傾斜して育成したクロマツ材の構造

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Structure of Inclined Grown Japanese Black Pine (*Pinus Thunbergii* Parl.) (1)

Distribution of Compression Wood and Cell Wall Structure of Tracheids

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傾斜して育成したクロマツ材の構造（I）

—あて材の分布と仮道管の壁構造—

吉 沢 伸 夫・出 井 利 長・岡 本 健 治

Summary

The correlation between the compression wood formation and the stimulus of inclination was investigated in the inclined grown japanese black pine (*Pinus Thunbrgii* Parl.)

Sample disks at vertical intervals of 20cm from the base were taken from the inclined stem and distribution of compression wood was surveyed on each disk. The cell wall structure of tracheids were examined with polarizing and scanning electron microscopy.

It was surmised that the stimulus of compression wood formation varied within stem in the process of the righting in tree.

The proportion of compression wood increased up to the first 3 years after the bending treatment but then decrsaed as increasing annual rings. In annual rings formed at the same growing season, the maximum proportion of compression wood within stem was found, at first, near the center of the curved stem, but then it was observed that it removed gradually upwards as diminishing the bow-like form of stem.

Slightly different modifications of the tracheid wall structure of the early spring wood were observed within an annual ring and also between annual rings.

In sever compression wood, there is no distinct difference in occurrence of intercellular spaces. However, they occurred later in mild compression wood than in sever compression wood.

From these results, it is considered that the early wood tracheid is less affected by

the compression wood forming stimulus than the late wood tracheid, and that if a leaning tree keeps on growing under the mechanically impossible condition of the righting, the saturation or decline in the stimulus of compression wood formation might occur within stem.

要　旨

傾斜して育成したクロマツ（*Pinus Thunbergii* Parl.）材を用いて，傾斜刺激とあて材形成との関連性を調べた。

あて材の樹幹内分布を測定し，偏光顕微鏡及び走査型電子顕微鏡を用いて仮道管の壁構造を観察した。

あて材形成の刺激は，樹幹の直立化に伴って樹幹内で変化することが観察された。

あて材の割合は傾斜後3年位までは増加するが，その後減少した。同一年輪において，最初あて材の割合は屈曲した樹幹の中央で最も大きいが，傾斜年数が経つにつれてあて材の割合の最大値は樹幹の上部に移行した。

あての程度の異なる壁構造をもつ早材イニシャル仮道管が，年輪内及び年輪間で観察された。早材仮道管は晩材仮道管よりもあて材形成の刺激の影響を受けにくいものと思われる。

程度の強いあて材では，細胞間隙の出現に差が見られないが，軽微なあて材では程度の強いあて材よりも細胞間隙の出現が遅い。

直立化が物理的に不可能になった樹幹では，あて材形成の刺激の飽和あるいは減退がおこるものと思われる。

1. Introduction

A large number of study has been made so far to investigate the correlation between the mechanism of compression wood formation and the bending of stem.

Compression wood was produced artificially by many experimental treatments. For instance, tree stem was directly tilted, or a growth hormone was applied to vertical stem, and also seedlings were subjected to the centrifugal force.[1), 2)] More recently, compression wood was produced under no bending stress by the application of an IAA transport inhibitor.[3)]

As a consequence, the nature of stimulus, the receptive system of stimulus, and the physiology of compression wood formation have been gradually made clear.

As to changes of wall structure of compression wood tracheids induced by the stimulus of inclination, however, many problems have remained unsettled. For example, there are some disagreements about the ultrastructural cytology of developing compression xylem, or about the origin of helical cavities in compression wood tracheid.[4)~7), 16)]

The cell wall structures of typical compression wood tracheids have been studied numerously, while the transitional tracheids were seldom examined.

Fukazawa observed the structural changes of the transitional tracheids between normal wood and compression wood in his study on the process of righting and xylem development in tilted seedlings of *Abies sachalinensis,* in which materials were inclined artificially and then recovered naturally, using scanning electron microscopy.[8)] And he also observed the transition from compression wood to lateral wood using ultraviolet microscopy and reported some attractive informations.[9]

More recently, extensive investigations on the formation of the secondary wall in compression wood of *Cryptomeria japonica* have been carried out by Fujita et al.[10]~[12] They observed the cell wall structure of transitional tracheids relating to the differentiation of tracheids and showed accurately the sequence of the secondary wall formation in the differentiating compression wood tracheids.

