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STUDIES ON THE FORMATION AND STRUCTURE OF THE COMPRESSION WOOD CELLS INDUCED BY ARTIFICIAL INCLINATION IN YOUNG TREES OF *PICEA GLAUCA*

III. Light microscopic observation on the compression wood cells formed under five different angular displacements

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Introduction

Compression wood is a particular type of wood formed generally on the lower side of leaning stems or branches in gymnosperms (except for Cycadopsida and Gnetopsida)[26,27]. The occurrence of this reddish wood has been known since several hundred years ago and concerning to the causal factor to evoke its formation, considerable number of hypotheses were proposed by earlier workers[18,19,25,26]. A strong indication of the primary involvement of gravity in compression wood formation was first given by an ingenious experiment of EVART and MASON-JONES[7] and this was confirmed repeatedly by later investigators[3,17,18,28]. Compression wood formation is, at present, thought to be a geotropic manifestation of the secondary tissue in those gymnosperms[23,26,27]. In geotropism in herbaceous plants, responses are known to occur depending on angular displacement from the equilibrium position (generally vertical) and this would be also the case in compression wood formation, though many factors are known to affect the formation[16,26,27].

Thus, the relation between the degree of stem deviation and the severity of compression wood formation is considered of primary importance in the study of this phenomenon, however, there has been no sufficient experimental studies such as that made by ROBARDS[22] in tension wood. The degree of compression wood formation would be manifested in two different ways,

namely, in structural alteration and amount of cells formed. LITTLE[15] noted that compression wood formation increased to a maximum between 0° and 60°, whereas the relatively greater growth on the lower side increased to a maximum between 90° and 120°, based on an experiment with *Pinus strobus* grown at angles of 0°, 60°, 90° and 120°. Recently, HARRIS[9] tilted trees of *Pinus echinata* at angles of 20°, 30° and 45°, and observed the wood formed using SEM. He reported that the transition from earlywood to latewood progressed from abrupt to gradual as the severity of compression wood increased and that the modification of the tracheids was notably more pronounced in the latewood than in the earlywood. Although other reports suggesting the relation between the amount of compression wood and the degree of lean[3,10,11,20,33], in any case, these reports were not made on compression wood cells but the wood itself. Thus, no carefull cytological studies on the present problem seems to have been performed.

In the present study, structural features of compression wood cells in young trees of *Picea glauca* grown under five different angular displacements are investigated light microscopically. The chief interests are the relation between the degree of the angular displacement and the severity of compression wood cells, and the adaptation of trees to new equilibrium positions. Several aspects in growth of sample trees and preliminary macroscopic and light microscopic observations were already reported in a brief note[29].

Materials and Methods

Young trees of *Picea glauca* ca. 2 m high grown in the nursery of The Laboratory of Forest Tree Breeding in Nayoro, College Experiment Forests, Hokkaido University, were bent in July 1978 at some 30 cm above the ground level to be inclined at 5°, 10°, 20°, 45° and 90° from the vertical and the 1st and 2nd internodes were tied to woody stakes with strings. No compression and tension is expected to have been exerted on these internodes. Two trees were used on each, but three for the displacement of 5°. In winter, protections were given against snowfall. After about a year, the 2nd and 3rd internodes, which were the 1st and 2nd in the previous year, were harvested in August 1979 for a light microscopic observation. Materials were severed from three portions, *i. e.*, distal, middle and proximal, of each internode and fixed in Zirkle's reduced chromium solution[34] and embedded in paraffin. Sections of 10 μ were cut on a sliding microtome and stained with an iron haematoxylin — orange G combination.

Details of sample trees are presented in Table 1.

TABLE 1. Details of sample trees

Tree (Code)	Angle of stem deviation at the beginning of the experiment	Angle of stem deviation at harvest	Length of the 2nd internode	Diameter of the middle portion of the 2nd internode	Length of the 3rd internode	Diameter of the middle portion of the 3rd internode
90-a	90°	89°	36.0 cm	18.8 mm	29.5 cm	28.4 mm
90-b	90°	91°	29.0 cm	19.3 mm	14.0 cm	24.6 mm
45-a	45°	41°	38.5 cm	19.6 mm	26.5 cm	27.3 mm
45-b	45°	42°	41.5 cm	21.7 mm	24.5 cm	30.0 mm
20-a	20°	17°	40.5 cm	21.6 mm	30.0 cm	30.0 mm
20-b	20°	18°	47.0 cm	21.7 mm	21.5 cm	30.9 mm
10-a	10°	9°	36.0 cm	22.8 mm	26.0 cm	30.3 mm
10-b	10°	9°	43.0 cm	21.8 mm	26.0 cm	31.3 mm
5-a	5°	6°	40.0 cm	22.0 mm	30.0 cm	29.9 mm
5-b	5°	4°	50.0 cm	24.2 mm	23.5 cm	34.6 mm
5-c	5°	5°	41.5 cm	20.6 mm	35.0 cm	31.3 mm

Results

In the following description, sample trees will be called by code names presented in Table 1. No marked differences but a steady increase of the severity of compression wood cells towards the distal portion within a internode was observed. On the other hand, often notable differences were found between internodes. Therefore, description will be focussed on the middle portions of the both internodes and the number of the internode will be given in Roman numerials after the code name. For example, 45-a-II means the middle portion of the 2nd internode of a tree inclined at 45°.

Angular displacement of 90° from the vertical

Photos 1 to 3 show disks of 90-a-II, -III and 90-b-III respectively. Compression wood dark in colour developed strongly and is widened laterally to give a roughly triangular shape especially in 90-a-II. Crescents of compression wood contain bands of different colours arranged tangentially and the depth of colour is markedly reduced in the second year. Minute spots bright in colour are vertical resin canals and sharp lines running radially are leaf traces.

In these disks typical compression wood was formed thoroughly except for the close vicinity of the growth ring boundary. A dark band found in the inner portion of the first crescent in disk 90-a-III was found to be caused by smaller cell diameter and thick cell wall. No other appreciable differences

could be found between sample trees and between internodes, and cells formed shortly after the inclination (Photo 4) and those formed shortly before the harvest (Photo 5) have all the features of typical compression wood cells.

On the other hand, the region near the growth ring boundary showed particular features differing between sample trees and between internodes. The most prominent and peculiar one is abnormal latewood developed most typically in 90-a-III (Photo 6). Insufficient lignification as compression wood cells (since haematoxylin was destained to differentiate compression wood cells from normal ones, walls bright in colour means lesser degree of lignification than compression wood cells, if no account of physical effects in staining[2] is taken) is found up to 10- to 20-cell deep back from the growth ring boundary and walls become thinner towards the boundary, the last 5 to 7 cells being crushed radially or tangentially. Many of these cells are filled with yellow (pressumably stained with orange G) frothy or gummy substances, or contain relatively small dark materials. Abnormalities resembling frost injury are also found in ray cells. The occurrence of these cells are reduced in another sample tree (90-b) and strongly favoured in the 3rd internode (compare Photo 8 with Photo 6). These cells give an impression that they were killed in the course of differentiation. On the other hand, earlywood cells showed features of frost injury. In sample tree 90-a, in which the severe abnormalities in latewood were found, frost injury developed more seriously than in sample tree 90-b and did not show conspicuous differences in the severity between internodes. Although these abnormalities seem to affect structural features of compression wood cells, further description exceeds the sphere of the present work.

