### Studies on the Formation and Structure of the Compression Wood Cells Induced by Artificial Inclination in Young Trees of Picea glauca: IV. Gradation of the Severity of Compression Wood Tracheids

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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*

IV. Gradation of the Severity of Compression Wood Tracheids*

By

Masahide YUMOTO**, Shigeo ISHIDA**
and Kazumi FUKAZAWA**

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Introduction

Compression wood tracheids are known to have rounded outline in cross section with intercellular spaces and thicker walls in which spiral grooves run obliquely and lignin is distributed in a characteristic pattern, and to lack in the S3 layer (Casperson 1965, Côté and Day 1965, White 1965, Timell 1981). However, it is only a so-called typical compression wood tracheid that shows all these structural features and indeed, there are intermediates between the typical compression wood tracheid and the normal wood tracheid, in other words, compression wood tracheids show various degrees of the development.

Although increasing attention has been called to the severity of compression wood recently (Wooten et al. 1967, Shelbourne and Ritchie 1968, Harris 1977, Seth and Jain 1977, 1978), little is known as to the fine structure of these intermediates. The occurrence of intermediate compression wood tracheids seems not well recognized by many workers, because in the literature such confusion is often seen that the wood shown to be “normal wood” is apparently mild compression wood, or some of the wood samples which should be normal wood are obviously slight compression wood, or to the contrary, the compression wood stated as “typical” seems actually moderate compression wood for us, judging from the photographs presented there.

The recognition of mild or slight compression wood tracheids is of critical significance especially in experiments on the threshold value of stimulation or on the artificial induction of compression wood by chemical agents of others. If the wood formed is not so-called typical compression wood, how does the investigator judge whether the reaction is positive or not without any information on intermediate compression wood tracheids? Furthermore, there could be a possibility that the wood is of another type other than compression wood.

On the nature of compression wood a lot of discrepancies can be found in the literature. Some of the discrepancies are believed in part to come from the difference in the severity of compression wood examined, because the degree of development of compression wood is variable among reports as expected from above statements. Intermediate compression woods of lesser degrees are difficult to detect macroscopically (Pillow and Luxford 1937, Core et al. 1961, Fukazawa 1974) and therefore, there would be a good possibility that in physical, chemical and even in anatomical investigations on “normal wood” deviations of values might be caused by the presence of mild compression wood of macroscopically indiscernible
Severity of compression wood tracheids (Yumoto et al.)

degrees. Therefore, it is apparently indispensable to reveal the nature of intermediate compression wood tracheids not only for the study of compression wood tracheids itself, but also for general surveys on woody materials.

Intermediate or atypical compression wood tracheids are found in the following situations; (1) on the lower side of slightly leaned trees (Harris 1976, Yumoto and Ishida 1979, 1982); (2) on the lower side of trees which were tilted strongly but for only a short period (Onaka 1937, Kennedy and Farrar 1965); (3) on the lower side of trees which have long enough been inclined strongly (Fukazawa 1973, 1974, Harris 1977, Yumoto and Ishida 1979, 1982, Yoshizawa et al. 1981); (4) on the lateral sides of strongly leaned trees (Fukazawa 1974); (5) in the vicinity of the growth ring boundary especially in early-earlywood of enoughly leaned trees (Côté et al. 1967, Wood and Goring 1971, Timell 1972, Fukazawa 1974, Höster 1974, Yumoto 1982); (6) in the transitional zone from normal to compression wood (Kennedy and Farrar 1965, Fujita et al. 1979, Yumoto et al. 1982 b); (7) in the transitional zone from compression to normal wood (Kennedy and Farrar 1965, Fujita et al. 1979, Yumoto et al. to be published). However, a simple linear gradation of the degree of development of compression wood tracheids is not necessarily applicable in all the cases above mentioned: one or some of the characteristic features of compression wood tracheids are known to lack at least in the cases (2), (5), (6) and (7), even though other features develop typically. Such a particular type of intermediate is apparently formed by a differential stimulation, namely, tracheids are differently stimulated through the change in the strength of the stimulus depending on their position in the cambial and differentiating zone. On the other hand, the tracheids formed under the cases (1), (3) and (4) are believed to be formed under nearly constant strength of the stimulus, and therefore, there could be expected a possibility of a linear gradation of the severity of compression wood tracheids.

Although the degree of compression wood tracheids could be studied on woods formed under these three cases, it is preferable to perform this on the case (1) by the comparison of tracheids formed under several different angular displacements, because compression wood formation is considered as a geotropic manifestation of the secondary tissue of conifers (Westing 1965, 1968, Robards 1969), and therefore, the degree of compression wood formation can be thought to basically depend on the angle of stem deviation from the vertical, though many factors are known to affect the formation (Low 1964, Westing 1965, 1968).

However, the possibility to conduct such an experiment over the full range of the severity was denied in a previous paper (Yumoto and Ishida 1982), in which we studied compression wood tracheids formed under five different angular displacements by light microscopy. The woods formed shortly after tilting were found to be mostly higher in degree even if the stem deviation was 5°. And it was expected that at the stem deviation below 5° the degree of development of compression wood tracheids would strongly fluctuate and no suitable materials for this kind of study could be obtained. In the previous paper we found also that the reduction of the severity occurred in the course of time as an adaptation to
the new equilibrium positions, *i.e.*, the fixed leaning positions, and that the woods formed after about a year covered full range of the severity. Although the wood formed through the adaptation cannot be thought to reflect the relation between the severity of compression wood tracheids and the angle of stem deviation, if the strength of stimulus and the sensitivity of the differentiating tracheids are enoughly constant, the wood thus formed could provide also good materials for the study of the degree of development of compression wood tracheids.

It should be noted here that our interest lies in the gradation of the severity of observed compression wood *tracheids* and not in that of *wood*. There are several reasons for this; *i*) in the present series of studies we deal with biological aspects of compression wood formation and the main biological unit of coniferous wood is the tracheid; *ii*) intermediate or atypical compression wood tracheids formed under the cases (2), (5), (6) and (7) can only be studied as tracheid and it is preferable to compare the structure of these tracheids with those formed under the case (3) revealed in the present study; *iii*) a close examination often revealed substantial differences among tracheids in the degree of development of the characteristic features even in a limited area of wood (*Harriss* 1977); *iv*) structural particularities of compression wood appear mainly in tracheids (*Onakas* 1949, *Westing* 1965, *Timell* 1972 b).

In the present paper structural features of compression wood tracheids formed a year after the displacements to five different angles are studied. The observation on the inner surfaces of tracheids along a radial file by SEM (scanning electron microscopy) corresponds strictly to that by UVM (ultraviolet microscopy) on the same tracheids in the matched thin cross section. The aptitude of each feature for the marker of the severity of compression wood tracheids is discussed in detail. And, after selecting reasonable markers, a variety of compression wood tracheids observed are gradated according to a criterion with selected markers.

**Materials and Methods**

All samples were taken from the same trees with those examined in the previous paper by light microscopy (*Yumoto and Ishida* 1982).

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 late July 1978 at some 30 cm above the ground level to be tilted at 5°, 10°, 20°, 45° and 90° from the vertical and the 1st and 2nd internodes were tied to wooden stakes with strings. Two trees were tilted on each stem deviation, but three for the displacement of 5°. After about a year (early August 1979) these trees were harvested. The angles of the stem deviation were found to have been kept almost unchanged throughout the experimental period. Details of the sample trees were presented in the previous paper.

For a SEM-UVM combination method disks of 1 cm in thickness were cut from the middle portions of the 2nd and 3rd internodes, which had been the 1st and 2nd in the previous year respectively, and fixed in FAA. A small sample (*ca.* 2 × 2 × 2 mm)
Severity of compression wood tracheids (YUMOTO et al.)

was severed from the most newly formed xylem on the lower most side of a disk including the cambium, and dehydrated, and embedded in methacrylate resin mixture. A thin transverse section of ca. 1 μ was cut from a sample and photographed under an UV-microscope (Carl Zeiss, type MPM-01) at a wavelength of 280 μ using ordinary commercial films.

The remainder of the sample was cut out from the resin block and a radial surface of the sample was finished on a ultramicrotome to expose the inner surfaces of the tracheids aligned in a radial file. After finishing, a small tangentially flat piece with the finished surface was cut from the sample to give a new radial surface, the latter was also finished in the same manner. These pieces were soaked in acetone to remove the embedding resin, dried at room conditions, mounted on specimen stubs with pieces of bouble-face-adhesive tape and coated with gold in an ion coater. Photographs were taken in a JSM-2 microscope at 15 kV.

Other than the SEM-UVM combination method, observations were also made by SEM and UVM separately on these specimens.

For the details of the procedure, the reader refers YUMOTO et al. (1982 b).

Observations

The observation by the SEM-UVM combination method was made on three to five radial files on each sample, and each file comprises generally 50 to 70 tracheids. Therefore, the observation involves a total of more than 5,000 tracheids.

In the following description, sample trees will be called by the code name presented in Table 1 of the previous paper (YUMOTO and ISHIDA 1982). The number of the internode will be shown by Roman numerals after the code name as in the previous paper, e.g., 45-b-III represents the middle portion of the 3rd internode of tree b tilted at 45° from the vertical.

1. Angular displacements of 90° and 45° from the vertical

All specimens from the trees grown under the displacements of 90° and 45° showed features of the so-called typical compression wood tracheids. Photos 1 and 45 show common features of such compression wood tracheids. They are round in cross section with well-developed intercellular spaces and have thick walls, in which spiral grooves and strong UV-absorption especially in the S 2 (L) layer are evident. The S1 and the inner region of the S 2 layer also show strong absorption to lessen the contrast to the S 2 (L) layer. On the other hand, a close observation on the inner surfaces of tracheids by SEM revealed considerable variations in the features of spiral grooves and the form of bordered pits. Tracheids shown in Photo 2 have distinct grooves and ridges are wide and dilated. On the contrary, those shown in Photo 3 possess relatively narrow ones, especially the tracheid at right has fine grooves. Photos 5 to 10 show front views of bordered pits. Many of them do not have definite outlines of the inner pit aperture. In Photo 5 the inner pit aperture assumes a wide depression along the grooves, and the depression in Photo 6 is shallow and loose. Those in Photos 7 and 8 are confluent to spiral grooves. Inner pit apertures are generally slit-like (Photos 7 to 9), but some are
not (Photos 5 and 6). Most tracheids did not show the rising of the pit dome, but some, especially those situated near the tip of tracheids had the rising (Photo 10). The width and length of the inner pit aperture or the depression varied considerably as shown in photographs.

The angle of spiral grooves, which represents the angle of microfibrils in the S2 layer, seemed not to differ markedly among specimens though it is difficult to estimate accurate angles from a SEM observation (specimens were tilted at 45° descending toward the upper side of photographs). There seemed to be rather a tendency that the microfibrilar angle of the S2 layer increased as the width of the tracheid increased. But a limited number of tracheids found in 90-b-II (Photo 4) had greater angles nearly perpendicular to their long axes, though being narrow in diameter.

No appreciable anatomical differences were obtained between samples of the stem deviations of 90° and 45°. However, a difference in physical nature was observed during the specimen preparation. Namely, methacrylate-embedded samples from trees at 45° could be easily split radial-longitudinally, but those from trees at 90° were generally difficult to split along the grain.

2. **Angular displacement of 20° from the vertical**

Tracheids found in 20-b-II showed almost the same features with those found in the greater stem deviations. However, cell walls seemed slightly thinner (Photo 46) and many of the bordered pits had slight risings of the pit dome as shown in Photo 11, though some had no rising resembling those shown in Photos 8 and 9 which were found in the specimens from trees at 90° and 45°.

In the third internode of the same tree (20-b), especially on the pith side of the sample, cell walls were apparently thinner and in places, spiral grooves were not typically developed. Most of bordered pits did not have typical slit-like openings. The pit opening shown in Photo 19 is one of the most slit-like ones found in this sample. Spiral grooves around the pit openings were generally only poorly developed (Photos 20 and 21).

