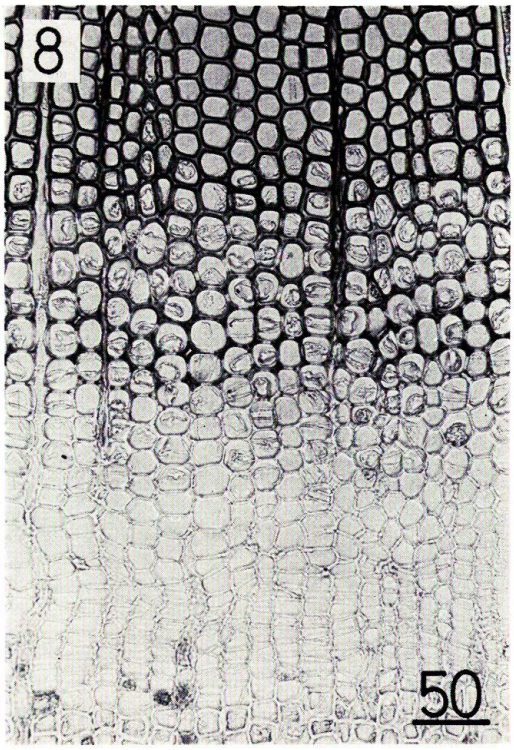
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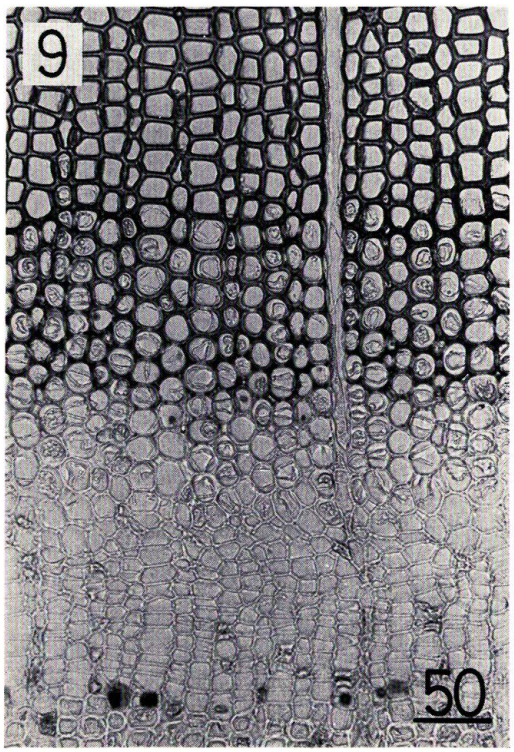
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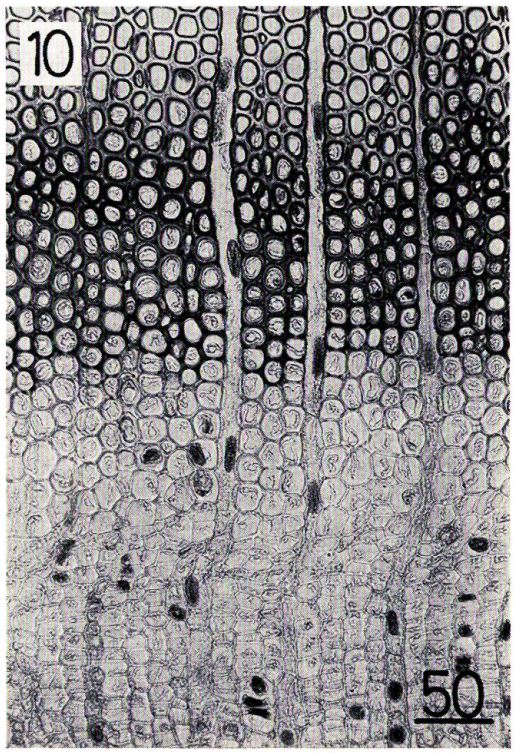
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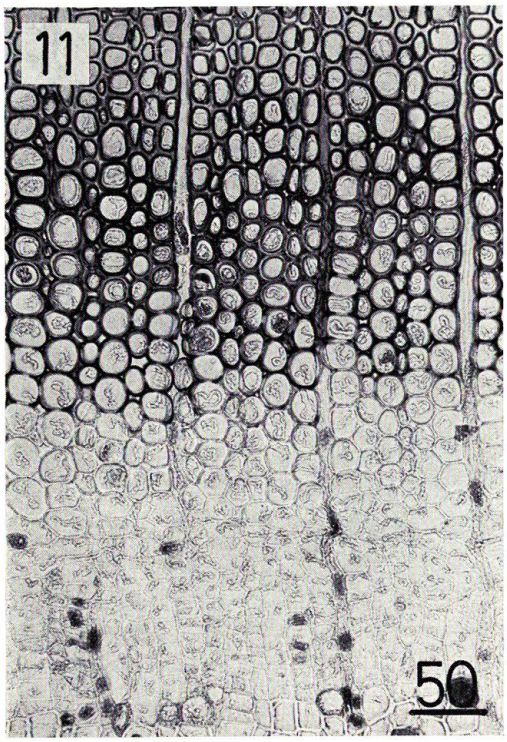