Latewood and earlywood cells in the close vicinity of the growth ring boundary were found to lack in some of the characteristic features of this type of wood. Intercellular spaces are not formed around the last 3 to 5 latewood cells (Photos 7 and 8) except for 90-a-III (Photo 6), in which the last 7 to 10 abnormal latewood cells lack in the spaces. In earlywood of 90-a-II (Photo 7) the first formed cells have rounded outline and heavily lignified thick cell walls, some of them comparing with typical compression wood cells, though lacking in intercellular spaces, which did not appear until approximately the 10th cell from the ring boundary. In 90-b-II, the first earlywood cells showed slightly reduced features, however, intercellular spaces were found at about the 6th cell. In the 3rd internodes of both sample trees, lesser degree of lignification and cell wall thickness were observed as compared with those in the 2nd. Intercellular spaces first appeared approximately at the 10th cell in 90-b-III and at the 15th cell in 90-a-III

(Photo 6), and typical compression wood cells were formed ca. 15-cell deep from the growth ring boundary. Generally the formation of intercellular spaces follows the full development of the thick cell wall but in 90-b-III, in which the first several rows of the earlywood cells had considerably thinner wall, the reverse was observed.

Thereafter, typical compression wood cells continued to be formed by the end of the experimental period.

Angular displacement of 45°

Disks formed under the displacement of 45° (Photos 9 to 11) are not so different from those formed under 90°, however, their triangular forms are less obvious especially in 45-b-III (Photo 11). In the 2nd internodes (Photo 10), disks show more angular form than those of the 3rd internodes. In 45-a-III and 45-b-III, early formed wood of the second crescent is brighter than that of 45-b-II (Photo 10).

Typical compression wood cells (Photo 12) are exclusively formed in these sample trees except for the region near the growth ring boundary as those inclined at 90°.

The abnormal latewood cells mentioned above developed to the same intensity with those formed under the displacement of 90°. The number of the latewood cells lacking in intercellular spaces is almost the same (3 to 5 cells, Photos 15 and 16) or slightly greater (ca. 10 cells, in 45-a-III, Photo 14) than in horizontally placed stems. There seems a general rule that the number of cells without the spaces increases, as the severity of the abnormal latewood increases. Frost injury in earlywood also developed, however, wall thickness of the first earlywood cells is generally thinner than in the horizotal stems especially in 45-a-III (Photo 14), where earlywood gives brighter colour in the disk (Photo 9). Intercellular spaces were formed around the 9th to 12th cells from the ring boundary in 45-a-II and the 7th to 9th cells in 45-b-II. In these samples, walls of the first formed earlywood cells are considerably thicker and the thickness reaches that of typical compression wood cells up to 5th cell or so (earlywood cells in Photo 15 are affected by frost injury and have thinner wall than those in other regions). On the other hand, in the 3rd internodes, in which the first cells have considerably thinner wall, intercellular spaces are found approximately from the 10th cell (45-b-III) or more than 20-cell deep (45-a-III, Photo 14) where cell wall thickness first developed fully.

From these region to the differentiating zone (Photo 13) typical compression wood cells were formed exclusively.

Angular displacement of 20°

Disks are no longer triangular and the colour is apparently brighter in 20-a-II and -III (Photos 17 and 18), but in 20-b-II and -III (Photo 19) the colour is still considerably deep as those of greater angular displacements. The depth of the colour decreases apparently in the second year. Striations in early formed wood of the second crescent are distinct in 20-a-II and -III (Photos 17 and 18) and both show a similar pattern.

Typical compression wood cells are formed also under this angular displacement (Photo 23). Cells formed shortly after the inclination (Photo 23) show almost the same structural features with those formed under the displacement of 90°, though the depth of colour on disks is decreased especially in a sample tree (20-a). In the region of the growth ring boundary (Photos 20 to 22), the formation of the abnormal latewood is markedly reduced; in the 3rd internodes 5 to 10 cells show insufficient lignification but no crushed thin-walled cells is found (Photo 20); in the 2nd internodes almost no abnormalities is formed (Photos 21 and 22). The number of the cells lacking in intercellular spaces is not so different from those of greater stem deviations (4 to 8 cells), but in 20-a-II the last 8 to 10 cells lack in the spaces and assume considerably square outline (Photo 21). A trace of frost injury was found in 20-b-III. In the 2nd internodes the first several rows of earlywood cells have generally thinner wall and assume more square outline (Photos 21 and 22) than those formed under the displacement of 45°. However, in the 3rd internodes cell wall thickness was similar or thicker than that of 45° displacement in which serious frost injury was observed. Interestingly, intercellular spaces are found in earlier stage than in the samples of 45° inclination, namely, at the 5th to 10th cell from the boundary (Photos 21 and 22) except for 20-b-III (Photo 20), in which the spaces first appear at the 10th to 15th cell. In 20-a-II (Photo 21) and -III cell wall thickness reaches a temporal maximum at the 15th to 20th cell, which is, however, not that of typical compression wood cells, and moderate compression wood cells with few intercellular spaces and reduced roundness are formed at the harvest (Photo 24). Striations found in disks 20-a-II and -III seemed to be caused by differences in cell wall thickness and cell diameter. In the other tree (20-b) the thickness reaches that of typical ones at about the 10th cell in the 2nd internode (Photo 22) and a temperal maximum was found in the 3rd internode at the 10th to 15th cell, though slightly thinner than typical ones. In this tree typical compression wood cells were formed at the harvest in both the internodes.

Angular displacement of 10°

The degree of the development of compression wood crescents is markedly reduced as compared with those formed under 20° displacement particularly in 10-a-II and -III (Photos 25 and 26), in which decrease of the depth of the colour is apparent in the first year and only faint bands of darker colour in earlywood are found in the second year. In 10-b-II and -III (Photo 27) the crescents of the first year are considerably dark in colour, however, in the second year the depth of the colour markedly decreases, though deeper than 10-a-II and -III.

Cells formed under angular displacement of 10° show all characteristics of typical compression wood cells, however, they are by no means typical ones (Photo 28). Cell wall thickness and the number and size of intercellular spaces seem apparently reduced especially in the 3rd internodes (Photo 29). In all the specimens intercellular spaces became not formed in the course of time, and cells assumed more square outline in the 3rd internodes, though in 10-b-II the spaces are formed up to approximately the 25th cell back from the growth ring boundary (Photo 30). Particularly, in 10-a-III the degree of compression wood cells decreases conspicuously towards the boundary (Photo 31). The abnormal latewood was not formed, however, slight frost injury rather in favour of the lower side was observed in the 2nd internodes. Latewood cells are considerably round (10-a-II, Photo 32, and -III) or nearly square (10-b-II, Photo 33 and -III). The first several rows of earlywood cells of all the specimens have slightly thicker wall than normal ones and have somewhat rounded outline, however, no intercellular spaces was formed except for 10-b-II, in which small and a fewer number of the spaces were found after the 15th to 20th cell from the boundary. Thereafter, the degree of compression wood cells fluctuated to decrease in all the specimens. Seemingly normal wood cells are formed at the harvest (Photo 34), but in 10-b-II, where intercellular spaces appeared in the middle of the growth layer and slight compression wood cells showing somewhat thicker wall with slightly rounded outline but lacking in intercellular spaces are formed at that time (Photo 35).