In 20-a-III the severity of compression wood tracheids were more reduced in all the aspects and intercellular spaces were partially not formed (Photo 48). The greater part of the sample was composed of tracheids with spiral grooves, but most of them were not fully developed. The tracheids on the most pith side (Photo 47) had well-developed grooves, which were mainly fine (Photo 12). In the sequence of the reduction of the severity of compression wood tracheids, the disappearance of distinct grooves seemed generally to occur slightly before intercellular spaces disappeared, however, tracheids with distinct grooves but no spaces were also found (Photo 14). In the middle of the sample, grooves were mainly wide in interval (Photo 13). Photo 15 shows a type of tracheid which appeared in the course of the lowering of the degree of development of spiral grooves. The inner surfaces of the tracheids seem to be somewhat veiled, whereas the matched UV-photograph shows radially oriented striations, which would represent the presence of spiral grooves. Where the grooves were poorly developed, its degree of formation was
found to vary considerably within and among the radial files (Photos 16 and 49). In Photo 49 all tracheids in the third radial file from right have spiral grooves, but in the second file only tracheids A and B have the groove. Spiral grooves became not distinct towards the cambial side (Photo 50) and in the youngest tracheids (the most newly formed) only poorly developed fine grooves were observed on the inner most surfaces (Photo 17). In Photo 17 no trace of grooves can be found in the matched UV-photograph. The striations on the radial walls seem to be caused by folds in the section. Most of bordered pits found in this sample have apparent risings of the pit dome resembling those found in 20-b-III (Photos 20 and 21) and some were nearly normal (Photo 24), and others were intermediates between these types. A channel or depression over the pit opening running parallel to the microfibrilar orientation was often seen (Photos 22 and 23). Bordered pits with and without such a channel were occasionally found in a tracheid in the close vicinity to each other.

In 20-a-II developed grooves were not formed throughout the sample and the outer half (cambial side) of the sample did not contain intercellular spaces. Radially oriented striations in UV-photographs were apparent in some tracheids but not in others. Bordered pits had the round domes with or without the depression along the microfibrilar orientation. Resembling the 3rd internode, the degree of development of spiral grooves was variable where they were poorly developed. In addition, a different type of tracheid was found in the middle of the sample. As shown in Photo 18, they are relatively thin-walled and round in cross section with well-developed intercellular spaces. UV-absorption in the secondary walls is lower and their inner surfaces are smooth without grooves. They made a layer ca. 10 cells wide oriented tangentially and were situated between the zones of tracheids with the radial striations and strong UV-absorption resembling those shown in Photo 16.

3. **Angular displacement of 10° from the vertical**

Materials taken from trees at 10° showed a considerable reduction in all the aspects of the severity of compression wood tracheids. On the pith side of 10-b-III the most severe ones in these samples were observed. The tracheids had spiral grooves, though not typically developed, with partial occurrence of intercellular spaces, resembling those found in 20-a-II and III (Photos 16, 48 and 49). Tracheids of different degrees in the development of spiral grooves were found to be intermingled. In this sample (10-b-III) the severity of compression wood tracheids became reduced considerably in most respects towards the cambial side. Photos 25 to 32 show the sequence of the reduction. Photo 25 shows tracheids with veiled grooves similar to those seen in Photo 15. The occurrence of charges along grooves is an artifact caused by drying during specimen preparation. However, in contrast to those shown in Photo 15, radial striations in the UV-photograph are found only in the radial walls. This implies that these striations are largely artifacts. In Photos 26 and 27 grooves on the inner surfaces are reduced to fine streaks. Cracks indicated by the occurrence of charge are found in Photo 26 and radial striations can be recognized in Photo 27, but are obscure in Photo 26. Tracheids
seen in Photo 28 have fairly smoothed surfaces and no trace of the striation can
be found in the matched UV-photograph. From Photo 27 to Photo 32 the
roundness of outline, cell wall thickness and the strength of UV-absorption of the
secondary wall seem reduced nearly in parallel, the feature of the inner surface
remaining unchanged. Strong UV-absorption became confined at cell corners.
Intercellular spaces were generally absent, but can be present occasionally and
sporadically as shown in Photos 28, 29 and 52, irrespective of the degrees of de­
velopment of other features. Photo 52 represents a stage of the reduction at a
lower magnification and may correspond to Photo 30 in degree. The most newly
formed tracheids of a specimen had the S 3 layer and faint UV-absorption in the
S 2 (L) layer at cell corners (Photo 32). Cell walls of these tracheids (Photo 53)
were thinner than those of the corresponding normal wood tracheids (Photos 40
and 56).

In the second internode of this tree (10-b) the degree of development of com­
pression wood tracheids was found more lowered in all the aspects than in the
third internode. Photo 51 shows tracheids on the most pith side of the sample
in cross section. The most newly formed tracheids (Photo 54) had traces of UV­
absorption in the S 2 (L) layer at cell corners. Cell wall thickness of these tracheids
was apparently thinner than the normal. No S 3 layer was observed in these
tracheids. Intercellular spaces were present only on rare occasions in this sample.

In 10-a-III similar features to those found in 10-b-II were observed.

On the pith side of 10-a-II tracheids had smoothed inner surfaces and faint
UV-absorption in the S 2 (L) layer at cell corners (Photo 33) resembling those seen
in 10-a-III, 10-b-II and -III. The severity of compression wood tracheids were
reduced in most aspects towards the cambial side and the characteristic UV-absorp­
tion in the S 2 (L) layer was not appreciably observed on the cambial half of the
sample. Whereas, most of tracheids showed slightly higher UV-absorption than the
normal distributed evenly in the S 2 layer (Photo 55). They seemed also to have
somewhat rounded outlines. The S 3 layer was present (Photo 36) but sometimes
thinner than the normal (tracheid at right in Photo 35) or occasionally not formed
(Photo 34), or instead of the S 3 layer, the transition layer between the S 2 and
S 3 was observed (tracheid at left in Photo 35, that at right in Photo 34). No
intercellular spaces were found in 10-a-II and -III.

4. Angular displacement of 5° from the vertical

Three trees were tilted at 5°. On the pith side of 5-a-II and -III slight
compression wood tracheids with faint UV-absorption in the S 2 (L) layer at cell
corners were observed. They had no S 3 layer and were similar to those shown
in Photos 30, 31 and 33. Following these tracheids those with the S 3 layer and
traces of the UV-absorption in the S 2 (L) were formed (Photo 37). The cambial
halves of the samples comprized apparently normal tracheids (Photos 40 and 56).
Interposed between these regions tracheids similar to those found in 10-a-II were
observed (Photo 39). Namely, they had slightly higher UV-absorption evenly dis­
tributed in the S 2 layer and seemed to be somewhat round in cross section. They
Severity of compression wood tracheids (YUMOTO et al.)

Occasionally lack in the S3 layer, but possessed the transition layer between the S2 and S3 instead.

In the second internode another type of tracheid was found (Photo 38). They lack in the S3 layer and characteristic UV-absorption in the S2 (L) layer, whereas their S2 layer shows fairly strong UV-absorption distributed evenly, the strength of the absorption being apparently higher than that of the above mentioned type of absorption. They were found between more rounded tracheids with thicker walls and the characteristic UV-absorption in the S2 (L) layer.

Structural features of compression wood tracheids in 5-b-II were similar to those found in 10-a-III and 10-b-II.

In the third internode of the same tree (5-b) tracheids were especially thin-walled on the most pith side of the sample (Photo 41). These tracheids were followed by relatively thick-walled ones, though their outlines were similar in roundness (Photo 42). From the middle to the cambial side of the sample the severity of compression wood tracheids was reduced in most respects and the S3 layer became formed. But UV-absorption in the S2 (L) layer remained considerably strong (Photo 43) and occasionally the S3 layer was found even in the tracheids with considerable roundness and strong UV-absorption in the S2 (L) (Photo 44). The most newly formed tracheids resembled those found in the cambial half of 10-a-II and the middle portions of 5-a-II and -III, which were somewhat round in outline and had slightly excessive UV-absorption distributed evenly in the S2 layer.

On the pith side of 5-c-II traces of spiral grooves similar to those seen in Photo 25 were found. Intercellular spaces were distributed sporadically. The remainder of the sample was composed of tracheids of various degrees of UV-absorption and roundness as found in 10-b-II, both decreasing towards the cambial side. In this sample no S3 layer was formed with one exception, in which a tracheid adjacent to an axial parenchyma cell of a resin canal tissue had the S3 layer, others situated around the resin canal being without the layer. The tracheid had also lesser strength of UV-absorptino.

The pith side of the third internode of the same tree (5-c) consisted of compression wood tracheids with characteristic UV-absorption in the S2 (L). No S3 layer was observed in these tracheids. These were followed by the tracheids with both the UV-absorption in the S2 (L) and the S3 layer. On the most cambial side normal wood tracheids were formed, and in the transitional zone to these normal tracheids, the above mentioned type of tracheid, i.e., those with slight roundness being somewhat darker in UV-photographs, were observed.

Discussion

As stated earlier, our chief interests lay in biological aspects of compression wood formation and the gradation of the severity of given tracheids, and therefore, the gradation should be of biological significance and characterized by structural features of tracheids. As characteristic features of compression wood tracheids,
the occurrence of spiral grooves, excessive lignification particularly in the \( S_2 \) (L) layer, the roundness of outline in cross section, thicker cell walls, and the changes in the form of bordered pits and the angle of the microfibrils in the \( S_2 \) layer, and the absence of the \( S_3 \) layer were listed for consideration in the present study. The occurrence of intercellular spaces is also a prominent feature, though it is rather that of compression wood.

At a glance, the gradation of the severity might be easy to make. Namely, in the most severe compression wood tracheids all characteristic features are typically developed and in moderate ones the roundness, cells wall thickness and the strength of UV-absorption, etc. are reduced, and mild compression wood tracheids have no spiral grooves, traces of the \( S_2 \) (L) layer and slightly thicker walls than the normal and lack in intercellular spaces.

However, difficulties arise when we try to grade the severity of given compression wood tracheids, because the observed degree of development of a feature did not necessarily change in parallel with that of another. For example, tracheids in Photo 25 have spiral grooves though not typically developed, on the other hand, those found in Photo 27 have apparently thicker walls than these but lack in grooves. The groove can be formed even in the tracheids of fairly angular outline without intercellular spaces (Photo 14), but some have more rounded outline than those with the spaces, though their inner surfaces are smooth and free from the groove (Photo 18). Tracheids in Photo 34 are angular in outline and have no characteristic UV-absorption in the \( S_2 \) (L) layer as if they were normal, but they have no \( S_3 \) layer. On the contrary, those in Photo 44 seem to be of considerable degree showing fairly rounded outlines and characteristic UV-absorption in the \( S_2 \) (L) layer, but possess the \( S_3 \) layer. Which tracheids should be regarded to be more severe in such cases? Can the degree of development of a particular feature represent the severity of a compression wood tracheid as a whole?

This nonparallelism in the degree of development among features is thought to be brought about by at least three factors essentially different in nature, i.e., 1) fluctuation of the strength of the stimulus which affects all the cambial and differentiating tracheids at the same time, 2) influences of factors not essentially involved in compression wood formation, and 3) difference in the stimulation or response for the formation of each characteristic feature in a tracheid, which is not caused by the factor 1). Aside from nonparallelism caused by the factor 3), those evoked by factors 1) and 2) should be at least excluded from the gradation. In the present paper the fluctuation of the strength of stimulus will be first mentioned, and then the influences of extrinsic factors will be discussed together with causal relations among features, the behavior of each feature along the severity. The gradation can only be made after reasonable markers are selected according to such considerations, and the markers should be essentially involved in compression wood formation and should not be subject to the influences of extrinsic factors.

1. **Fluctuation of the strength of compression wood stimulus**

Although the strength of the stimulus which exerts its effects on all the cambial
and differentiating tracheids, and the sensitivity of tracheids to the stimulus were expected to be relatively constant under fixed stem deviations, this was not always the case. It is generally difficult to distinguish the participation of the strength of stimulus from that of the sensitivity on an anatomical observation, nevertheless, an apparent example of the fluctuation of the former was observed in 20-a—II. As mentioned above, the tracheids shown in Photo 18 have considerable roundness but other features such as cell wall thickness, the strength of UV-absorption and the feature of the inner surfaces are apparently those of lower degrees. These tracheids are quite reminiscent of a type of tracheid which is found in the transitional zone from compression to normal wood formed by the interruption of stimulation (i.e., by returning the inclined stem to the vertical position) (KENNEDY and FARRAR 1965, FUJITA et al. 1979, YUMOTO et al. to be published). In this case tracheids in different developmental phases are thought to be differently stimulated depending on their positions and destined to show corresponding differences in anatomical features. And the tracheids in the most outer zone would be stimulated only for the formation of rounded outline with the occurrence of intercellular spaces. Tracheids in Photo 18 would have been formed under a similar condition, though the stem had been kept constant in the angle of the deviation.