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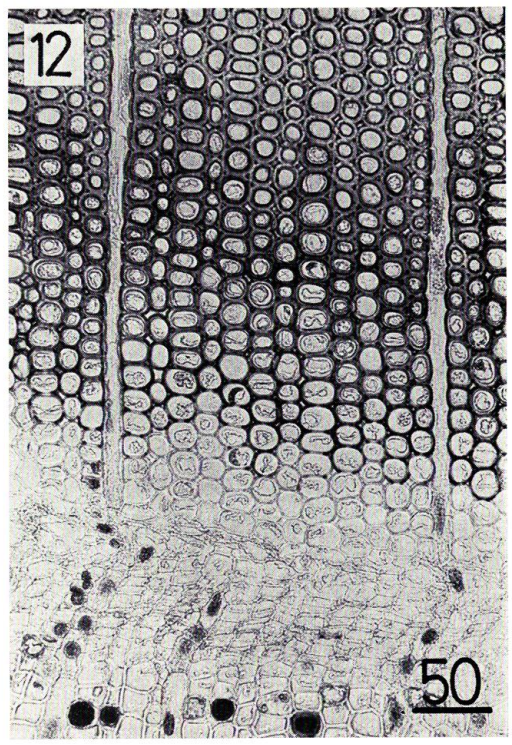
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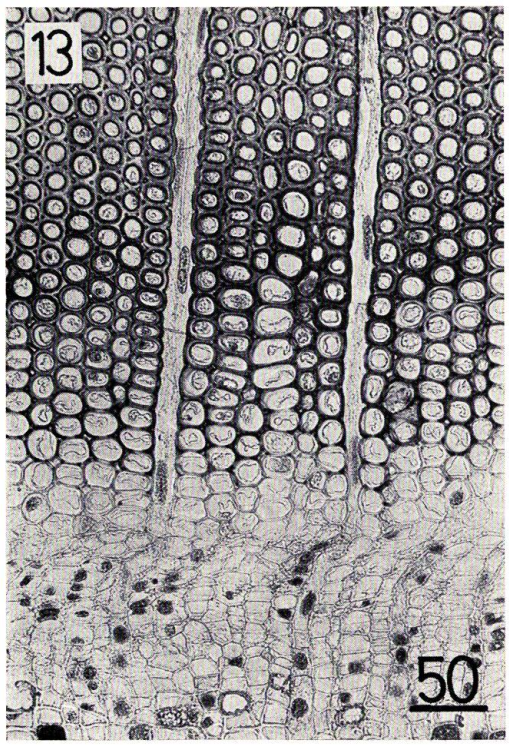
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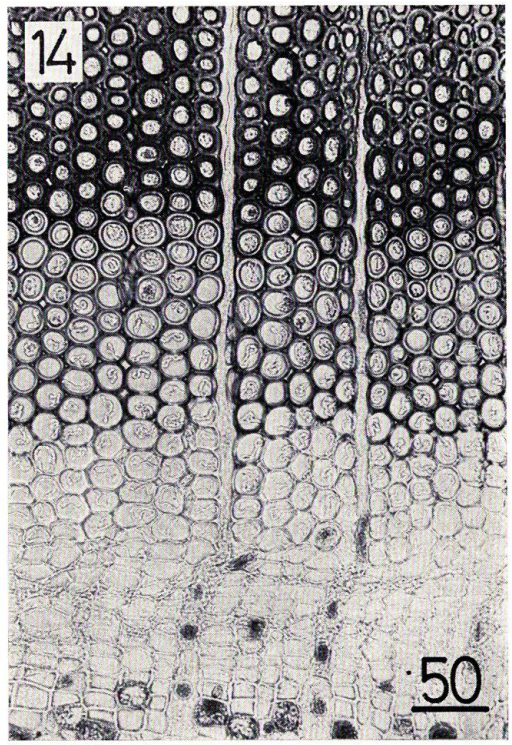
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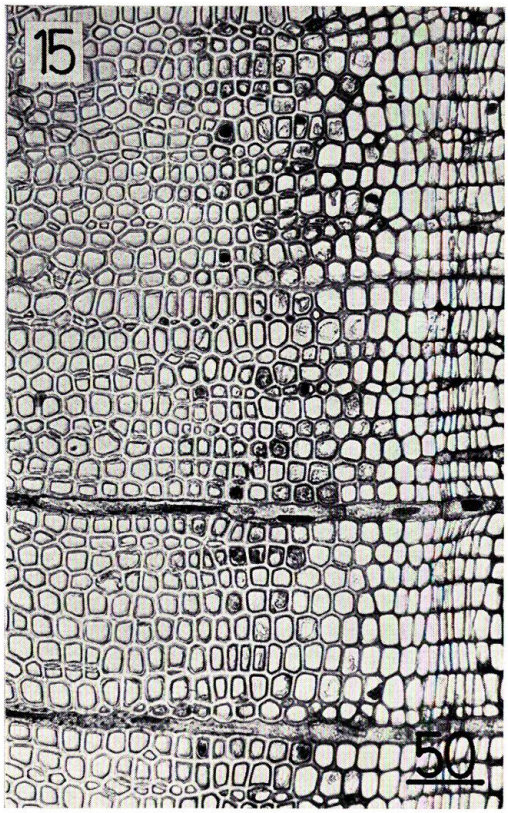