Angular displacement of 5°

Three trees were inclined at 5°. Disks 5-a-II and -III (Photos 36 and 37) show the slightest crescents or arcs. The decrease of the depth of the colour in the first year is abrupt and no compression wood can be distinguished macroscopically in the second year. On the other hand, other disks showed considerable depth of colour in the first year, especially in disk

5-b-II (Photo 38) the colour is apparently deeper than that of disk 10-a-II (Photo 25). In these disks only a few bands of faint colour are found in the second year, but in 5-c-II (Photo 39) a band is thick and deep in colour making an apparent crescent.

Mild compression wood cells are formed shortly after the inclination and intercellular spaces are small but abundant (5-a-II, 5-b-II and 5-c-III, Photo 41) or occasional and few (5-b-III and 5-c-II, Photo 42) or absent (5-a-III, Photo 43). Towards the growth ring boundary, cell wall thickness remains almost unchanged with decreasing occurrence of intercellular spaces in 5-b-II (Photo 44) or the degree of compression wood cells decreases rather abrupt as shown in the disk (5-a-II, Photo 45) or fluctuates showing wavy appearance in others (Photo 46). Latewood cells seem almost normal in 5-a-II (Photo 47) and -III or slightly round in 5-b-II (Photo 48), -III and 5-c-II or apparently round in 5-c-III (Photo 49). The first several rows of earlywood cells seem to assume slightly rounded shape in many of the specimens. However, those of the opposite side showed also the same appearance, particularly if frost injury was accompanied. Therefore, it is difficult to judge whether these cells are actually slight compression wood cells or not, from the slight roundness of the outline. However, cells found in 5-c-II and -III (Photo 49) especially in 5-b-II (Photo 48) must be those of the lowest degree of compression wood. In the second year all the specimens showed fluctuation of the degree from normal to slight compression wood, but in 5-a-II and -III normal wood was formed in major part of the growth layer. At the harvest apparently normal wood cells are formed in all the specimens (Photo 50).

Discussion and Conclusions

From the observation on disks, it is apparent that the depth of the colour of compression wood increases, as the angle of stem deviation increases. However, this is not always the case. Colour of the wood formed under the displacement of 90° and 45° gave almost the same depth. This would be explained by the saturation in the response mechanism. And the first crescent of compression wood in disk 20-b-III (Photo 19) showed almost the same depth of the colour with that of 45-b-III (Photo 11), 10-b-III (Photo 27) with 20-a-III (Photo 18) and 5-b-II (Photo 38) with 10-a-II (Photo 25) etc. (Photographs are not necessarily reliable for the reproduction of the true depth of the colour). Compression wood found in the crescents of deeper colour generally showed greater severity except for the difference between the first and second year found in disks formed under

greater angular displacements. The depth of colour decreased in the course of time after inclination, especially in the second year the depth was markedly reduced. This means apparently the reduction of the severity of compression wood, which was confirmed by the light microscopic observation.

The reduction would be caused by adaptation of trees to new equilibrium positions, *i. e.*, fixed leaning positions. This is also suggested by the fact that if a tree which has long been inclined is returned back to the vertical position, compression wood is formed on the former upper side[13,32]. In herbaceous plants, it is also known that no response occurs after prolonged gravitational stimulation[1]. However, such a drastic reduction of the degree of compression wood has not been reported in adult trees. Plausibly, younger trees have greater adaptabilities than adult ones. The reduction, in most cases, did not occur steadily but rather fluctuatingly to make bands of different colours. This means that the degree of compression wood is strongly affected by a factor or factors other than gravity and that threshold value for the formation of slightest compression wood is difficult to determine.

The difference in the depth of the colour between the first and second year found in disks of greater angular displacements seems not caused by the difference in the degree of compression wood cells. The depth of colour is thought to be determined mainly by the degree of lignification and wall percentage. The participation of the latter is apparent in latewood and dark bands in the first year in disk 90-a-III (Photo 2) and in the second year in disks 20-a-II and -III (Photos 17 and 18) were shown to be caused by thicker cell wall and smaller cell diameter. In disks formed under the displacements of 90° and 45°, typical compression wood cells were formed exclusively except for the close vicinity of the growth ring boundary and no appreciable differences in cell wall thickness and cell diameter was found between the first and second years. The degree of lignification was not studied in the present work. This difference between years is not thought to be brought about by the aging of the cambium, because the 2nd internodes showed almost the same depth of the colour and similar degree of the difference.

Thus, a tree grown under a fixed angular displacement can form various degrees of compression wood cells. However, the relation between the angle of stem deviation and the degree of compression wood cells should be considered from the observation on the wood formed shortly after the inclination, because compression wood cells of lesser degrees formed through the adaptation to the fixed leaning position can not be thought to reflect directly this relation. Compression wood cells formed shortly after the inclination

at 20° or more showed typical features and those formed at 10° were of slightly decreased degree. In the latter all characteristics of compression wood cells were found, but cell wall thickness was apparently reduced. Cells formed under the displacement of 5° had far more reduced wall thickness and considerably square outline, though intercellular spaces could be found among these cells. From these evidences, it can be said that the response mechanism for the compression wood formation is saturated on the lower most side of trees inclined at angles of 20° or more. However, cell wall thickness, roundness, the degree of lignification, the number and size of intercellular spaces were not measured in the present study. Differences might perhaps be shown among these typical compression wood cells and this leads to a question to be solved what a typical compression wood cell is. In the compression wood formed under the displacement of 5°, a scanty occurrence of intercellular spaces was observed in a half of the specimens. This implies that the threshold value for the formation of intercellular spaces would be nearly 5°.

As mentioned above, compression wood cells formed in the 2nd internodes showed higher degree than in the 3rd with an exception. In a previous paper[30], the sensitivity to the gravitational stimulus was suggested higher in the 1st internode than in the 2nd. Younger internodes would have higher sensitivities in general.

Under the displacements of 90° and 45°, typical compression wood cells continued to be formed in all the specimens, however, in the region near the growth ring boundary, different features were observed. Compression wood cells in the close vicinity of the boundary especially those in earlywood are known to lack in some of the typical features even in strongly developed compression wood[4,8,12,24]. Furthermore, the abnormal latewood and frost injury were observed in the present study. To our knowledge, the former has not been reported and is apparently different from late frost injury[6]. These cells seem to have been killed in the course of the differentiation. In the trees equivalent to those used in the present work inclined at 45°, the activity of the cambium on the upper side ceased in early autumn, however, on the lower side many differentiating cells were found even in mid December especially in the proximal internodes, and the cambial activity seems to be initiated earlier on the lower side than on the upper[32]. DADSWELL and WARDROP[5] reported earlier commencement of the activity on the lower side of leaning stems and branches of gymnosperms, though PRIESTLEY and TONG[21] stated the reverse and KUTCHA *et al.*[14] reported to be same. The occurrence of the abnormal latewood cells in favour of the

proximal internode and the fact that no abnormalities in both latewood and earlywood was found on the upper side[29] would indicate that many latewood cells remaining immature even at the end of growing season were killed in the winter or early spring, and earlywood cells were injured by frost, because of earlier initiation of the cambial activity on the lower side.

These abnormalities seem to affect the severity of compression wood cells. In the abnormal latewood more number of cells without intercellular spaces was found. This would imply also later cessation of the activity on the lower side. Frost injury in earlywood seems to cause thinner wall and this would mean earlier initiation of the cambial activity. Frost injury also gives increase of the roundness in normal and compression wood cells of lesser degrees. Therefore, the degree of compression wood cells is difficult to judge, if these abnormal features are present.