Another case is illustrated in Photo 38. The tracheids were found between those with characteristic UV-absorption in the S 2 (L) layer. Their relatively strong UV-absorption distributed nearly evenly in the S 2 layer is quite similar to that found in the transitional zone from normal to compression wood (YUMOTO et al. 1982 b). These tracheids would have been formed during a sudden increase in the strength of stimulus which occurred shortly after a sudden decrease. The occurrence of the fluctuation of the strength of stimulus under fixed stem deviation implies a condition of disturbed physiological balance in the trees. Since this kind of fluctuation necessarily causes the zonation of different types of tracheids, it can be easily recognized by an observation on transeverse sections. In the present paper the tracheids modified by the fluctuation are excluded from description except for the above mentioned cases.

In addition, it is appropriate to note here a case which showed a difference in the sensitivity of differentiating tracheids to the stimulus. It is clearly shown where tracheids have poorly developed spiral grooves. As shown in Photo 49, all tracheids in the 3rd file from right have grooves, whereas in the 2nd file grooves are not formed except for tracheids A and B. Whether a tracheid have grooves or not would be determined by the sensitivity of the tracheid in this case, because no difference in the strength of stimulus is expected between these two files. However, in these tracheids the roundness, cell wall thickness and the strength of UV-absorption seem to increase in parallel accompanying the occurrence of spiral grooves, and therefore, such a difference in sensitivity does not stand against a linear gradation.

2. Nature of each feature and its behavior along the severity
As mentioned above, influence of extrinsic factors should be excluded from
the criterion of gradation. However, it is practically quite difficult or impossible, because even if a feature is essential in compression wood formation, many physiological processes are involved between the perception of stimulus and the final response, some of which must be not intrinsic or may be common with those involved in the formation of other features. Therefore, in the strict sense none of the features can be said free from the influences of extrinsic factors and to be independent from other features. However, the intensity of their influences on a feature would be different among features and it would be possible to distinguish features formed under greater influences of extrinsic factors from those formed under relatively small influences by considering their courses of formation and the relations among the behaviors of respective features along the severity.

Furthermore, the occurrence of some features seems more unstable than others and the degrees of development of certain features appear to be determined by those of others. Therefore, causal relations among features are also important to gradate the severity of compression wood tracheids appropriately, and this can only be revealed by similar considerations stated above.

Prior to this, however, it is necessary to think over the theoretical basis for the description of the behavior of each feature along the severity. It is apparently impossible to make this directly along the severity before the severity gradated. The severity could be replaced by the magnitude of stimulation, which is thought to have a direct relation to the biological gradation of the severity. Since compression wood formation is regarded to be a geotropic manifestation of conifers (Westing 1965, 1968, Robards 1969), the intensity of stimulation is thought to basically depend on the angle of stem deviation. However, this is not the case in the tracheids formed through the adaptation to the fixed leaning positions observed in the present study. And if the intensity is known, the gradation of the severity itself could be made easily. Therefore, the basis for the description of the behavior of a characteristic feature along the severity is theoretically ambiguous and encounters difficulties.

Of the characteristic features, the roundness in cross section, excessive lignification and enhanced cell wall thickness are quantitative in nature and it can be admitted that the degrees of development of these features are presented by the quantity of deviation from the normal. Although the response mechanism would be saturated above a certain magnitude of stimulation, the response would never occur reversely to the increase of the stimulation. However, as will be mentioned later, such a relation seems not applicable to cell wall thickness of mildly stimulated compression wood tracheids. On the other hand, description of the behaviors along the severity of rather qualitative features, such as spiral grooves, the form of bordered pits and the distribution pattern of UV-absorption, are generally difficult to make by itself. The solution of this difficulty can be found only in the relation to the degrees of other features.

i. **Spiral grooves**

Although Jaccard (1940) reported the occurrence of striations in normal wood
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of several species of Pinus, it can be admitted that the grooves occur only in compression wood tracheids. On the other hand, the groove is known to lack in such genera as Ginkgo, Taxus and Torreya (TAKAOKA and ISHIDA 1974, TAKAOKA 1975, TIMELL 1978 a, b, 1981, YOSHIZAWA et al. 1982). This suggests its ontogenically younger nature. However, so far as the grooves are formed through an active involvement of biological processes, as will be discussed, it should be thought that the groove is an essential feature of compression wood tracheids in the species that have the ability to develop this feature.

There have been two entirely different theories as to the formation of the grooves. Some authors claimed that the grooves were produced by a tangential contraction of the originally continuous S2 layer in a direction perpendicular to that of the microfibrils (WARDROP and DAVIES 1964, CÔTE et al. 1968, KUTSCHA 1968, cf., BOYD 1973). On the other hand, CAsPERSION and ZINSSER (1965) and FUJITA et al. (1973) provided the evidences to prove that the spiral grooves were formed as a consequence of intermittent deposition of wall materials. Whether the spiral grooves are thought to be independent from other features or not hangs on the choice between the two. In the history of biology we can find a number of instances that a mechanical explanation for a biological structure or function was denied and replaced by a biological explanation through the progress of the study. Considered from improved methods used in FUJITA et al., by which they proved that the other theory was based on artifacts caused by an inadequate fixation, and also from other evidences, especially the finding of the presence of plasma membrane penetrating deeply into the groove, the latter would be the case. If so, there would be an active involvement of biological processes and the formation of spiral grooves can be thought fairly independent from that of other features.

Because the grooves are thus formed through certain biological processes, it can hardly disputed that the tracheid with the grooves is biologically more severe than that without the grooves. However, the depth and interval of the grooves seem to vary irrespective of the degrees of development of other features. As shown in Photo 3, shallow grooves can be found in a compression wood tracheid which was formed under the displacement of 90° and is thick-walled and highly round. Similarly, the interval of the grooves or the width of the ridge is sometimes wide (Photos 2 and 13) or sometimes narrow (Photo 14) irrespective of the cell wall thickness and roundness, though TAKAOKA (1975) stated that as the degree of development of spiral grooves increased, the width of ridges became wider. In addition, the degree of development of the groove is known to lower towards cell tips (WARDROP and DADS WELL 1952).

As the degree of development of the grooves lowers, they become not distinct in both SEM- and UVM-photographs as shown in Photos 16, 17, 25 and 26. In Photo 16 the degrees of the development of the grooves observed by SEM correspond well to those by UVM. Spiral grooves shown in Photo 25 seem somewhat veiled and the corresponding UV-photograph shows distinct striations only in the radial walls. This would be largely an artifact caused during sectioning. Charges along grooves indicate a liability of the secondary wall of this degree to split along
the microfibrils. Radially oriented striations in UV-photographs, which implies the latent occurrence of the grooves, are no longer apparent in Photos 17 and 26, and become not present in the course of the lowering of the degree (Photo 28). In this respect a tracheid shown in the middle of Photo 27 is of interest. The tracheid has apparently no grooves and no drying checks, whereas in the matched UV-photograph traces of fine striations can be seen. However, these striations are different from above mentioned usual striations in a respect. Namely, in the former dark fine striations are found on a relatively bright background, whereas the reverse is the case in the latter. Timell (1978 b) found similar striations in some of cross sections of lignin skeleton of compression wood tracheids in Ginkgo in which spiral grooves are known to lack, and states this might be an artifact. The dark striation in Photo 27 would be also an artifact brought about by minute folds of the section. In some cases grooves were found veiled as a result of the lowering of the degree (Photos 15 and 25). However, the matched UV-photograph of Photo 15 shows relatively distinct radial striations. Thus, the degree of development of spiral grooves cannot be estimated only by an observation on the inner surfaces. It is desirable to observe also on the matched cross sections.

Spiral grooves were not observed in compression wood tracheids with relatively thin walls and lower UV-absorption, but fine streaks were sometimes found (Photos 27 and 28). They might represent a preliminary degree of the groove formation. Thin-walled and fairly angular compression wood tracheids have generally smooth inner surfaces on which no streaks are to be seen.

ii. Absence of the S 3 layer

Although the absence of the S 3 layer is thought to be one of the characteristics of compression wood tracheids, the layer was often observed in those with no spiral grooves and relatively angular outlines. In the course of the reduction of the severity of other features, the layer was generally first observed as a very thin lining on the inner surface, through which the orientation of the underlying S 2 layer could be recognized (Photos 32 and 35). As the severity reduced, the S 3 layer became thicker to give a texture differing from that of the S 2 layer. Occasionally, transition layer between the S 2 and S 3 (Imamura et al. 1972, Hirakawa and Ishida 1981) was found to be the inner most instead. These evidences suggest a gradual transition in the secondary wall structure from compression to normal wood tracheids.

However, the S 3 layer can be formed even in considerably round and thick-walled tracheids with strong UV-absorption in the S 2 (L) layer (Photo 44). As will be reported elsewhere, in the transitional zone from compression to normal wood formed by an artificial interruption of stimulation, the S 3 layer was found occasionally in thick-walled compression wood tracheids with spiral grooves. However, as mentioned above, the cases evoked by the fluctuation of the strength of stimulus were excluded from the description in the present paper except for Photos 18 and 38, and tracheids shown in Photo 44 were by no means formed under such a condition. Harris (1977) reported capricious occurrence of the S 3 layer in all
severities of compression wood, however, in the present study the layer was not observed in tracheids with more round and thicker walls than those shown in Photo 44.

On the other hand, in some seemingly normal tracheids by UVM, a SEM observation failed to detect the presence of the S 3 layer. WARDROP (1964) states that in *Picea* and certain other genera the S 3 layer is absent or so poorly developed that it is not apparent when transeverse sections are examined between crossed nicols. CÔTE and DAY (1965) states a similar content. However, there remains a doubt that they might have observed compression wood tracheids of light microscopically indiscernible degrees. During the course of the present series of studies on *Picea glauca*, no tracheids without the S 3 layer have been found freed from compression wood formation. Although the stable occurrence of the S 3 layer in normal tracheids in *Picea* has not been confirmed sufficiently, its absence in seemingly normal tracheids is thought to be rather evoked by gravitational stimulation.

In the present study most aspects of the severity of compression wood tracheids were found to reduce generally towards the cambial side especially in the samples from trees at smaller stem deviations. Whereas, tracheids with the S 3 layer were observed sometimes scattered in the specimens independently of the reduction. Our observation on the transitional zone from compression to normal wood (YUMOTO et al., to be published) also revealed an unstability in the reappearance of the layer. Thus, the occurrence of the S 3 layer in compression wood tracheids is not in parallel with the changes in the degrees of development of other features and should be regarded to be unstable rather than others are unstable. It might be controlled by a different factor. As discussed in a previous paper (YUMOTO et al. 1982 b), whether the S 3 layer appears or not seems to be determined by the degree to which normal wood formation is disturbed.

iii. Form of bordered pits

Although the pits in compression wood tracheids are simply described in many papers to have oval or slit-like openings, its form was rather variable. The inner pit aperture was generally difficult to define, as reported by COCKRELL (1974). However, the definite inner aperture was also found (Photo 9). In most cases the presence of spiral grooves obscured the outline of the inner pit aperture. The variability of the form could be classified by the length and width of the opening, and the definiteness of the inner aperture. Although the relation between the variability and the stimulation is difficult to know, two types of pits shown in Photos 5 and 7 were not found in the trees grown at 20° or less, and therefore, these types might represent the maximum response.

The rising of the pit dome seems to occur as a result of the reduction of cell wall thickness, because bordered pits in the tracheids with very thick wall did not show such risings (cf., JUTTE and LEVY 1972), though the size of pits may be variable (cf., OHTANI 1981). Even in such thick-walled tracheids, the rising was often found near the tip of the tracheid, where cell wall is known to be thinner than in other parts of the tracheid (OKUMURA et al. 1974, YOSHIZAWA et al. 1981).
Spiral grooves tend to be not distinct or absent on and around the rising. A similar content is seen in SCURFIELD and SILVA (1969). This would occur also as a result of the reduction in cell wall thickness. On the other hand, a channel or depression passing over the pit aperture as shown in Photo 23 is thought not necessarily related to the compression wood formation, because the pits with and without such a channel were sometimes found in a tracheid in the close vicinity to each other, and also because even in normal wood tracheids pits were occasionally found to have similar channels especially when they were situated near cell corners.