On the other hand, it has become important that the more preciser observation on the ultrastructural cytology of compression wood tracheids must be made to explain the mechanism of its formation. Fujita et al. observed the role of cell organelles in relation to the cell wall development and found that microtubules took part in the deposition of cellulose microfibrils, and that lignin was synthesized in the Golgi apparatus.[13], [14] And also Timell reported, in a series of studies on the formation of compression wood in balsam fir (*Abies balsamea*), that the compression wood stimulus must be received by the differentiating xylem tracheids and not by the cambial initials or any of the phloem cells.[15]~[17]

The cell wall structures of opposite wood tracheids have been also studied as well as those of typical compression wood tracheids. It is known that normal coniferous wood might be regarded as intermediate between opposite wood and compression wood.[18]

And it was also reported that transitional tracheids were formed frequently in initial and terminal zone of an annual ring.[19], [20]

The present paper is concerned with the process of compression wood formation accompanied with the righting in tilting tree in order to research the mechanism of its formation.

Althoough xylem developments in tilting trees have been studied numerously, only compression wood formed in the single growing season has been investigated so far. However, since the righting mechanism of the inclined tree is appeared to be complicated, it will be necessary that the within-tree variation in compression wood forming stimulus is examined continuously through several seasons.

Therefore, the inclined grown japanese black pine, at angle of 45°from vertical during 5 years, was used in this paper. And the process of compression wood formation was observed and then the variation of its stimulus within the inclined stem was surmised.

Because it is often stated that the compression wood severity of tracheids formed in the zone of the annual ring boundary is weak, whether or not the differences in severity among those cells are present were observed. Changes of characterization of compression wood within stem, namely the distribution of compression wood, the cross shape of tracheids, the cell wall structures of tracheids, and the occurrence of intercellular spaces were examined.

2. Materials and Methods

A sample studied here was obtained from the vigorous, 3-year-old japanese black pine

(*Pinus thunbergii* Parl.) which was inclined, fixed firmly at lm of height above ground, at the angle of 45° from vertical in May 1975 and then which has grown in the same condition during 5 years.

In October 1979, sample disks at vertical intervals of 20cm from the base were collected. Disks were numbered from 1 to 9 from the base. After stem analysis, soft X-ray photographs of compression wood arc were taken. Areal proportion of compression wood was obtained by a cut-and-weight method.

Small wood blocks taken from each disk, after fixed by FAA, were embeded in celloidin as usual and then transverse and radial sections of 6–14μm thickness were cutted from the blocks. These sections were mounted in Canada balsam directly without staining or after safranin staining.

The cell shape, cell wall thickness, intercellular spaces were observed in transverse sections by ordinary light microscope and the lack of S_3, cell wall checks were also examined in transverse or radial sections using polarizing microscopy. The structure of inner surface of tracheids was observed in radial sections of non-embeded materials fixed by glutaraldehyde, using scanning electron microscopy.

And also, variation in the cell wall thickness and diameter along the length of compression wood tracheid was examined using successive transverse sections of 14μm thickness.

3. Results and Discussion

3.1 Distribution of compression wood

The process of righting in japanese black pine is shown in Fig. 1. Immediately after

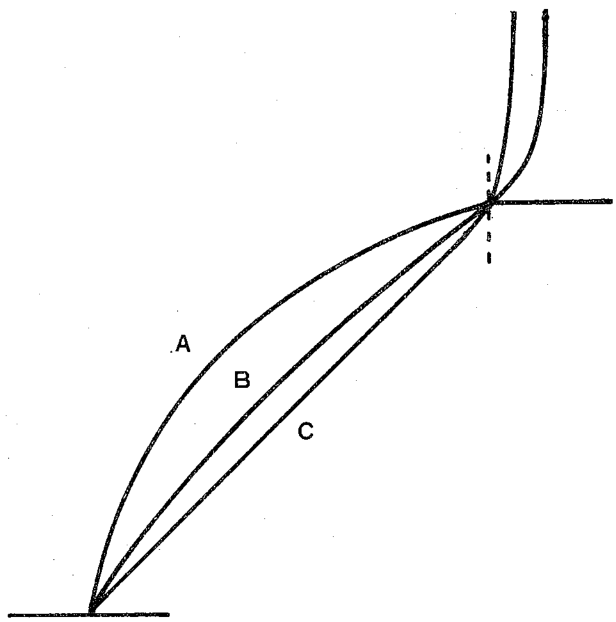


Fig. 1. Diagrammatic representation of righting process of japanese black pine. A; Immediately after bent B; After a year C; After five years

bent, the stem below the fixed portion showed a bow-like form as (A). After a year, the stem above the fixed portion recovered vertically. When cut down in October 1979, as (C) in Fig. 1, no bow-like form was found in the stem below the fixed portion and the stem leaned at the angle of approximately 45°, besides straightly, except of the vertically recovered upper stem.