However, general tendency could be shown. The most well-developed compression wood cells in this region were found in the 2nd internode of a tree inclined at 90°. Although the last formed latewood cells had thinner wall, a feature of the abnormal latewood, walls of the first formed earlywood cells were as thick as those of typical compression wood cells though intercellular spaces were not formed. The last and first formed cells in other specimens showed lesser degrees than these and apparently normal wood cells were found in a tree inclined at 5°. Thus, in this region all degrees of compression wood cells from normal to typical ones were observed over the full range of the angles of stem deviation. In comparison with the cells formed shortly after the inclination in July, these cells are thought to be not so sensitive to the geotropic stimulation, however, they can be typical compression wood cells if the angle of stem deviation is great enough, though lacking in intercellular spaces and flattened radially in latewood. In earlier works[4,12,24] apparently no account for the degree of stem deviation was taken and compression wood cells in the vicinity of the growth ring boundary should be reexamined closely from such a point of view.

It is of interest that the number of cells without intercellular spaces seems not affected greatly by the angle of the deviation, if the angle is great enough. HÖSTER[12] found in 30-year-old stems of *Picea abies* that the first formed earlywood cells in compression wood looked like normal and attributed this to a possibility that they were derived from xylem mother cells of the previous year and not destined to differentiate into compression wood cells, because of low IAA-availability in late summer. However, the most severe first formed compression wood cells found in 90-a-II had no intercellular spaces, though all other characteristic features developed typically,

and this leads to another possibility that formation of intercellular spaces is controlled by a different factor. Intercellular spaces are occasionally found to occur in normal wood and in some species their occurrence in normal wood is common and regarded as a diagnostic marker. A question whether xylem mother cells are distined in the previous year or not could be solved by an experiment in which trees inclined in the previous year are returned to the vertical position or, to the contrary, vertically grown trees are inclined during the dormant period.

The wood formed about a year after the inclination, namely, shortly before the harvest, showed full range of the degrees of compression wood cells. However, they represented rather two extremes of the severity. All trees inclined at 90° and 45°, and a tree at 20° continued to form typical compression wood cells. On the other hand, those inclined at 5° and that at 10° formed apparently normal wood at the harvest. The limit of the angle of stem deviation, at which adaptation of trees to the leaning position can occur, might lie between 10° and 20°. However, if trees of greater stem deviations had been kept inclined for a more longer period, normal wood might have been formed.

In a tree inclined at 10° very slight compression wood cells were observed (Photo 35). Detection of the compression wood cells of lesser degree than those is apparently beyond the limit of light microscopy. The slightest compression wood cells observed by ultraviolet microscopy are normal other than faint characteristic UV-absorption in the outer region of the S 2 layer at cell corners[8]. However, whether these cells possess the S 3 layer or not has not been known. Structural features of the slightest compression wood cells will be studied by a SEM-UVM combination method[3,10] in a following paper.

Summary

Young trees of *Picea glauca* ca. 2 m high were bent in July 1978 at some 30 cm above the ground level to be inclined at 5°, 10°, 20°, 45° and 90°, and fixed with stakes and strings; two sample trees on each but three for the deviation of 5°. After about a year, materials were severed from three portions of both the 2nd and 3rd internodes and fixed, dehydrated and embedded in paraffin. Sections of 10 μ thick were cut and stained with an iron haematoxylin — orange G combination. Following results were obtained.

i) The depth of the colour of compression wood on disks generally increases as the angle of stem deviation increases and the depth decreases

in the course of time especially in the second year. ii) The compression wood cells formed shortly after the beginning of the experiment were typical in trees inclined at 20° or more, moderate at 10° and mild at 5°, in which some of them lacked in intercellular spaces. The degree of compression wood cells were higher in the 2nd internodes than in the 3rd and also higher in distal portions within a internode. iii) Latewood and earlywood cells near the growth ring boundary showed lesser degrees of compression wood cells than in other regions of the growth layer. In trees inclined at 45° or more abnormal latewood cells with insufficient secondary wall deposition and lignification were found especially in the 3rd internodes. They seem to be killed in the course of differentiation because of the later cessation of the cambial activity on the lower side. The first formed earlywood cells were almost typical in a specimen from a tree inclined at 90° and normal in some of the specimens at 5°, and all intermediates were observed in the others. iv) Cells formed shortly before the harvest were typical in trees grown at 45° or more and a tree at 20°, and were normal in trees at 5° and a tree at 10°. v) From these evidences relation between the angle of stem deviation and the severity of compression wood cells, and adaptation of trees to new equilibrium positions, *i. e.*, fixed leaning positions, were discussed.

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EXPLANATION OF PHOTOGRAPHS

PLATE I. Angular displacement of 90°

Photos 1, 2 and 3. Disks 90–a–II, –III and 90–b–III respectively. Compression wood dark in colour developed fully to give a nearly triangular form. The first inner crescent of compression wood is darker than the second crescent. Sharp lines brighter in colour oriented radially are leaf traces and minute spots are vertical resin canals.

Photo 4. Typical compression wood cells formed shortly after the inclination. (90–b–III).

Photo 5. Typical compression wood cells formed shortly before the harvest. (90–b–III).

Photo 6. Abnormal latewood and frost injury in earlywood found in 90–a–III. In the former, cells are not sufficiently lignified and walls become thinner towards the growth ring boundary. The last 5 to 7 cells are crushed radially or tangentially. Cell inclusions different in kind are also found.

Photo 7. Growth ring boundary in 90–a–II. Abnormal latewood cells insufficient in lignification are found. The last 3 to 5 latewood cells lack in intercellular spaces. The first formed earlywood cells are heavily lignified and thick-walled, some of them are thought typical compression wood cells though lacking in intercellular spaces. Abnormalities associated with frost injury are also seen.

Photo 8. Growth ring boundary of 90–b–III. The degree of the formation of the abnormal latewood is decreased in this tree. The first several rows of the earlywood have considerably thinner wall as compared with that of 90–a–II (Photo 7). Abnormal shape of ray cells widened in tangential direction is a feature of frost injury.