Although bordered pits in compression wood tracheids are reported to be smaller in diameter than the normal (ONAKA 1949, OHTANI 1981), its inner structure presented by CASPERSON (1968) seems not different from that in normal tracheids except for the general differences in cell wall structure between these two types of tracheid. Possibly the modification of the form of bordered pits in compression wood tracheids is not genetically determined but caused passively by the structural changes in cell wall.

iv. Roundness of tracheids in cross section

The rounded outline in cross section is one of the most prominent features of compression wood tracheids. TAKAOKA (1975) concluded from detailed observations on compression wood of eight gymnosperms including primitive species that the rounded outline was the most essential and common feature associated with compression wood formation in all gymnosperms. However, it is not a feature found only in compression wood tracheids. Frost injury tends to increase the roundness of the outline (YUMOTO and ISHIDA 1982), and the rounded outline can be brought about by casual occurrence of intercellular spaces which are formed by unknown causes other than compression wood formation (see later). However, if such interferences are not concerned, the averaged roundness seems to reflect a delicate difference in an aspect of the severity of compression wood not only in severe ones (Photos 45 to 47) but also in very mild ones (Photos 53 to 56).

However, when we are concerned with the roundness of a given compression wood tracheid, its possibility as marker encounters difficulties. The word “roundness” seems to have been used ambiguously for the description of compression wood tracheids. When used as “roundness of outline”, the word means that of the line which makes the outer edge of tracheids in cross section in the true sense of the word. But the word appears to be often used for the line making the inner edge of tracheids or the outline of the cell lumen. Generally speaking, if intercellular spaces are large and abundant, the roundness of the former stands out, but if they are absent, that of the latter attracts more attention than the former. Observed by UVM, the roundness of the boundary line between the S1 and S2 (L) layer is most impressive over all the severity.

At a glance, the roundness of the outline or the line of the outer edge of mature tracheids is strongly affected by the shape and size of cell corner middle lamella or intercellular spaces and the arrangement of the neighbouring cells (com-
pare Photos 12 and 15 with Photos 14 and 16). Simply thought in a transverse section, the stiffness of the middle lamella counteracts the tendency of compression wood tracheids to round, and this gives the tracheids various degrees of roundness of outline which would represent an aspect of the severity of compression wood tracheids. However, in contrast to the case of normal wood formation in which surface growth is thought to occur symplastically, there would be involved a sliding and/or an intrusive type of growth in compression wood formation, judging from the fact that the tips of tracheids are highly distorted in this type of wood (Münch 1940, Wardrop and Dadswell 1952). Therefore, in highly developed compression wood where sliding and/or intrusive growth occur intensively, not only the shape and size of cell corner middle lamella or intercellular spaces but also the arrangement of the neighbouring cells should be regarded as a result of complicated three-dimensional cellular events brought about by compression wood formation. Naturally, many extrinsic factors must be involved there. This would explain in part the fact that in highly developed compression wood such as that shown in Photo 45, the arrangement of the neighbouring cells exerts less influence on the roundness of the outline with the occurrence of large intercellular spaces, as compared with the case of compression wood of fairly lower degrees than that. The influence of the neighbouring cells seems also relatively small in far lower compression wood where intercellular spaces are absent and tracheids have fairly angular outlines. However, if so, the outline of a given tracheid in a cross section cannot be free from their influences. Although such a difficulty could be cleared to some extent by averaging the value of the roundness measured on a statistically sufficient number of sections obtained along the length of each tracheid, such an observation was not made in the present study.

The roundness of the outline may also be modified slightly through the secondary wall formation as observed in the transitional zone from normal to compression wood (Yumoto et al. 1982 b).

The line of the inner edge of tracheids in cross section is determined by the outline and the pattern and quantity of cell wall formation. Closely observed, the inner line of compression wood tracheids is more round than the outline. On the contrary, in normal wood tracheids the former is more angular than the latter (Photos 40 and 56). In other words, the secondary wall formation tends to increase the roundness of the inner line in compression wood and to decrease it in normal wood. Therefore, if the roundness of the inner line is compared with that of the outline, the influences of extrinsic factors, such as arrangement of the neighbouring cells, unstable occurrence of intercellular spaces, could be relieved to a considerable extent. However, if the outline is round enough, the inner line would be also round irrespective of the intensity of this tendency (cf., Photo 18). Furthermore, the intensity of the tendency to modify the roundness of the inner line may differ tree-to-tree and/or species-to-species, and also between juvenile and mature wood, since in some of photographs presented in other papers or textbooks, normal earlywood tracheids are seen to have also rounded inner lines, though there remains a doubt that the “normal wood” might actually be slight compression wood.
In this respect the tracheids seen in Photos 35, 36, 39 and 55 are of special interest. Their outlines and especially their inner lines seem to be slightly rounder than the normal. In the region where they were found, tracheids had generally no appreciable UV-absorption in the S2 (L) layer but slightly higher UV-absorption evenly distributed in the S2 layer, and the S3 layer was often poorly developed or absent (Photos 34, 35 and 39). The lack of the S3 layer would be brought about by geotropic stimulation as stated above. Judging from our experience in the study of the structure of normal and compression wood tracheids in young trees of *Picea glauca*, they are believed to be somewhat different from normal ones (Photos 40 and 56). Although such a degree of the roundness might be within the range of normal variation, it is quite questionable whether they are normal ones.

The roundness of the inner line is also subject to the annual variation of cell wall thickness. If cell walls are thin, there would be little difference in roundness between the outer and inner line. As the thickness increases, the difference in roundness would become greater. However, little information is available concerning to the influence of the thickness of the secondary wall on the roundness. From these considerations, it can be said that many factors are also involved in the establishment of the roundness of the inner line.

The boundary line between the S1 and S2 (L) layer most attracts our attention in UV-photographs. The roundness of the boundary line is determined by that of the outline and the pattern and thickness of the S1 layer deposition. Similar to the case of the total secondary wall, the S1 layer in compression wood tracheids is thicker than the normal and deposited preferentially at cell corners. From the present observation, it can be said that its thickness and pattern of deposition represent an aspect of the severity of compression wood tracheids; the increase of the degree of the S1 layer formation is represented by the increases in thickness and tendency of the preferential deposition. In contrast to the S2 layer, the influence of the S1 layer on the roundness in normal wood tracheids is negligible because of its thinness. Only in compression wood tracheids the S1 layer augments the roundness of the outline diminishing the influences of extrinsic factors depending on its degree. The higher the degree of the S1 layer formation as an aspect of compression wood formation is, the more the influences of extrinsic factors are relieved (cf., Photos 1, 4, 14 and 28). However, as is the case of the total secondary wall, if the outline is highly round, the S1 layer also does not participate in the increase of the roundness of the boundary line (cf., Photo 18).

The thickness of the S1 layer in normal wood is reported to show an annual variation (SAIKI 1970, SIDDIQUI 1976). Although the relation between its annual variation in pattern and quantity, and the intensity of stimulation in compression wood is not known, the net reflection of its annual variation in thickness on the roundness of the boundary line would be considerably less than that brought about by compression wood formation.

From above discussion, it is concluded that the roundness of the boundary line between the S1 and S2 (L) layer most effectively represents an aspect of the
Severity of compression wood tracheids (YUMOTO et al.)

severity among the three, relieving the influences of extrinsic factors, though it is not yet completely free from them.

v. **Cell wall thickness**

As discussed in the previous paper (YUMOTO et al. 1982 b), cell wall thickness or wall percentage can be thought to be the primary factor to determine the specific gravity of wood, and the specific gravity is reported to increase as the severity of compression wood increases or to have correlations with some aspects of the compression wood severity (PILLOW and LUXFORD 1937, PEREM 1958, 1960, SHELBOURNE and RITCHIE 1968, WEOCH 1975, HARRIS 1977, SETH and JAIN 1978). More directly, YOSHIZAWA et al. (1981) reported increases of cell wall thickness from the opposite to the lower most sider of a leaning stem of a young tree in *Pinus thunbergii*, and our preliminary study showed a fairly good correlation between the thickness and the angle of stem deviation in young trees of *Picea glauca* (YUMOTO, unpublished).

However, as well known, cell wall thickness also changes under the influences of external and internal factors other than gravity. In normal wood of temperate species the thickness shows a more or less periodical change (SAIKI 1963 a, b, c, 1965 a), whereas in compression wood, if the gravitational stimulation is strong enough, the thickness is kept almost unchanged throughout the annual increment (YUMOTO and ISHIDA 1982). Most of compression woods show intermediates between these two patterns; walls are thin in earlywood and at a certain point to the latewood they thicken gradually to have the thickness of so-called typical compression wood tracheids (cf., PARK et al. 1979, YOSHIZAWA et al. 1981).

To complicate the subject further, cell wall thickness of mildly stimulated compression wood tracheids seems to be a little thinner than that of the corresponding normal wood tracheids. For instance, compression wood tracheids shown in Photos 53 and 54 have apparently thinner walls than the corresponding normal wood tracheids shown in Photo 56, all of which were taken from the most cambial sides of the specimens. The relation between the degree of the thinning of cell wall in compression wood tracheids and those of development of other features in a tracheid appears also to change seasonally. For example, tracheids shown in Photo 41, which are situated on the most pith side of a specimen, have extremely thin walls, which are probably thinner than those of the corresponding normal tracheids. Whereas, the tracheids found ca. 35 cells later in the same radial file (Photo 42) have relatively thick walls, despite the fact that the strength and distribution pattern of UV-absorption and the roundness do not change so markedly. Probably, as a result of this thinning, cell wall thickness in early formed wood does not reach to a great value until the stimulation exceeds a certain limit. The cell wall thickness of the tracheids shown in Photo 25, which was taken from the most pith side of another specimen, is obviously thinner than later formed ones in the same sample shown in Photo 27, whereas, in contrast to the lack of spiral grooves in the latter, traces of grooves are present in the former. However, since the tracheids shown in Photos 25 and 41 are situated ca. 100 cells apart from the
most newly formed ones, they are believed to have been formed apparently earlier than other tracheids examined in this study (a radial file consists of 50 to 70 tracheids in most specimens). Cell wall thickness of compression wood tracheids near the growth ring boundary especially in late wood is reported to be similar or even a little thinner than the normal (White 1907, Onaka 1949, Panshin and de Zeeuw 1980), though no mention is made as to the severity of the tracheids they examined. Thus, the behavior of cell wall thickness in compression wood is very complicated. However, within 50- to 60-cell depth from the most newly formed tracheids in the present materials, i.e., in the middle of the growth ring, the thinning generally occurs in the tracheids with fairly angular outline and traces of the S2 (L) layer at cell corners, and the relations between the behavior of cell wall thickness and the degrees of development of some other features such as UV-absorbance, spiral grooves, seem relatively fixed.

Another problem is the variation in thickness along the length of the tracheid. According to Okumura et al. (1974), the thickness of the S2 layer in a normal latewood tracheid in Pinus densiflora was relatively uniform along the length of the tracheid in the tangential wall, whereas in the radial wall it conspicuously decreased towards cell tips and showed a linear relationship to the tangential cell diameter. In an earlywood tracheid, on the other hand, the thickness was rather constant through the length both in the tangential and radial wall. Yoshizawa et al. (1981) studied cell wall thickness and diameter of compression wood tracheids along the length in a young tree of Pinus thunbergii and recognized two different types of variation. However, differing from the normal wood tracheid reported by Okumura et al., not only in the radial wall but also in the tangential wall the thickness was found to decrease towards cell tips in both the types of tracheid showing a common pattern of the variation. Judging from the figures presented in these papers, it can be said that the pattern of the variation in cell wall thickness of the radial and tangential wall are similar to those of the tangential and radial diameter respectively. Therefore, if the ratio between them is taken, a relatively uniform value along the length would be given irrespective of the type of tracheid (cf., Okumura et al. 1974). Okumura et al. reported also increased thickness of cell wall at ray crossings in a normal earlywood tracheid. It may be preferable to avoid estimating the thickness of the tracheids adjoining rays.

The thickness and diameter are expected to show tracheid-to-tracheid variations. In a previous paper (Yumoto et al. 1982 b) we found a linear correlation between the tangential* single wall thickness and the radial cell diameter in normal and compression wood of a young tree of Picea glauca. Therefore, the ratio between them can be thought to be also available among tracheids, though this apparently reflects partly the above stated relation along the length of the tracheid.