The transverse variation in the proportion of compression wood is shown in Fig. 2. After a year from the bending treatment, compression wood area occupied about 20 to 35% of disk area. The proportion of compression wood increased up to the first 3 years after bent and then decreased as increasing annual rings, except for the slight increase in disk 5. And after 5 years, in the outermost annual ring, the proportion of compression wood formed near the fixed portion showed the most high value within stem. The vertical variation in the proportion of compression wood formed in the same annual ring is shown in Fig. 3. Until 2 to 3 years from the bending treatment, as seen in the ring number 5 and 6 from pith, the maximum of the proportion of compression wood within stem was found in the center of the curved. But thereafter, as seen ring number 7 and 8, the peak removed upwards. As a result, the proportion of compression

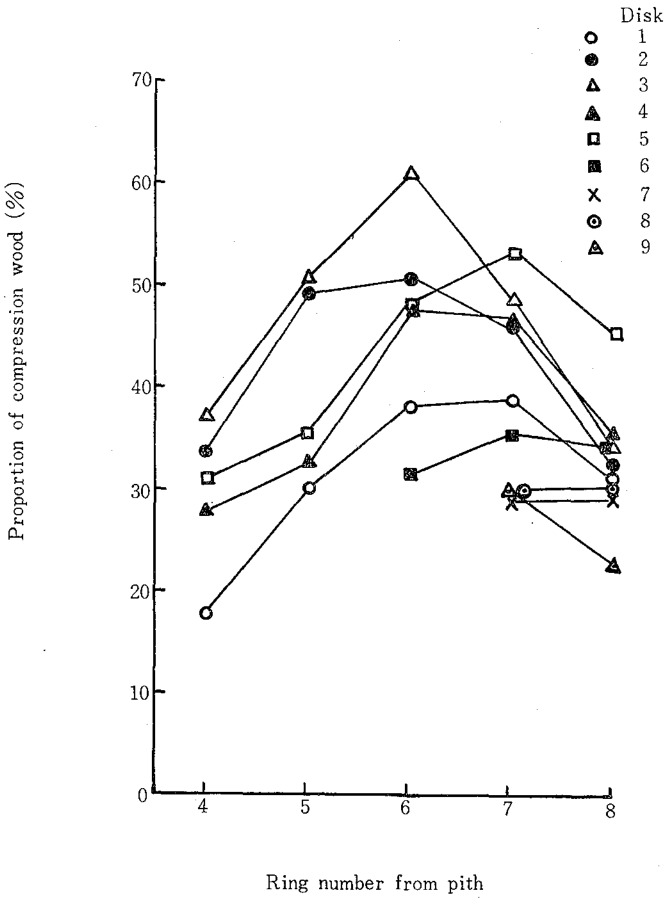


Fig. 2. Horizontal variation in proportion of compression wood area within stem.

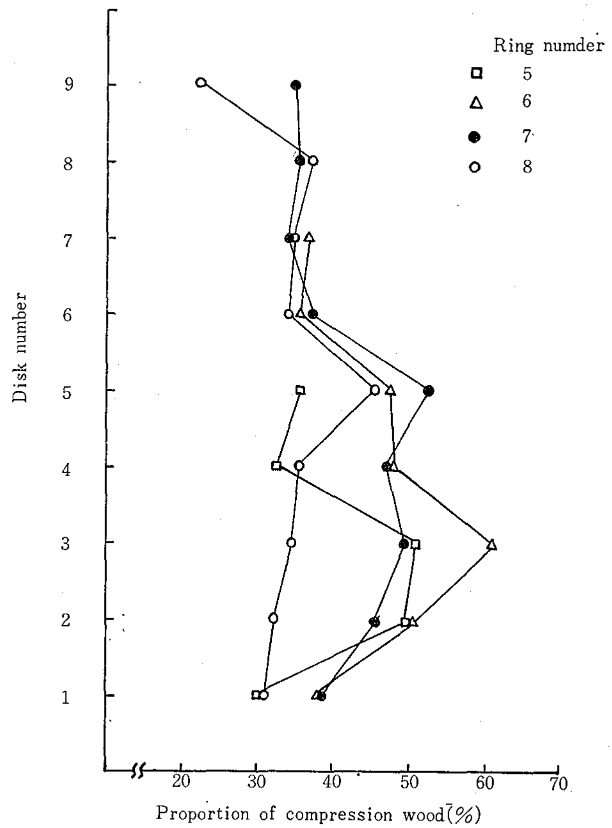


Fig. 3. Vertical variation in proportion of compression wood area within stem.

wood attained to the maximum in disk near the fixed portion, then gradually decreased towards the apex.