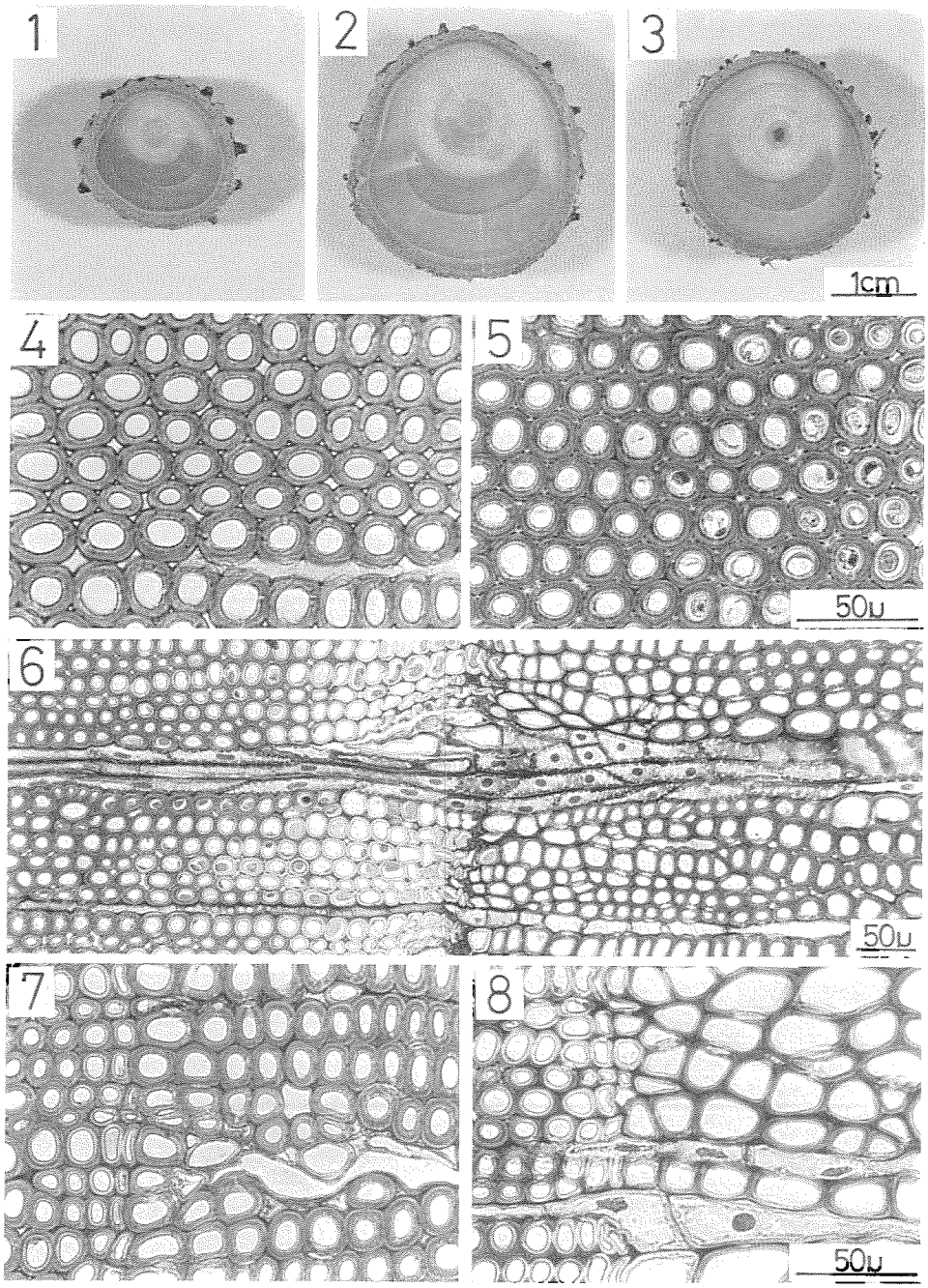

1
2
3
1cm
4
5
50μ
6
50μ
7
8
50μ

PLATE II. Angular displacement of 45°

Photos 9, 10 and 11. Disks 45-a-III, 45-b-II and -III respectively. Triangular shape of the disk is slightly decreased as compared with those of 90°, especially in 45-b-III (Photo 11).

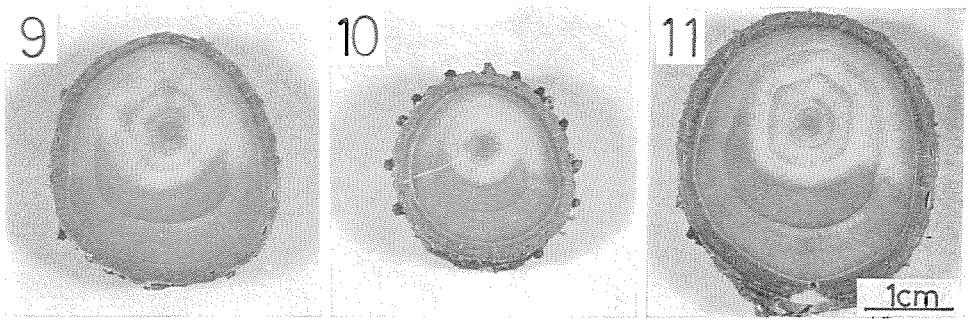
Photo 12. Typical compression wood cells formed shortly after the inclination. (45-a-III).

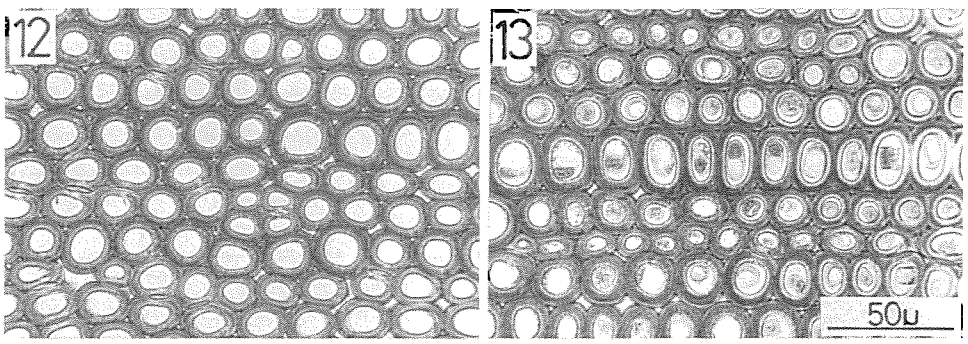
Photo 13. Typical compression wood cells in the course of the formation at the harvest. (45-a-III).

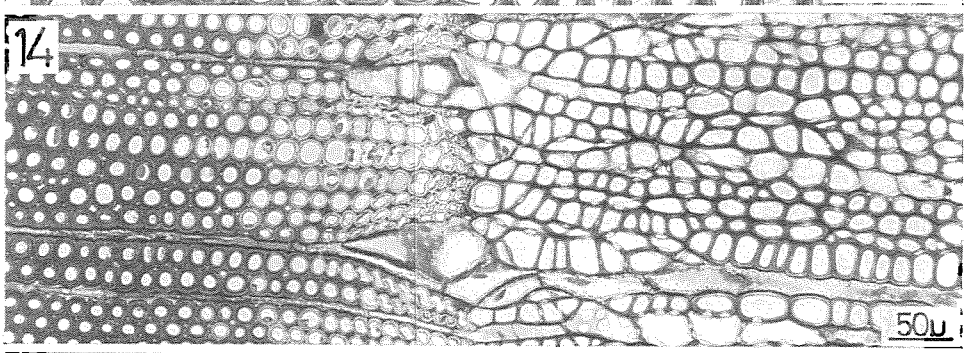
Photo 14. Growth ring boundary of 45-a-III. Abnormal latewood developed to the same intensity as 90-a-III (Photo 6) and frost injury is also seen. Cell wall thickness of the earlywood is decreased as compared with 90-a-III.

Photo 15. Growth ring boundary of 45-b-II. Cell walls of both latewood and earlywood is thinner than those of 90-a-II. Other features are not so different from 90-a-II.

Photo 16. Growth ring boundary of 45-b-III. Walls are thicker than those of 45-a-III and similar to those of 90-a-III (Photo 6), though earywood cells are more angular.