The cell wall thickness and diameter, or the ratio between them are also known to differ among species and between juvenile and mature wood (Saiki 1965 b, Larson

* In Yumoto et al. (1982 b) where it says radial wall or radial single wall should correctly read tangential wall or tangential single wall respectively; they appear on p. 322, 2nd par., 1st line; on p. 323, 1st par., 2nd line; and in 1st lines of the explanation of Figs.1 to 5.
1966, France and Mexal 1980). Therefore, the ratio is only available in a comparison of an aspect of the severity of compression wood tracheids among which above mentioned difficulties are negligible.

vi. Excessive lignification particularly in the S2 (L) layer

The occurrence of the characteristics lignin distribution particularly in the S2 (L) layer can be thought to be the most essential feature of compression wood tracheids, because it is the only feature that can be found in all the species that produce this type of wood including Ginkgo, Taxus and Torreya (Takaoka and Ishida 1974, Takaoka 1975, Timell 1978a, b, 1981 Yoshizawa et al. 1982), and also found only in compression wood tracheids, and at same time, covers nearly full range of the severity of compression wood tracheids except for the tracheids with slightly higher UV-absorption evenly distributed in the S2 layer (Photos 39 and 55).

Observed by UVM, two different aspects of this feature can be distinguished, i.e., the distribution pattern and the absolute strength of the absorption (absorbance). Although the absorbance was not measured in the present study, it is represented partly in the distribution pattern.

The distribution pattern of the UV-absorption changes as the degrees of development of other features lower, and the strength of the absorption also changes supplementing the change in the pattern. In thick-walled and highly rounded compression wood tracheids with spiral grooves, the strong absorption in the S2 (L) layer is distributed almost evenly around the circumference of the tracheids, and the S1 and the inner region of the S2 layer also show a considerable strength of the absorption to lessen the contrast between these parts of cell walls and the S2 (L) layer in 1-μ-thick sections (Photos 1 to 4). The first appreciable change in the reduction of the severity is found in the strength of the absorption. The decrease in absorbance seems more apparent in the S1 and the inner region of the S2 layer than the S2 (L) layer to make the presence of the latter prominent. In UV-photographs the presence of the spiral grooves is represented as radial striations. Accompanying the lowering of the degree of development of spiral grooves, the striations become not distinct and finally disappear.

As the degree further lowers, strong UV-absorption becomes concentrated near the cell corners. This concentration seems to be caused mainly by the reduction of the roundness in cross section, namely the strong absorption tends to be accumulated to the part of cell wall which shows a greater curvature than the surrounding parts. Even in thick-walled compression wood tracheids with spiral grooves and higher absorption, if a tracheid has strongly curved wall in a part, the part shows strong UV-absorption or has the wider S2 (L) layer than its surrounding parts (Photos 4 and 14). On the contrary, if tracheids, in which the degrees of other characteristic features are totally lower, are round in cross section, strong absorption is distributed nearly evenly around the circumference as shown in Photo 18. However, in this photograph, the S2 (L) layer presents a considerable contrast to other parts of cell walls because of the lower absorption in the latter. There-
fore, the degree of development of this feature should be estimated not only from the distribution pattern but also from the relative absorbance between the S 2 (L) layer and other parts of cell walls (e.g., inner region of the S 2 layer).

The decrease in the width of the S 2 (L) layer also plays an important role in determining the distribution pattern of more lower degrees. As shown in Photos 30 to 32, the S 2 (L) layer other than that near the cell corners is reduced to fine lines along the middle lamella, and this gives an impression that the strong absorption is confined at cell corners.

Traces of the UV-absorption in the S 2 (L) layer at cell corners are in most cases the only apparent feature that distinguishes compression wood tracheids from the normal ones by the method used in the present study. However, this type of absorption does not seem to represent the lowest degree of the excessive lignification. In the sequence of the lowering of the degree, tracheids with slightly higher UV-absorption evenly distributed in the S 2 layer were observed between compression wood tracheids with traces of the S 2 (L) layer and apparent normal ones. Although there remains a doubt that this might be an optical artifact, this type of absorption would represent the lowest degree of the excessive lignification, judging from the fact that these tracheids generally have a trace of the roundness and often lack in the S 3 layer.

There is little information concerning to the cause which evokes the characteristic distribution of lignin in the secondary wall of compression wood tracheids. However, as discussed in a previous paper (Yumoto et al. 1982 b), the distribution pattern is possibly intimately associated with the secondary wall deposition. Therefore, if there are some seasonal differences in wall structure (Wilson and Wellwood 1965), the difference might be reflected in the lignin distribution pattern. The lignin concentration in the secondary walls is also known to show an annual variation (Fergus et al. 1969, Wood and Goring 1971, Siddiqui 1976, Fukazawa and Imagawa 1981). Although the net influence of the annual variation on the lignin concentration and distribution pattern in the secondary wall of compression wood tracheids has not been sufficiently studied (cf., Wood and Goring 1971, Fukazawa 1974), its extent would be far less than that caused by compression wood formation, and could be neglected.

VII. Angle of the microfibrils in the S 2 layer

The angle of the microfibrils in the S 2 layer of compression wood tracheids is known to be greater than that of normal tracheids (Wardrop and Dadswell 1950, Matsumoto 1957). Matsumoto (1957) reported a positive correlation between the angle of the microfibrils and the degree of stem deviation. Nečesáný (1955) mentioned, on the other hand, a positive relation between the microfibrilar angle and the degree of lignification.

However, in the present study, the angle observed by SEM seems to be kept nearly constant irrespective of both the degrees of development of other features and the angle of stem deviation. Although increased angles were observed in a tree grown under the displacement of 90° (Photo 4), this should be regarded as
an exceptional case. In UV-photographs spiral grooves which run in parallel with the microfibrils were not so clearly shown in the specimens from the trees grown at greater stem deviations (e.g., Photo 45) as in those at smaller deviations (e.g., Photo 47). This might imply the difference in the microfibrilar angle in the S2 layer. However, this would be rather a sectioning artifact brought about by the difference in hardness of the samples, since UV-photographs of the differentiating zone of the former showed also distinct grooves. The materials examined in the present study are juvenile wood and the microfibril angle of this type of wood is known to be greater than that of mature wood (DADSWELL and WARDROP 1949, ZOBEL et al. 1959). Therefore, it can be well understood that no appreciable difference in angle was observed in the present study. In a previous paper (YUMOTO et al. 1982b) also no appreciable change in angle was observed through the transitional zone from normal to compression wood, using equivalent trees to those used in the present study. HARRIS (1977) failed to detect the difference in mean microfibrilar angle between compression wood and the corresponding opposite wood using 3-year-old young trees of Pinus radiata, though the angle in opposite wood is reported by some authors to be greater than the normal (MATSUMOTO 1957, TIMELL 1973).

However, whether the angle of the microfibrils in mature wood is related to the severity of compression wood tracheids remains to be solved. FUJITA et al. (1979) reported a sharp increase in the microfibrilar angle occurred accompanying the transition from normal to compression wood in a 20-year-old tree of Pinus densiflora. CÔTÉ et al. (1976) states that in the earlywood cells in Larix laricina, despite their lack of rounded outline and helical cavities, the orientation of the microfibrils in the S2 layer was similar to that in the more typical compression wood tracheids formed at a later stage. PARK et al. (1980) made a similar observation in a 15-year-old branch taken from a 25-year-old tree of Pinus densiflora.

Some investigators attributed the greater microfibrilar angle in compression wood tracheids (WARDROP and DADSWELL 1950) and in juvenile wood (WESTING 1965) to their shorter length. At any rate in this study, the angle of the microfibrils in the S2 layer observed by SEM cannot be said to represent any aspect of the severity of compression wood tracheids.

viii. Intercellular spaces

Although the occurrence of intercellular spaces is not a characteristic of a compression wood tracheid, it is adequate to mention it, since the formation of intercellular spaces can be thought to be evoked by their surrounding tracheids.

The occurrence of intercellular spaces seems the most capricious feature of compression wood. They do not necessarily appear at all cell corners even among thick-walled and highly rounded compression wood tracheids with spiral grooves such as those shown in Photos 2 to 4. As mentioned earlier, the disappearance of the spaces generally occurs at a slightly later stage than that of spiral grooves in the sequence of the reduction of the severity. However, the spaces are sometimes entirely excluded from all the cell corners among tracheids with distinct
grooves as shown in Photo 14. Mio and Matsumoto (1982) made a similar observation. On the contrary, the spaces can be formed among relatively thin-walled tracheids without spiral grooves as those shown in Photos 28 and 29.

Mio and Matsumoto (1979) reported the occurrence of longitudinal intercellular spaces between rays and their adjacent tracheids in normal wood of all the coniferous species they examined. In the course of the present series of studies on *Picea glauca*, the spaces have also occasionally been found in normal wood, though their association with rays could not be confirmed in a section (Yumoto, unpublished). On the other hand, in a young tree of *Abies sachalinensis* all intercellular spaces in a certain zone of compression wood comprising tracheids with thick walls and spiral grooves were once found to be filled with intercellular substances to make an apparent band of several-cell depth arranged tangentially covering the entire crescent of compression wood (Yumoto, unpublished). Although this is apparently exceptional, this implies the existence of a factor or factors other than gravity essentially concerned in the formation of intercellular spaces.

Intercellular spaces are known to be formed in an early developmental stage (Wardrop and Davies 1964, Casperson and Zinsser 1965). Whether intercellular spaces are formed or not would be determined by the volume of the room among several immediately adjacent tracheids and the amount of intercellular substances to fill up the room. The former is thought to be determined by a complicated process mentioned earlier as to the establishment of the outline of tracheids in cross section. Probably, the middle lamella is partially dissolved (Esau 1965) and there would be enzymatic involvements as is the formation of resin canals (Fahn and Benayoun 1976). Thus, the formation of intercellular spaces should be thought rather a result of the involvement of many essentially different factors, and little information is available for the effects of gravitational stimulation on these factors.

As well known, the occurrence of intercellular spaces is a common feature of normal wood in some genera (McGinnes and Phelps 1972, Bolton et al. 1975). In compression wood the occurrence of intercellular spaces can be said generally to represent an aspect of relatively severe one, however, it is not necessarily associated with compression wood formation and unstable in nature.

3. Selection of reasonable markers for the gradation of given tracheids

The influences of extrinsic factors on the formation of characteristic features of compression wood tracheids and relations among respective features are summarized in Fig. 1. Thick arrows indicate strong dependence. It should be noted that this figure shows only conceivable relations, and that many unrevealed physiological processes are involved for the formation of each feature, some of which may be common with those of another or not necessarily confined in compression wood formation.

Of extrinsic factors, the occurrence of intercellular spaces evoked by casually, though being rare in young trees of *Picea glauca*, cannot be distinguished from that caused by compression wood formation. The arrangement of the neighbouring
Severity of compression wood tracheids (YUMOTO et al.)

Fig. 1. Influences of extrinsic factors on the formation of characteristic features and interrelation among the features.

Int. S.: intercellular spaces, Ex. L.: excessive lignification, R outer, R bound, R inner: roundness of the outline, boundary line between S1 and S2 (L), and the inner line in cross section respectively, CWTs1: cell wall thickness of the S1, CWTtot: total cell wall thickness, Sp. G.: spiral grooves, F. B. P.: form of bordered pits, L. D. P.: lignin distribution pattern; thick line: reliable features with independence, thick dotted line: features of little intrinsic involvement, fine dotted line: unstable features, fine line: other characteristic features; thick arrow: strong influence, fine arrow: mild influence, thick bar: strong relation.

cells can be recognized on observations. Although its influence on the roundness of the outline is generally difficult to eliminate, it seems to be relatively small in highly rounded compression wood tracheids with large intercellular spaces and in far lower ones without the spaces. And the roundness of the boundary line between the S1 and S2 (L) layer is more reliable than that of the outline or inner line of tracheids in cross section. Cell wall thickness is strongly subject to the annual variation. The variation of cell wall thickness as an aspect of the severity of compression wood tracheids is further complicated by the thinning of cell wall which occurs in mildly stimulated compression wood tracheids, however, in the middle of the growth ring, there is a relatively fixed relation between cell wall thickness and the degrees of development of several other features.

As discussed above, intercellular spaces and the S3 layer in compression wood were found to occur fairly regardless of the degrees of development of other features, and their occurrence would be unstable in nature rather than others are unstable. However, if they are primarily involved in compression wood formation, the occurrence should be regarded to have the same significance as marker with others. The problem is that the cause of the unstability is not known, and their importance as marker hangs on whether they are primary in nature, or if not, hangs on the degree to which they are concerned. The absence of the S3 layer in
compression wood tracheids seems to be caused simply by the disturbance of normal wood formation, and the formation of intercellular spaces is thought to be controlled by many essentially different factors and their involvement is more complicated than in the case of other features. Therefore, in the present study, it can be permitted to regard these two features to be of secondary importance as marker and to exclude them from the criterion of gradation.