These facts suggest that because the righting function is still maintained in the upper stem, the rate of decrease of compression wood forming stimulus is small as compared with that of other portion. It is probable that the stimulus of compression wood formation varied within stem in the process of the righting and of the dissolution of the bow-like form. Such variation in the distribution of compression wood might be connected with the physiolosical phenomenon that the curved stem, leaning at an angle of approximately 45°, was recovered straightly. It is probable that if an inclined tree keeps on growing under the mechanically impossible condition of the righting, the saturation or decline of the stimulus of compression wood formation might occur within stem, as pointed out by Fukazawa.[8] These facts, indicating the physiology of the transitional process between compression wood and normal wood, are very interesting.

3.2 Variations in tracheid diameter and wall thickness

Figure 4 and 5 show variations in tracheid diameter and wall thickness within an annual ring. In compression wood, tangential diameter was relatively constant, with the exception of tracheids formed in the region of an annual ring boundary, whereas radial diameter decreased gradually from early wood to late wood. On the other hand, radial diameter in opposite wood decreased rapidly towards late wood. Cell wall thickness in compression wood was slightly thicker in tangential direction than that in radial direction. On the contrary, in the initial zone of opposite wood, tangential wall was slightly thicker than radial one.

The typical compression wood tracheids usually have the circular shape in transverse section. In this experiment, however, many tracheids showed freqently the elliptic shape with the long axis in tangential direction. why tracheides did not show the circular shape, cannot be explained at present. And also, there is no saying that whether or not the stimulus of compression wood formation attained to the maximum.