9
10
11
1cm


12
13
50μ


14
50μ

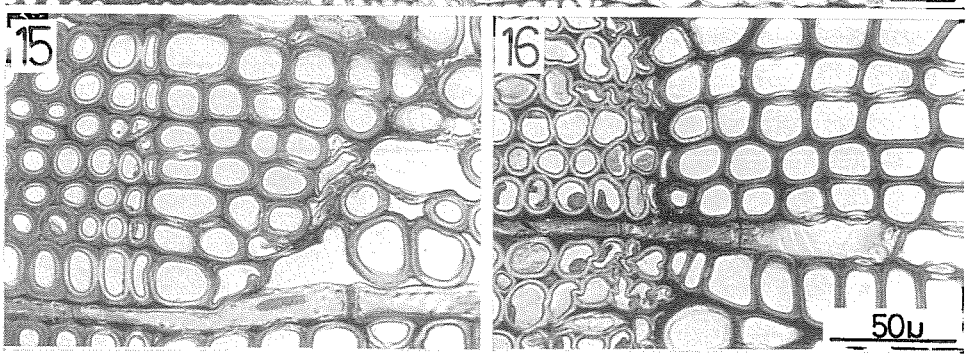

15
16
50μ

PLATE III. Angular displacement of 20°

Photos 17, 18 and 19. Disks 20-a-II, -III and 20-b-III respectively. Disks are no longer triangular. The depth of the colour of the second crescents is markedly reduced.

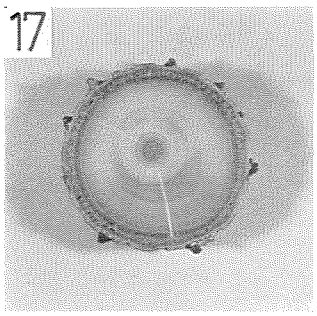
Photo 20. Growth ring boundary of 20-b-III. The deficiency in lignification in latewood is also found, though the degree of the development of the abnormalities is markedly reduced as compared with that of the greater stem deviations. No crushed cells is found.

Photo 21. Growth ring boundary of 20-a-II. The last 8 to 10 cells in latewood lack in intercellular spaces and assume considerably square outline. Cell walls of the first several rows of earlywood cells are thiner than those found in Photos 20 and 22, though thicker than those of 45-a-III.

Photo 22. Growth ring boundary of 20-b-II. Latewood cells have thick wall as those formed under 45° displacement. Intercellular spaces are found up to the 4th to 6th cells back from the boundary in latewood and from the 5th to 10th cells in earywood.

Photo 23. Typical compression wood cells formed shortly after the inclination. Although cells seem to have slightly square outline, such cells can be found in sections of greater angular displacements. (20-a-III).

Photo 24. Compression wood cells of reduced severity with few intercellular spaces formed shortly before the harvest. (20-a-III).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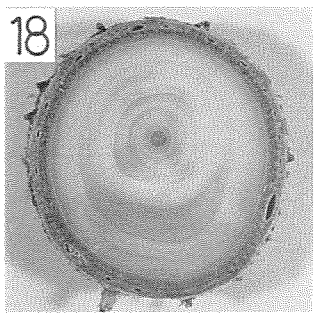
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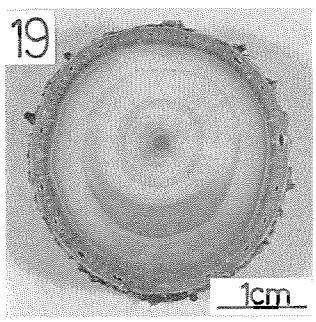
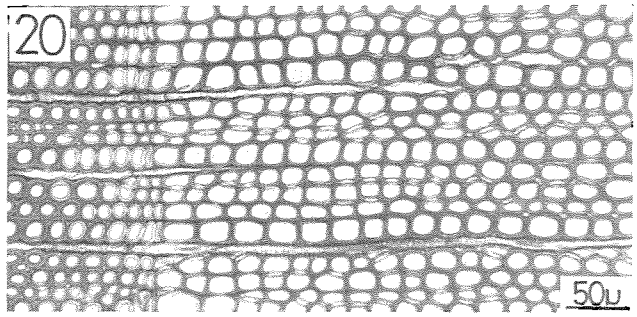
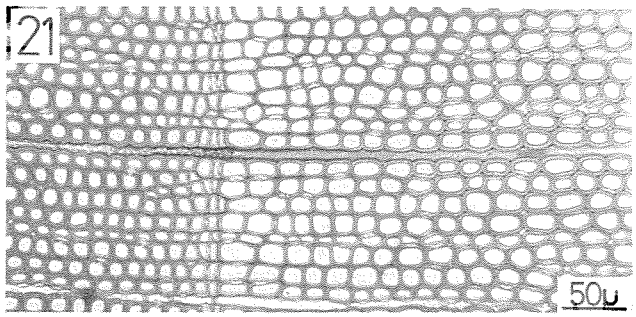

19
1cm


20
50u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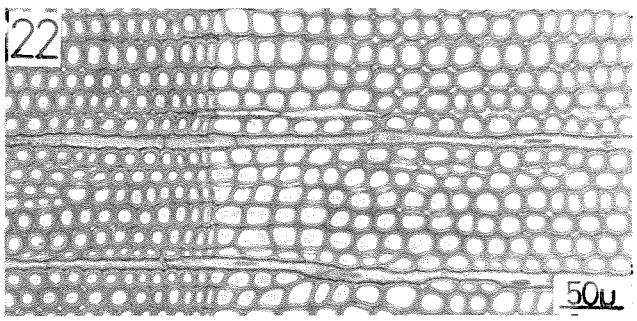
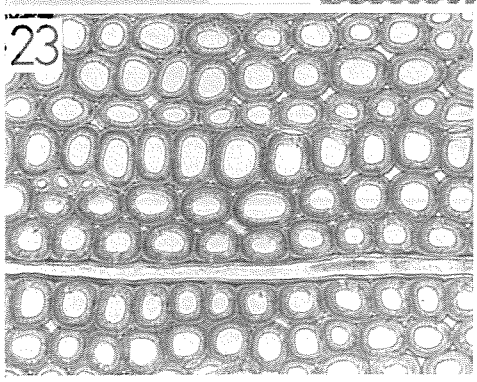
50u


22
50u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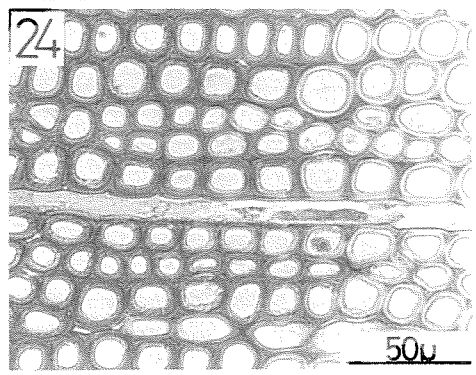

24
50u

PLATE IV. Angular displacement of 10°

Photos 25, 26 and 27. Disks 10-a-II, -III and 10-b-III respectively. Decrease in the depth of the colour in the first year is apparent in the former two disks. Disk 10-b-III shows almost the same depth of the colour with that found in greater angular displacements.

Photo 28. Moderate compression wood cells with reduced occurrence of intercellular spaces found in 10-a-II.

Photo 29. Moderate compression wood cells formed in the 3rd internode of the same tree (10-a). The severity is apparently lower than in the 2nd (Photo 28).

Photo 30. Compression wood cells of reduced degree found in the middle portion of the first crescent in 10-b-II. Walls remain considerably thicker with some intercellular spaces.

Photo 31. Slight compression wood cells in 10-a-III found in the similar position to the above photograph. No intercellular spaces and lesser degree of lignification and wall thickness are apparent.