The features surrounded by thick dotted lines in Fig. 1 are those whose degrees of formation are believed to be determined chiefly by the those of the indicated features. Namely, the form of bordered pit opening in compression wood tracheids is modified by the enhanced cell wall thickness and the occurrence of spiral grooves. The characteristic lignin distribution pattern is determined chiefly by the quantity of lignin, the roundness of the boundary line between the S1 and S2 (L) layer, and the presence of spiral grooves or structure of the S2 layer.

From these considerations, it can be concluded that the occurrence of spiral grooves and the excessive lignification are of primary importance and independent from other features and from each other. And if the gradation is set up only for the tracheids in the middle of the growth ring, cell wall thickness expressed as the ratio to the diameter is also available and independent, though it cannot be used alone because of the occurrence of the thinning in mildly stimulated compression wood tracheids. The severity of a given tracheid should be thought to be represented as a function of the degrees of development of these features and each has its own significance as marker.

The degrees of development of these features seem to change relatively in parallel to one another. This might imply that the formation of these features is stimulated by a common agent. However, even if this is the case, since the final response mechanisms are apparently different to one another, there must be nonparallelism in degree between them. Such a nonparallelism is an essential attribute of the organism and cannot be avioded at any rate.

It should be pointed out that abnormal deviations from the normal features of compression wood tracheids occasionally happen to occur. During the course of the present study, two tracheids with no grooves and thick walls having lower strength of UV-absorption were found in a file of tracheids with grooves and strong UV-absorption having thinner cell walls than those. In a previous paper (YUMOTO et al. 1982 a) we found clusters of cells showing a lower degree of lignification in the transitional zone from normal to compression wood. SCOTT and GORING (1970) noted also the occurrence of abnormal compression wood tracheids in a branch wood of Picea abies. According to their report, these tracheids lacked in spiral grooves and possessed variable lignin content and a distinct lamellar structure in the secondary wall with concentric layers of high UV-absorbance separated by the layers of every low absorbance, and were dispersed through the regions of the "usual" compression wood tracheids. They would be not caused by the difference in the stimulation but caused by that in the sensitivity of the tracheids or by some disturbance in the response mechanism, and at any rate, they should be regarded to be abnormal and exceptional.
4. Gradation of given compression wood tracheids

As stated above, the severity of given compression wood tracheids is estimated by a combination of the degrees of development of three relatively reliable characteristics, *i.e.*, excessive lignification, spiral grooves and cell wall thickness compared with the diameter, permitting a certain degree of the latitude for each feature, though the third is not available for relatively thin-walled compression wood tracheids. However, unfortunately, the reasonable range of the latitude cannot be settled in the present study because of the lack in quantitative information. Therefore, compression wood tracheids are first classified for convenience by the degree of development of spiral grooves into three classes, *i.e.*, compression wood tracheids with distinct grooves, those with poorly developed grooves, and those without grooves. These three classes are further complemented and subdivided by the strength of UV-absorption (degree of excessive lignification), cell wall thickness, and by the degrees of development of other features whose degrees are determined chiefly by those of the three features.

The first class of compression wood tracheids is characterized by the presence of distinct grooves; the depth and interval of the groove are not important. This type of tracheid seems to cover a considerable range of the severity, and therefore, it is adequate to subdivide this class into two subclasses, *i.e.*, Grades I and I'. Grade I compression wood tracheids are the most severe ones and distinguished from those of Grade I' most apparently by the relative absorbance in the inner S2 layer to the S2 (L) layer and the cell wall thickness. In this class the UV-absorption of the S1 and the inner region of the S2 layer is so strong that the presence of the S2 (L) layer does not stand out when observed on 1 μ thick sections as shown in Photos 1 to 4 and 11, and highly thickened cell wall generally hinders the bordered pit dome from rising, or if not, the rising is limited in a small extent (Photos 1 and 11). Generally, the boundary line between the S1 and S2 (L) layer in cross section is nearly circular and lignin in the S2 (L) layer is distributed almost evenly around the entire circumference. Intercellular spaces are generally present.

Grade I' compression wood tracheids show the rising of the pit dome, because of their decreased wall thickness, and the difference in UV-absorbance between the S1 or the inner region of the S2 layer and the S2 (L) layer stands out because of the reduced absorbance in the former as shown in Photo 12 to 14. Intercellular spaces are generally present but occasionally absent (Photo 14). The boundary line between the S1 and S2 (L) layer is round but not nearly circular as that of Grade I and sometimes fairly angular when intercellular spaces are lacking (Photo 14).

Compression wood tracheids of the second class have poorly developed spiral grooves. For the confirmation of this class, it is desirable to estimate its degree of development from both the transeverse and longitudinal view, as stated earlier. The cross-sectional shape of the boundary line between the S1 and S2 (L) layer is variable depending on the presence or absence of intercellular spaces. The
range of this class is relatively narrow. Tracheids shown in Photos 15 to 17 belong to this class.

In the third class of compression wood tracheids, spiral grooves are absent. Since this class covers also a considerable range of the severity, it may be appropriate to subdivide it into two subclasses as is the case of the first class. They are denoted Grades III and III'. Unfortunately however, there is no reasonable qualitative marker for the distinction of these subclasses. As shown in Fig. 1, lignin distribution pattern is thought to be determined by the degree of excessive lignification, the secondary wall structure and the roundness of the boundary line between the S1 and S2 (L) layer. Of these characteristics, the roundness is not so reliable. However, in the lower range of this class the degree of excessive lignification seems to be represented mainly by the width of the S2 (L) layer and the width plays an important role in determining the distribution pattern. This complements unreliability of the roundness, and therefore, in this class lignin distribution pattern can be believed available as marker. Grade III compression wood tracheids have thicker walls than the normal and are yet considerably round in cross section, and because of this the occurrence of fairly wide S2 (L) layer they do not give an impression that lignin is concentrated at cell corners. Fine streaks (not grooves) on the inner surface are occasionally found as seen in Photos 26 to 28. The S3 layer is generally absent but can be present (Photo 44). The tracheids shown in Photos 26 to 29 and 44 belong to Grade III.

In Grade III' compression wood tracheids, cell wall thickness is not reliable as marker. It is slightly thicker or similar, or even a little thinner than that of the corresponding normal wood tracheids. The strong UV-absorption tends to be distributed mainly at cell corners. Intercellular spaces are generally absent and the S3 layer is present or absent. The tracheids shown in Photos 30 to 33, 37, 42 and 43 belong to Grade III'.

Other than these classes, it may be preferable to provide a particular class of gradation for the tracheids shown in Photos 34 to 36 and 39. These tracheids are almost normal, but different in some respects; lacking in the S3 layer (Photos 34, 35 left tracheid, 39 left one) or having slightly rounded shape in cross section (especially Photo 36) or having slightly excessive UV-absorption evenly distributed in the S2 layer (especially Photo 39). As stated above, there is a doubt that they might be artifacts or be within the range of the normal variation. However, the fact that they are found between compression wood tracheids of Grade III' and normal ones in the sequence of the reduction of the severity strongly suggests that they are actually a type of compression wood tracheid. These tracheids can be said to be situated at the edge of the normal, and they constitute Grade IV.

In addition, Grade V is given for normal wood tracheids. The criterion of the gradation is summarized in Table 1.

The occurrence of unstable features such as intercellular spaces and the S3 layer can be represented by suffixes if necessary. Namely, when intercellular spaces are present among Grade III' compression wood tracheids, the tracheids are expressed as Grade III' + i, where i is an abbreviation of intercellular spaces. Simi-
Table 1. Criterion for the gradation of compression wood tracheids in the middle of growth rings.
Characteristic features are arranged in the order of importance from left. Spiral grooves, 
UV-absorption and cell wall thickness are of primary importance, though the availability 
of the third is limited. Roundness of the boundary line between $S_1$ and $S_2 (L)$, form of 
bordered pits are in the second class in importance. Unstable features are also incorpo­
rated at right. Cell wall thickness and form of bordered pits are only available in the 
middle of growth increments.

<table>
<thead>
<tr>
<th>Grade</th>
<th>Spiral grooves</th>
<th>UV-absorption</th>
<th>Cell wall thickness</th>
<th>Roundness of boundary line between $S_1$ and $S_2 (L)$</th>
<th>Form of bordered pits</th>
<th>Unstable features</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>distinct</td>
<td>totally strong; lower contrast between $S_1$ or inner region of $S_2$ and $S_2 (L)$; distributed nearly evenly around entire circumference of tracheid</td>
<td>very thick</td>
<td>highly round nearly circular</td>
<td>no or slight rising of pit</td>
<td>intercellular spaces generally present</td>
</tr>
<tr>
<td>I'</td>
<td>distinct</td>
<td>strong but less in $S_1$ and inner region of $S_2$ to stand out the presence of $S_2 (L)$</td>
<td>thick</td>
<td>round but not circular</td>
<td>pit dome rising</td>
<td>intercellular spaces generally present</td>
</tr>
<tr>
<td>II</td>
<td>poorly developed</td>
<td>considerably strong</td>
<td>considerably thick</td>
<td>round but variable depending on the presence or absence of intercellular spaces</td>
<td>generally no grooves or absent</td>
<td>intercellular spaces present or absent</td>
</tr>
<tr>
<td>III</td>
<td>absent</td>
<td>strong absorption not confined at cell corners</td>
<td>thicker than normal</td>
<td>fairly round</td>
<td>—</td>
<td>intercellular spaces generally absent; S3 layer generally absent</td>
</tr>
<tr>
<td>III'</td>
<td>absent</td>
<td>strong absorption confined at cell corners</td>
<td>slightly thicker or similar, or even a little thinner than normal</td>
<td>slightly round</td>
<td>—</td>
<td>intercellular spaces generally absent; S3 layer absent or present</td>
</tr>
<tr>
<td>IV</td>
<td>absent</td>
<td>no strong absorption in $S_2 (L)$ but slightly higher absorption evenly distributed in $S_2$</td>
<td>similar to normal</td>
<td>trace</td>
<td>—</td>
<td>S3 layer generally present</td>
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</table>
larly, the variations in the cell wall thickness, roundness and the degree of excessive lignification within a given grade can be described by suffixes $t$, $r$ and $l$ respectively, and if the variation occurs towards the lowering of the degree, or if an unstable feature is absent in a grade in which it is usually present, this is expressed with a subtraction sign, e.g., Grade I$-i$.

It should be noted that this criterion of gradation is only available for the middle region of tracheids situated in the middle of the growth ring in young trees of *Picea glauca*. As stated above, the degree of development of spiral grooves is known to lower near the tip of tracheids. And the behavior of cell wall thickness along the stimulation and its relation to the degrees of development of other features are apparently different in early formed wood and latewood. Furthermore, the relation among behaviors of respective features along the severity other than cell wall thickness might also not be applicable to other cases, though the selected features are believed to have universality in aptitude within a tree or among trees, or among species except for those without the ability to produce spiral grooves.

Since tracheids shown in Photos 25 and 41 are situated in early formed wood, the gradation is not given for these tracheids. The relations among the behaviors of respective features along the severity in early formed wood and latewood remain to be solved. However, they probably belong to Grade II and Grade III respectively, though cell walls are thinner than those in the middle of the growth ring.

The present criterion of gradation is a little similar to that of Fukazawa (1974). He made an observation on compression wood tracheids of *Abies sachalinensis* by UVM, and classified them into several grades based chiefly on the distribution pattern of UV-absorption and the cell shape in cross section. However, the observation on the inner surfaces in the present study made the gradation far more difficult, because of the strong nonparallelism found among different characteristic features.

Fukazawa (1973) also suggested a possibility of the depth of spiral grooves observed by SEM as marker, which was adopted by Park et al. (1980). However, this possibility was denied in the present study.

In the present criterion of gradation the occurrence of spiral grooves has priority over other features. It should be noted again that this is only a matter of practical convenience, and that properly speaking, the selected three features have the same significance as marker. In this respect the present gradation remains to be an artificial gradation.