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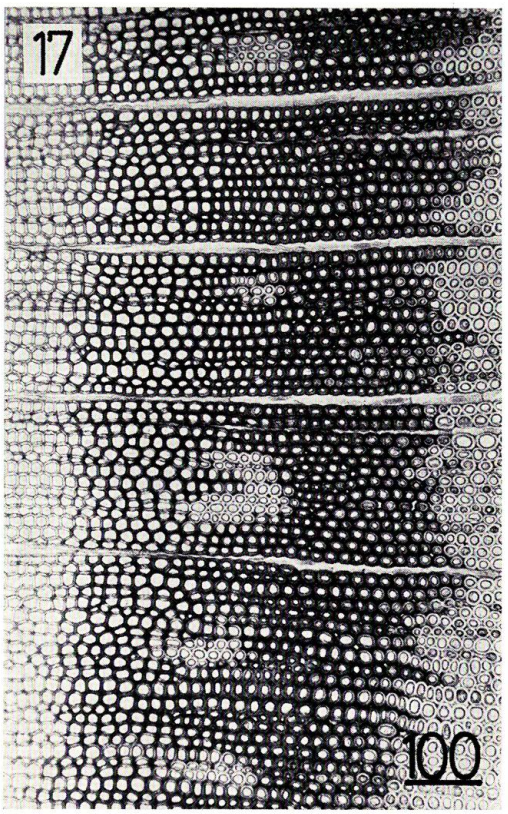
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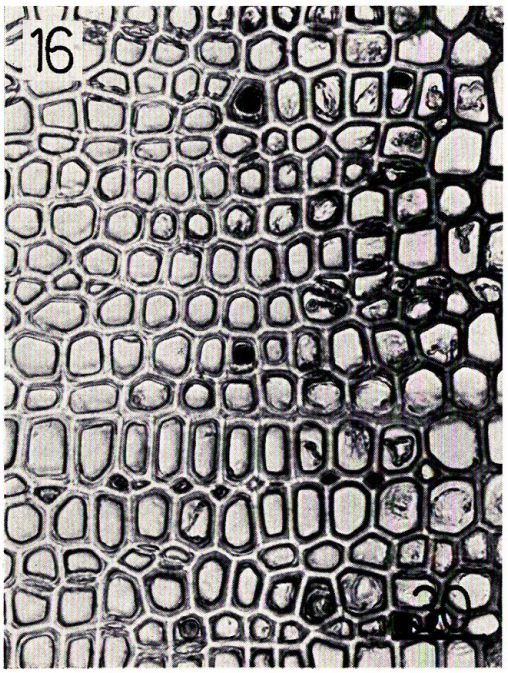
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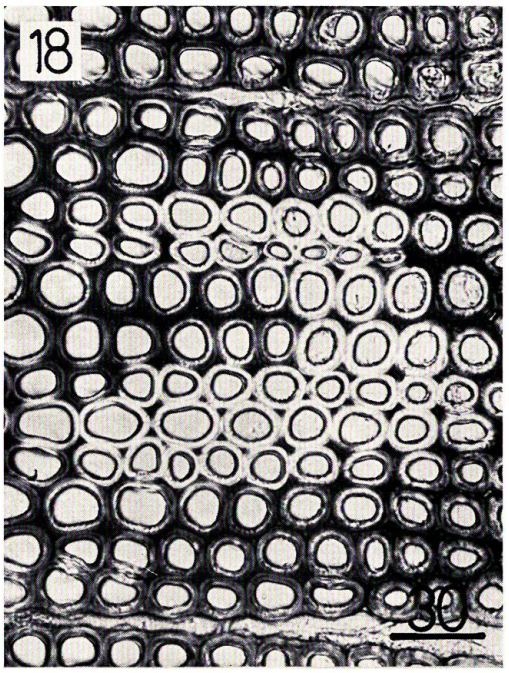
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