Photo 32. Growth ring boundary of 10-a-II. Latewood cells show reduced degree of roundness. First two to three rows of earlywood cells affected by frost injury assume more rounded outline than later formed cells.

Photo 33. Growth ring boundary of 10-b-II. Latewood cells are nearly square and earlywood cells have slight roundness.

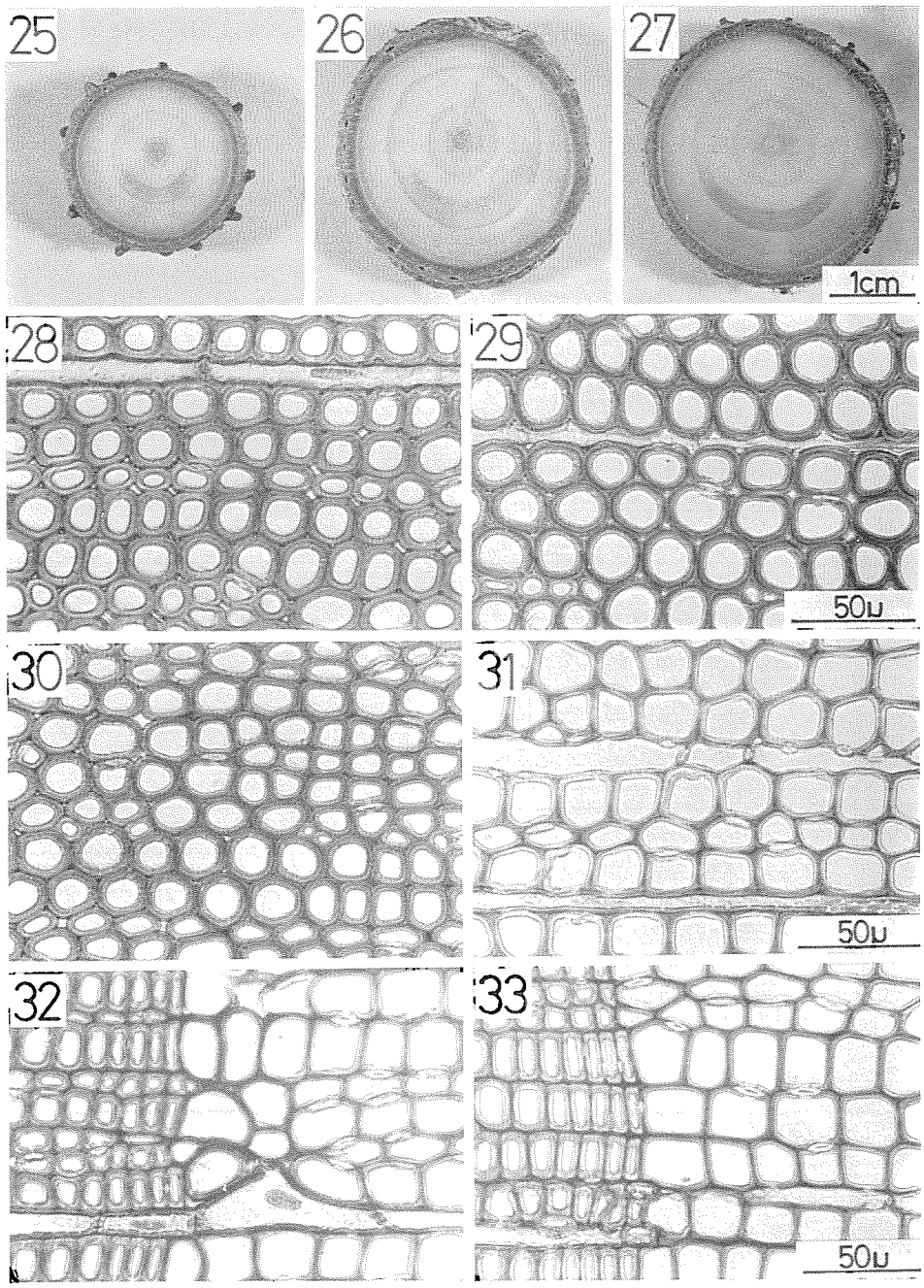

25
26
27
1cm
28
29
50μ
30
31
50μ
32
33
50μ

PLATE V. Angular displacements of 10° (Photos 34 and 35) and 5° (Photos 36 to 43)

Photo 34. Normal wood cells formed at the harvest found in 10-a-III.

Photo 35. Very slight compression wood cells formed at the harvest in 10-b-III. Cells are somewhat round and slightly thick-walled. Lignification seems slightly excessive.

Photos 36 to 40. Disks 5-a-II, -III, 5-b-II, 5-c-II and -III respectively. The slightest crescents of compression wood are found in the former two disks. Disks 5-b-II and 5-c-II show considerable depth of the colour in the first year.

Photo 41. Mild compression wood cells formed in 5-c-III. Many intercellular spaces are seen. Walls are still considerably thicker.

Photo 42. Mild compression wood cells found in 5-c-II. A few number of intercellular spaces are found at the lower right corner of the photograph.

Pohto 43. Mild compression wood cells found in 5-a-III. No intercellular spaces could be seen in this specimen. Cells are more square than those found in above two photographs.