As well known, the grooves are lacking in compression wood tracheids of primitive gymnosperms such as *Ginkgo, Taxus* and *Torreya*, though drying checks are often found (Takaoka and Ishida 1974, Takaoka 1975, Timell 1978a, b, 1981, Yoshizawa et al. 1982). This implies the lack of the response mechanism for grooves formation and raises a serious difficulty to grade compression wood tracheids of these genera. This also suggests that the secondary walls of well-developed compression wood tracheids in these genera would have a similar structure to that of moderate or mild ones (Grade III) of other genera being able to produce the grooves, though the former often reaches a comparable thickness.
Severity of compression wood tracheids (YUMOTO et al.)

and roundness to that of the typical one of the latter. The fact that drying checks are often found in this type of compression wood tracheid (PARK et al. 1980) leads to a possibility that their $S_2$ layer might not be composed of microlamellae as that of normal tracheids (IMAMURA et al. 1974, HIRAKAWA and ISHIDA 1981). Spiral grooves have been thought to be a feature presented in all-or-none manner, however, the present investigation revealed rather a gradual transition as to the degree of development of spiral grooves. There might be intermediates in the secondary wall structure between compression wood tracheids with spiral grooves and normal ones. It is hoped to disclose the cell wall structure of moderate or mild compression wood tracheids, and this might provide a reasonable basis to subdivide this grade of compression wood tracheids.

In the present study observations were made only on a limited area of tracheids. However, some anatomical features of compression wood tracheids appear as a whole trached. The reduced length (WARDROP and DADSWELL 1950, PETRIĆ 1962) and the undulating profile of the outline especially at cell tips (VERRALL 1928, MÜNZ 1940, WARDROP and DADSWELL 1952) are also characteristics of this type of tracheid. As stated above, samples taken from trees grown under 90° could not easily be split radial-longitudinally. This would mean the occurrence of a higher degree of the distortion of tracheids in the sample. The distorted shape and the irregular arrangement of tracheids in compression wood would enable to detect this type of wood by the use of a light box (PILLOW 1941).

5. Comparison with a light microscopic observation

The most newly formed tracheids of all the samples examined were gradated according to the present criterion (Table 2). Although the degree of compression wood tracheids varied considerably within a specimen, in this region it shows a relatively parallel relation to the angle of stem deviation; tracheids formed under the displacements of 90° and 45° all belong to Grade I; those of 20° to Grades I to III; those of 10° and 5° to Grades III' to V. The unstability of the occurrence of intercellular spaces and the $S_3$ layer is also clearly shown. This table would justify the existence of Grade IV compression wood tracheids. In a previous paper (YUMOTO and ISHIDA 1982) we examined similar portions of the same trees by light microscopy and found that they comprised typical compression wood tracheids in all trees grown at 45° or more and a tree at 20°, moderate ones in a tree at 20°, slight in a tree at 10°, and normal in a tree at 10° and all trees at 5°. Making a comparison between these results obtained by different methods, it is concluded that compression wood tracheids of Grades I and I are judged to be typical at a light microscopic level, those of Grades II and III to be moderate, those of upper Grade III' to be slight and those of lower Grade III' and Grade IV to be normal.

The fact that by light microscopy compression wood tracheids lower than Grade III in degree are estimated to be normal leads to a serious question that some of the investigations on “normal wood” would have been made on compression woods of not only macroscopically but also light microscopically indiscernible degrees. Judging from photographs presented in other papers and monographs, compression
Table 2. Grades of the most newly formed tracheids

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<td>90-a-</td>
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<td>90-a-</td>
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<td>I</td>
<td>45-a-</td>
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<td>90-a</td>
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The most newly formed tracheids are gradated according to the criterion shown in Table 1. Suffixes denote the presence or absence of unstable features; +: presence, -: absence, i: intercellular spaces, S 3: the S 3 layer.

woods investigated there consist generally of tracheids of Grade I to II, occasionally of Grade I, or even of Grade III. This must be one of the principal causes of the discrepancies which can be observed in the literature almost at every point of the subject.

Conclusions

In conclusion, the present work substantiated the above statement that it is indispensable to reveal the nature of intermediate compression wood tracheids not only for the study of compression wood tracheids itself but also for the general surveys on woody materials. The present subject, the severity of compression wood tracheids, seems to have been overlooked or evaded in spite of its great importance. Most studies on compression wood lack in mentioning the severity of the materials examined. Strictly speaking, we cannot settle results of such studies properly upon the “co-ordinates” of this phenomenon.

However, the present investigation covers only a fraction of a variety of compression wood tracheids, moreover of juvenile wood. The present criterion of gradation is not available for compression wood tracheids in latewood and early-
formed wood, as well as those situated near the growth ring boundary. In these regions cell wall thickness would show different behaviors. The influence of the annual variation of cell wall thickness on several aspects of the severity of compression wood tracheids is one of the most difficult and complex problems interfering with the establishment of an universal criterion of gradation. Cell wall thickness may affect lignin distribution pattern and the roundness of the outline of tracheids. It is hoped to reveal its influences in detail.

We believe the present gradation represents biological aspects of the severity of compression wood tracheids, though not quite satisfactory. This must provide a reasonable basis for the gradation of compression wood. On the other hand, chemical or physical gradations are also possible other than biological ones. They could be based on the concentration of lignin or characteristic substances in compression wood such as galactan (Stockman and Hägglund 1948, Jiang and Timell 1972) and callose (Brodzki 1972, Włoch 1975, cf., Timell 1982), or specific gravity, longitudinal shrinkage, the modulus of elasticity, etc. Such gradations might throw a new light reversely on the biological gradation, since chemical and physical aspects of compression wood also reflect the nature of the tracheid, the main biological unit of coniferous wood.

Summary

In the present study structural features of all intermediates from normal to the most well-developed compression wood tracheids are described, and after discussing the aptitude of each feature as marker, the observed tracheids are gradated by a criterion with the degrees of development of selected characteristic features.

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° from the vertical, and fixed to stakes with strings; two sample trees on each but three for the deviation of 5°. After about a year small disks were cut from the middle portions of the 2nd and 3rd internodes and fixed in FAA. Small samples were severed from the most newly formed parts of the current increments of disks and examined chiefly by a SEM-UVM combination method, by which the feature of the inner surfaces of tracheids and that in the cross section of the same tracheids along a radial file can be shown.

1) A variety of tracheids from apparently normal to the most well-developed compression wood tracheids were observed. Representatives of the observed tracheids are shown in photographs. At a glance the gradation of these tracheids along the severity might be easy to make. However, difficulties arose when tried to gradate them because of a considerable degree of nonparallelism in the degree of development found among respective features.

2) This nonparallelism was thought to be brought about by at least three essentially different factors, i.e., i) fluctuation in the strength of the stimulus which affects all the cambial and differentiating tracheids at the same time, ii) influences of factors not essentially involved in compression wood formation, and iii) difference
in the stimulation or response for the formation of each feature in a tracheid which is not caused by the factor i). Nonparallelism evoked by the factors i) and ii) should at least be excluded from the gradation.

3) The nature of each feature and its behavior along the severity was discussed to know the cause of nonparallelism in the case iii) and to check the aptitude for the marker. a) Spiral grooves were thought to represent an aspect of relatively severe compression wood tracheids and to be of primary importance and not to have any conceivable causal relations to other features. b) Although the S3 layer was absent in relatively severe compression wood tracheids, their occurrence in those of lower degrees was unstable and thought to be of secondary importance. c) Form of bordered pits in compression wood tracheids was believed to be modified chiefly by the increased cell wall thickness and the occurrence of spiral grooves in the S2 layer, and to have little intrinsic involvement. d) The roundness of the outline in cross section is strongly affected by the arrangement of the neighbouring cells, but its influence is relatively small in highly rounded compression wood tracheids with large intercellular spaces, and also in far lower ones without the spaces having fairly angular outlines. The roundness of the inner line in cross section is determined by that of the outline and the cell wall formation, the latter tends to round the inner edge in compression wood and to angulate it in normal wood tracheids. However, the participation of the annual variation of cell wall thickness on the roundness of the inner line is difficult to estimate. The roundness of the boundary line between the S1 and S2 (L) layer attracts a strong attention in UV-photographs, and is determined by that of the outline and the S1 layer formation. The latter tends to round the boundary line especially when the layer is thick and is less affected by the annual variation, and therefore, the roundness of the boundary line was thought to represent most suitably an aspect of the severity of compression wood tracheids among the three. e) Although cell wall thickness is strongly subject to the annual variation, and the net participation of compression wood formation in the cell wall thickness of given tracheids is difficult to estimate, if comparison is made on the tracheids in the corresponding positions in the annual ring of equivalent trees, it can represent an aspect of the severity. However, cell walls of mildly stimulated compression wood tracheids may be a little thinner than those of the corresponding normal tracheids, and therefore, cell wall thickness cannot be used alone as marker, if it is not substantially thicker than the normal. f) The occurrence of the excessive lignification was thought to be the most essential feature of compression wood tracheids and to have independence from other features. Its distribution pattern in the secondary walls is determined chiefly by the degree of excessive lignification, cell wall structure and the shape of the boundary line between the S1 and S2 (L) layer. g) The angle of the microfibrils in the S2 layer was found to be kept almost constant irrespective of the degrees of development of other features and the angle of stem deviation, and therefore, at least in the present study it cannot be said to represent any aspect of the severity of compression wood tracheids. h) Intercellular spaces were generally found in severe compression wood, however, it is not necessarily associated with
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compression wood formation and their occurrence in this type of wood was also unstable in nature.

4) From these considerations, the occurrence of spiral grooves and excessive lignification were thought to have the primary importance and to be independent from other features and from each other. And if comparison is made among tracheids taken from corresponding positions in the annual ring, cell wall thickness is also reliable within a limited range of the severity. Some other features whose degrees of development are chiefly determined by those of the above three features are also available as marker.

5) Based on the degrees of development of the above mentioned features, compression wood tracheids observed were gradated into six grades. They were first classified for convenience by the degree of development of spiral grooves into three classes, i.e., compression wood tracheids with distinct grooves, those with poorly developed grooves, and those without grooves. These three classes were further complemented and subdivided by the degree of excessive lignification, cell wall thickness, and also by the form of bordered pits and the distribution pattern of UV-absorption. The criterion of the gradation is given in Table 1.

6) The most newly formed tracheids in all the samples examined were gradated according to the criterion and the result was compared with that of a previous study made by light microscopy. Attention was aroused as to the importance of the recognition of the severity of compression wood tracheids not only for the study of compression wood itself but also for general surveys on woody materials.

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要約

正常材仮道管から最も良く発達したあて材仮道管へ至るまでの種々の中間的仮道管の構造について述べ、これらを適切な指標とするいくつかの特徴の発達程度により段階化した。

樹高約2mのグラウカトウヒ (*Picea glauca*) の若齢木を、1978年の7月に地上高約30cmの所から曲げて5°, 10°, 20°, 45°及び90°に傾斜させ、添え木にひもで固定した。供試木は各角度につき2本ずつであるが、5°傾斜のものは3本とした。約1年後に第2, 第3節間の中央部から小さな円板を取り主FAAで固定した。この円板の最外部の木部から試料を切り出し、観察は主に走査電子顕微鏡による1つの半径列に属する仮道管の内表面像を、その同一仮道管の横断面における紫外線顕微鏡像と対応させて行った。

1) 明らかに正常材仮道管から最も良く発達したあて材仮道管までの様々な仮道管が観察された。その代表的なものを写真に示した。一見これらの中間的仮道管の発達程度の段階化は容易に思えるかもしれない。しかし個々の仮道管において、あて材仮道管としての諸特徴の発達程度は必ずしも平行に変化しておらず、段階化は決して容易ではない。

2) この非平行性は少なくとも3つのまったく異なる要因によって引き起されていると考えられる。すなわち、i）すべての形成層及び分化中の仮道管に同時に影響をもたらすあて材形成刺激自体の強さの変動、ii）あて材形成には本来無関係な要素の関与、iii）1つの仮道管内における個々の特徴の形成に関する刺激量あるいは反応の強さの違い、である。このうちi), ii) の要
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因によるものは少なくとも段階化から除外しなくてはならない。

3) 上記のiii) の要因による非平行性の原因を知り、また各特徴の指標としての適性を見ることために、個々の特徴の性質及びそのあての程度にそった挙動について考察した。a) らせんみそは比較的高い让木仏仏道に見られ、他の特徴との間に相互関係はなく、指標として一義的な意味を持っていると考えられる。b) $S_1$ 層は比較的程度の高い让木仏仏道管では観察されないが、程度の低いものでは通常認められる。しかしその出現は不安定であり、指標として重要でないと判断される。c) 有縁壁孔の形は主に仏の肥厚とらせんみそょの出現によって変化させられ、そこで固有の独立した要素は少ないと考えられる。d) 仏仏道管断面の外側の丸身は隣接する細胞の配列によって強く影響されるが、その程度は大きな細胞間隙を持つ良好発達したあて仏及び間隙を欠かしたり方形な仏仏道からなるあて仏の中では比較的少ない。仏仏道管内壁の丸身は外側の丸身と壁形成によって定まる。壁形成は内腔の輪郭をあて仏では丸くし、正常仏では方形化する。しかし仏壁の年輪内変動が及ぼす影響を推測することは困難である。$S_1$ 層と$S(L)$ 層の境界線は紫外線顕微鏡観察で最も目立つが、その輪郭は外側の輪郭と$S_1$ 層形成によって決定される。後者はそれが厚い時に外側の輪郭の丸身を強め、またその年輪内変動の影響は比較的少ない。3 者の中ではあての程度を最も良く表わしていると言うえる。e) 細胞壁厚は年輪内変動を示し、その影響を分離することは困難であるが、年輪内の相当する位置についての比較には用いることが出来る。しかし過剰な刺激を受けたあて仏仏道管の壁厚は相当する正常仏仏道管のそれよりも薄い様であり、従って細胞壁厚はそれが正常仏仏道管のものよりも明らかに厚くない場合には、単独で指標として用いることは出来ない。f) 過剰の木化はあて仏仏道管の最も本質的特徴であり、また他から独立していると考えられる。その 2 次壁中の分布パターンはリグニン含量、細胞壁の構造及び$S_1$ 層と$S(L)$ 層との境界線の形によって定まる。g) $S_2$ 層のミクロフィブリル傾角は、他の特徴の発達程度あるいは供試木の傾斜角度と無関係にほぼ一定であった。従って少なくとも木研究ではあて仏仏道管発達程度の 1 側面を表わしているとは言えない。h) 細胞間隙は一般に程度の高いあて仏に見られるが、必ずしもあて仏形成のみに関係しているわけではない、またあて仏の中における出現も不安定である。指標としては重要であるとは考えられない。

4) 以上から、らせんみその存在と過度の木化があて仏仏道管の特徴として最も本質的であり、また他からの影響も少ないと考えられ。従って指標として適している。細胞壁厚も年輪内の相当位置にある仏仏道管の比較を行う場合にはある範囲内で信用度が高い。またこれらの特徴の発達程度によって主にその程度が定まるいくつかの特徴も指標として有効である。

5) 上記の特徴の発達程度を指標として、観察されたあて仏仏道管の程度を 6 つのクラスに段階化した。まずらせんみその発達程度によって、明瞭ならせんみぞを持つ仏仏道、良く発達していないらせんみぞを持つもの、らせんみぞを持たないものの、の 3 通りに便宜的に分け、これらをさらに木化の程度、細胞壁厚、有縁壁孔の形状、UV 吸収の分布パターンによって補
Explanation of photographs

Note: Photographs in a plate are the same in magnification and calibrations are given at the lower right corners. In Plates I, III, IV and VI to X, the upper photographs by UVM are matched exactly with the corresponding lower ones by SEM. For example, the tracheid in the middle Photo 1 have a pit pair on the cut surface and this is seen well in both the upper and lower photograph showing the same profile.

Plate I. Compression wood tracheids found in trees grown at 90° and 45° from the vertical; SEM-UVM combination method

Photo 1. Tracheids found in 45-b-III. They have highly thickened and rounded cell walls and distinct grooves. UV-absorption in the S1 and the inner region of the S2 layer is so strong that the presence of the S2 (L) layer does not stand out. A bordered pit in the left tracheid shows a slight rising of the pit dome.

Photo 2. Cell wall thickness is slightly reduced as compared with other photographs in this plate, though pits show no rising of the dome. Spiral grooves are relatively wide in interval (90-b-III)

Photo 3. Tracheids found in 90-b-III. The inner pit apertures assume large depressions. The right tracheid has fine grooves.

Photo 4. The angle of the microfibrils in the S2 layer represented as that of grooves is nearly perpendicular to the long axis of the tracheid. (90-b-II)

Plate II. Front views of bordered pits in compression wood tracheids formed under the displacements of 90° and 45°; (no corresponding UV-photographs)

Photo 5. Inner pit aperture, if can be said so, assumes a wide and long depression. (45-b-II)

Photo 6. Inner pit aperture is difficult to define. (90-a-III)

Photo 7. Inner pit aperture is narrow in width and long in the direction of spiral grooves. (45-b-II)

Photo 8. Inner pit aperture is narrow in width and short in the direction of spiral grooves. (90-b-III)

Photo 9. Inner pit aperture is well defined. The interval of the groove is wide. (90-a-III)
Photo 10. A pit with the rising of the pit dome found near the tip of a tracheid. (45-a-II)

Plates III and IV. Compression wood tracheids found in trees grown at 20°; SEM-UVM combination method

Photo 11. Cell walls are considerably thicker than those in other photographs shown in this and next plate. A slight rising of the pit dome can be seen (20-b-II)

Photo 12. Spiral grooves are fine and distinct but not formed around the pit opening at right. Walls are relatively thin and the presence of the S 2 (L) layer stands out because of the the reduced strength of UV-absorption in the S 1 and the inner region of the S 2 layer. (2-a-III)

Photo 13. Grooves are wide in interval but not so distinct as those in other photographs shown in this plate. (20-a-III)

Photo 14. Grooves are fine. The rising of bordered pit dome is apparent, around which no grooves are formed. The outline of the tracheid in cross section is fairly angular and no intercellular spaces are to be seen. (20-a-III)

Photo 15. Grooves are veiled but fairly distinct in the matched UV-photograph. The cross-sectional outline is round. (20-a-III)

Photo 16. The degree of development of spiral grooves is variable among tracheids. This is also shown in the UV-photograph. (20-a-III)

Photo 17. Some of the most newly formed tracheids in 20-a-III. Grooves are only poorly developed. Radial striations in the radial wall are caused by folds in the section.

Photo 18. A particular type of compression wood tracheid probably formed by a sudden decrease in the strength of stimulus. The outline is considerably round but their inner surfaces are smooth, and pits are nearly circular in front view as is the normal. The strength of UV-absorption is also lower. A linear gradation of the severity of compression wood tracheids is not applicable for these tracheids. (20-a-II)

Plate V. Front views of bordered pits found in tracheids formed under the displacement of 20°; (no corresponding UV-photographs)

Photo 19. One of the most slit-like openings in these sample. (20-b-III)

Photo 20. Spiral grooves are not formed around the pit opening. (20-b-III)

Photo 21. The region without grooves around the pit opening extends as the degree of development of the grooves lowers. (20-b-III)

Photo 22. A pit with a large depression and the rising of the dome. (20-a-III)

Photo 23. A pit with a large depression of channel over the pit opening. The formation of such channels at cell corners is not necessarily associated with compression wood formation. (20-a-III)

Photo 24. A pit with a rounded outline comparable to that of the normal tracheid. (20-a-III)
Plate VI and VII. Compression wood tracheids found in a tree tilted at 10° (10-b-III); SEM-UVM combination method.
Photographs are arranged according to the position of the tracheids in the sample from the pith to cambial side.

Photo 25. Tracheids found on the most pith side. Traces of grooves are seen in the radial walls. This would be an artefact formed during sectioning. Charges along grooves imply the occurrence of drying checks. The inner surfaces seem slightly veiled.

Photo 26. Tracheids with no grooves but drying checks.

Photo 27. Thick-walled compression wood tracheids without grooves found in the middle of the sample. Fine radial striations would be artefacts caused by minute folds in the section.

Photo 28. Cell walls are thinner than those in Photo 27 but intercellular spaces are present.

Photo 29. Even though intercellular spaces are seen, cell walls are thinner, and the strength of UV-absorption is also apparently lower than those found in Plate VI. Strong UV-absorption in the S2 (L) layer is considerably confined at cell corners.

Photo 30. The thickness of cell wall is not so different from the normal. Strong UV-absorption is apparently confined at cell corners.

Photo 31. The presence of the S2 (L) layer cannot well be recognized in the radial walls.

Photo 32. Some of the most newly formed tracheids. The S3 layer is present. Traces of the S2 (L) layer and slight roundness are found. The remnant of cell contents is seen in the left tracheid and at the bottom of photograph. Cell wall of the middle tracheid is very thin. Lignification seems not completed.

Plate VIII. Compression wood tracheids found in the other tree tilted at 10° (10-a-II); SEM-UVM combination method

Photo 33. Tracheids with traces of the S2 (L) layer. No S3 layer is present.

Photo 34. Tracheids without both the S2 (L) and S3 layer. The S2 layer shows somewhat higher UV-absorption than the normal. The transition layer can be faintly recognized in the right tracheid.

Photo 35. Very thin lining of the S3 layer is seen in the right tracheid but not in the left. In the latter the transition layer is formed instead of the S3 layer.

Photo 36. Considerably thick S3 layer is deposited, though the outlines remain slightly round and the S2 layer shows slightly excessive UV-absorption.

Plate IX. Compression and normal wood tracheids found in a tree tilted at 5° (5-a-II); SEM-UVM combination method

Photo 37. The S2 (L) layer is seen only as trace. Cell walls may be thinner than the normal.
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**Photo 38.** Compression wood tracheids found between the zones of tracheids with the characteristic UV-absorption in the S2 (L) layer. The S2 layer shows totally an apparent increase in the strength of UV-absorption. These tracheids is thought to have been formed through a sudden increase in the strength of stimulus, contrary to those shown in Photo 18. Gradation cannot be given for these tracheids.

**Photo 39.** The transition layer is found in the left tracheid and the S3 layer is present in the right. The S2 layer shows slightly higher UV-absorption than the normal and the cross-sectional outline may be somewhat round.

**Photo 40.** Apparent normal wood tracheids. Even if the stem is inclined, normal wood tracheids can be formed. The lines marking the inner edges of the tracheids are more angular than those of the outer.

**Plate X.** Compression wood tracheids found in another tree tilted at 5° (5-b-III); SEM-UVM combination method

**Photo 41.** Tracheids found on the most pith side of the sample. In spite of the occurrence of the S2 (L) layer and the rounded outline, cell walls are very thin. Since the sample is bigger in the radial direction, these tracheids are believed to have been formed earlier than those in most of samples examined in the present study.

**Photo 42.** Tracheids formed ca. 35 cells later in the same file with those in Photo 41. Cell walls are apparently thicker than those, though the roundness and distribution pattern of UV-absorption are not so different.

**Photo 43.** Cell walls are fairly thick and the strength of UV-absorption is also high, but the S3 layer is present.

**Photo 44.** Cell wall thickness, roundness and the strength UV-absorption are even higher than those shown in Photo 43, but the S3 layer is apparently deposited.

**Plates XI to XIII.** UV-photographs of transverse sections of compression and normal wood; (no corresponding SEM-photographs)

**Photo 45.** Cell walls are very thick and UV-absorption is very high even in the inner region of the S2 layer. Large intercellular spaces are seen. (90-a–III)

**Photo 46.** Compression wood in 20-b-II. Cell wall thickness, roundness and UV-absorbance are all reduced as compared with those shown in Photo 45.

**Photo 47.** Compression wood found on the most pith side of 20-a–III. Spiral grooves are clearly shown.

**Photo 48.** Compression wood found slightly to the cambial side from that shown in Photo 47. Grooves are not well-developed and intercellular spaces are partially not formed.

**Photo 49.** Compression wood in the middle of 20-a–III. The degree of development of spiral grooves is variable. In the 3rd file from right all tracheids show the presence of the groove, but in the 2nd file only cells A and B have grooves.
Photo 50. A part of the most newly formed compression wood in 20-a-III. No grooves but folds of the section are seen.

Photo 51. The most pith side of 10-b-II. No radial striation and no intercellular spaces are found. The lesser strength of UV-absorption in the inner region of the S2 layer stands out.

Photo 52. Compression wood found near the cambium of 10-b-III. The strength of UV-absorption decreases considerably. Small intercellular spaces are seen at lower left.

Photo 53. The most cambial side of 10-b-III. Strong UV-absorption tends to be concentrated at cell corners. Cell walls are thinner than that of the corresponding normal wood tracheids (Photo 56).

Photo 54. A part of the most newly formed compression wood of 10-b-II. Traces of the S2 (L) layer are recognizable. Cell walls are apparently thinner than the normal.

Photo 55. Compression wood of a disputable degree found near the cambium of 10-a-II. The S2 layer shows slightly higher UV-absorption. Trace of the roundness can be recognized.

Photo 56. Apparent normal wood found in the outer most side of 5-a-III. Tracheids are apparently more angular than those in Photo 55 in cross section and their UV-absorbance in the S2 layer seems lower.