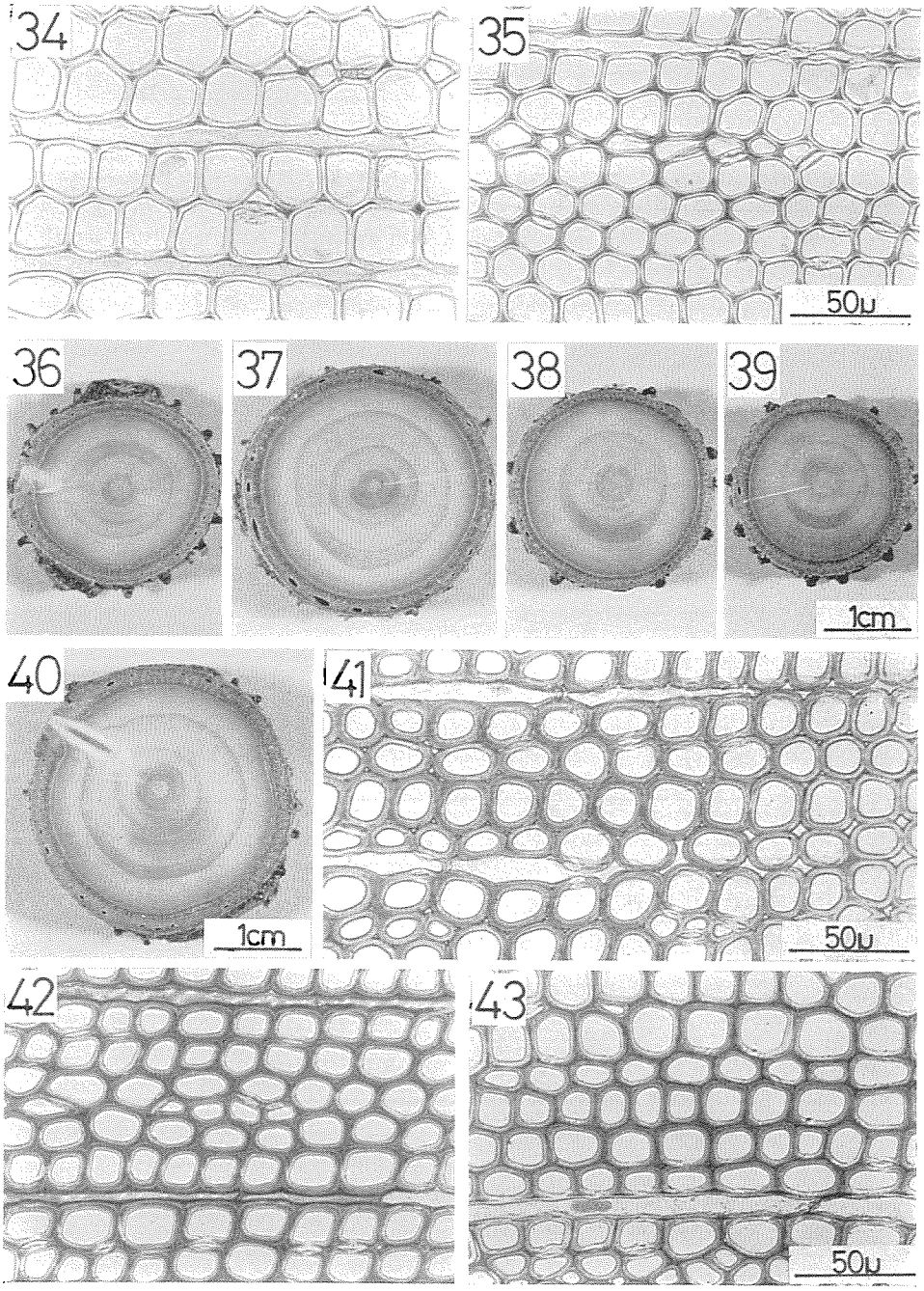

34
35
50μ
36
37
38
39
1cm
40
1cm
41
50μ
42
43
50μ

PLATE VI. Angular displacement of 5°

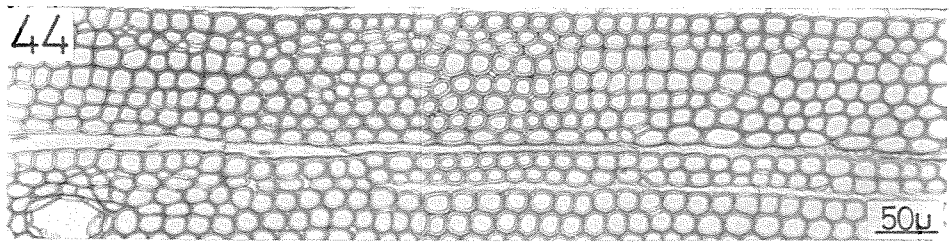
Photos 44 to 46. Decrease in the severity of compression wood cells in the first year. Cell walls remain thicker with decreasing occurrence of intercellular spaces in 5-b-II (Photo 44) or the decrease occurs rather abrupt in 5-a-II (Photo 45) or fluctuates to decrease in 5-c-II (Photo 46).

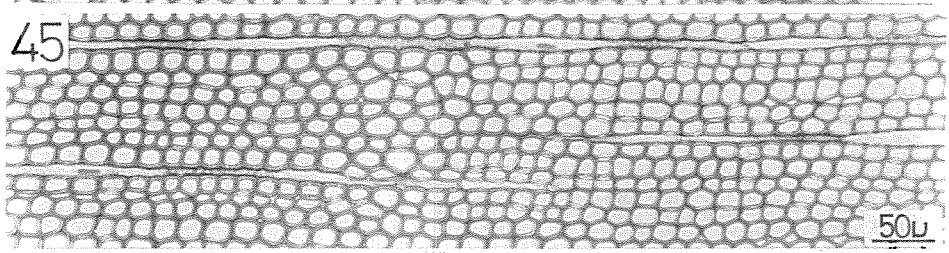
Photo 47. Growth ring boundary of 5-a-II. Latewood cells seem normal and earlywood cells may be slightly round.

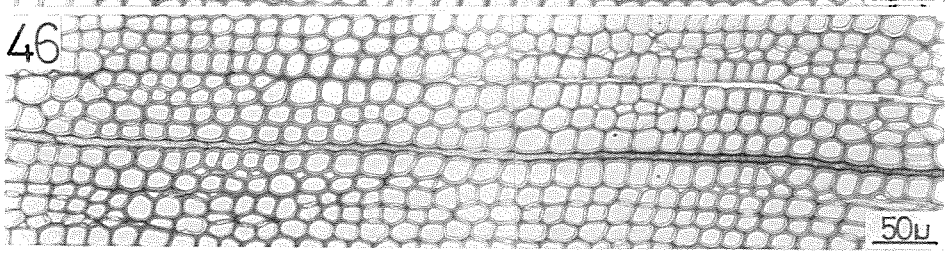
Photo 48. Growth ring boundary of 5-b-II. Latewood cells may somewhat round and earywood cells apparently show features of slight compression wood cells.

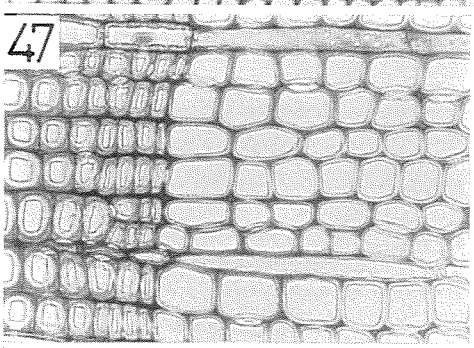
Photo 49. Growth ring boundary of 5-c-III. Latewood cells are apparently round and earlywood cells seem somewhat round.

Photo 50. Normal wood cells formed at the harvest. In all the trees inclined at 5°, normal wood was formed at that time.


44
50μ


45
50μ


46
50μ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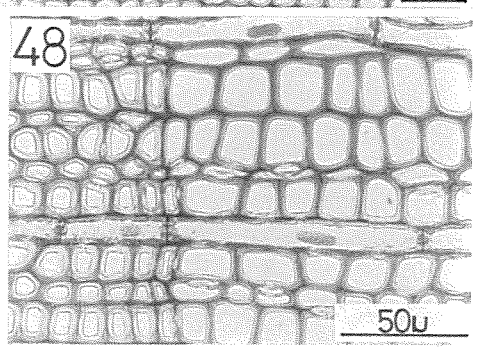
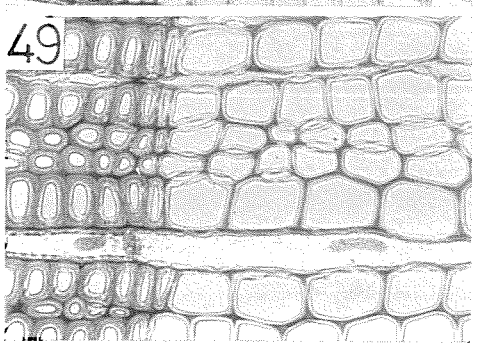

48
50μ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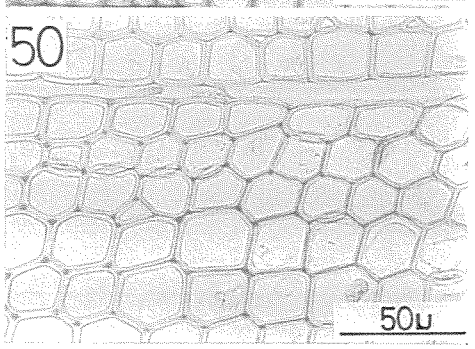
50
50μ