Thereupon, variation in tracheid dimension along the length was examined using

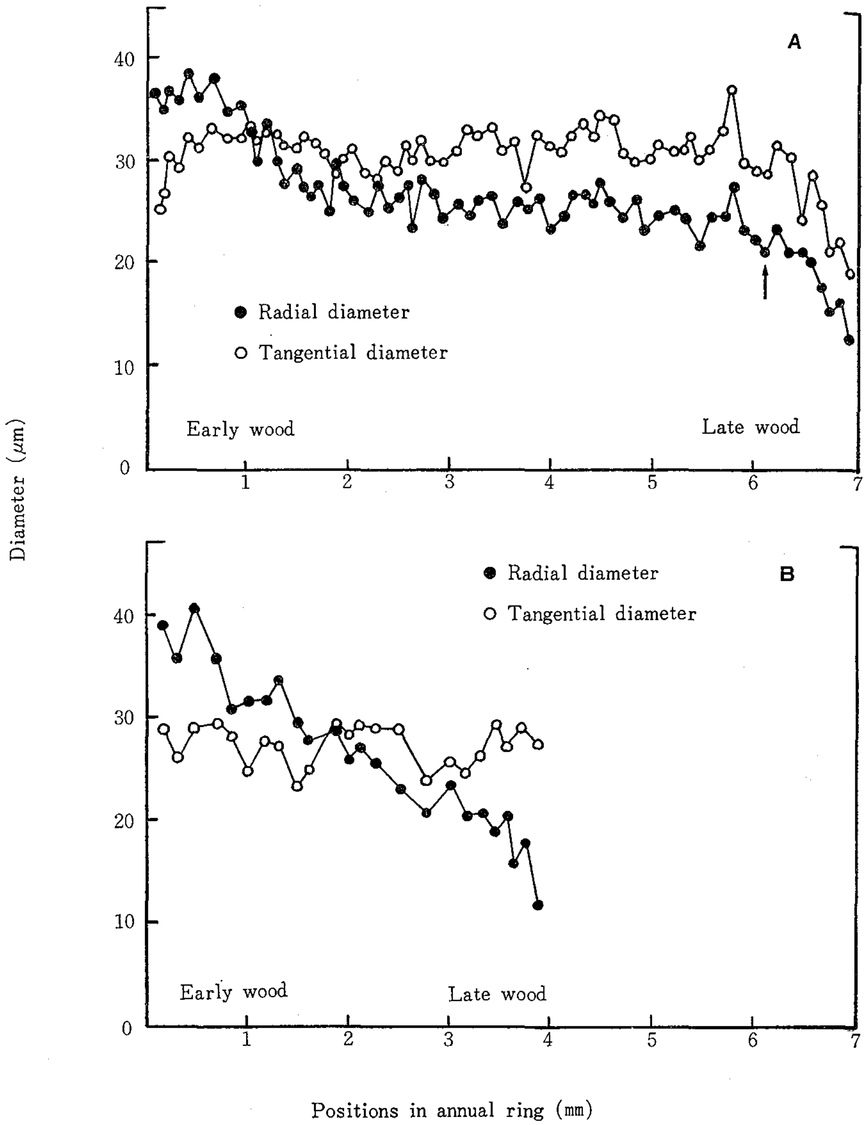


Fig. 4. Radial variation in tracheid dimension within the 7th annual ring in the 4th disk. A ; Compression wood B ; Opposite wood

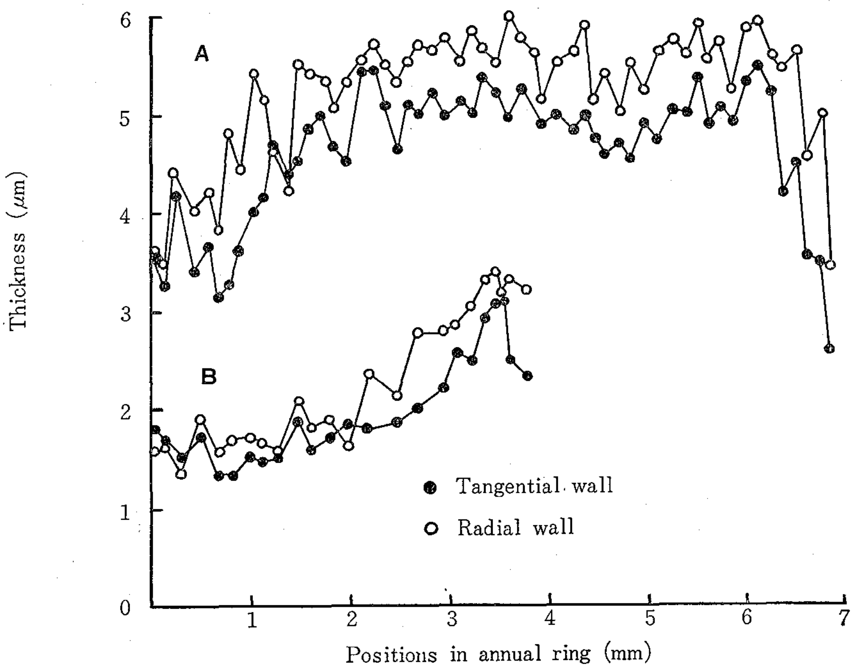


Fig. 5. Radial variation in thickness within the 7th annual ring in the 4th disk.
A ; Compression wood B ; Opposite wood

successive transverse sections of 14 μm thickness. The region selected for determination is shown by an arrow in Fig. 4. Because resin cannals are present in this region, it is easy to distinguish some numbered tracheids. After all, 35 tracheids could be examined. The results are shown in Fig. 6 and 7.

Figure 6 shows the changes of transverse shape of tracheids along the length. It indicates that the transverse shape of compression wood tracheid was not always uniform over the whole length. As a result, two different types were observed as shown in Fig. 7. The first type, which is shown in Fig. 7-A, is represented by tracheid (i). Cell wall thickness was relatively uniform along the major part of tracheid length in both radial and tangential direction, whereas it decreased rapidly from the mid-region of the tracheid, about 350μm length from the tip, towards the tip. In the center part of tracheid, cell wall thickness is thicker in radial direction than that in tangential direction, and tangential diameter is larger than radial one. Tracheid (1) is representative of the second type. In the major part of the tracheid length, tracheid diameter and wall thickness were relatively uniform, whereas no difference in direction was found differing from the first type. Most of this type was observed in tracheids with the long axis in radial direction.

In either type, cell wall thickness near the tip was thicker in radial direction. Considering of the tip's bending characteristic of compression wood tracheids, however, whether or not this result is right cannot be decided at present. It is probably difficult that variation in dimension along the full length of compression wood tracheid can be

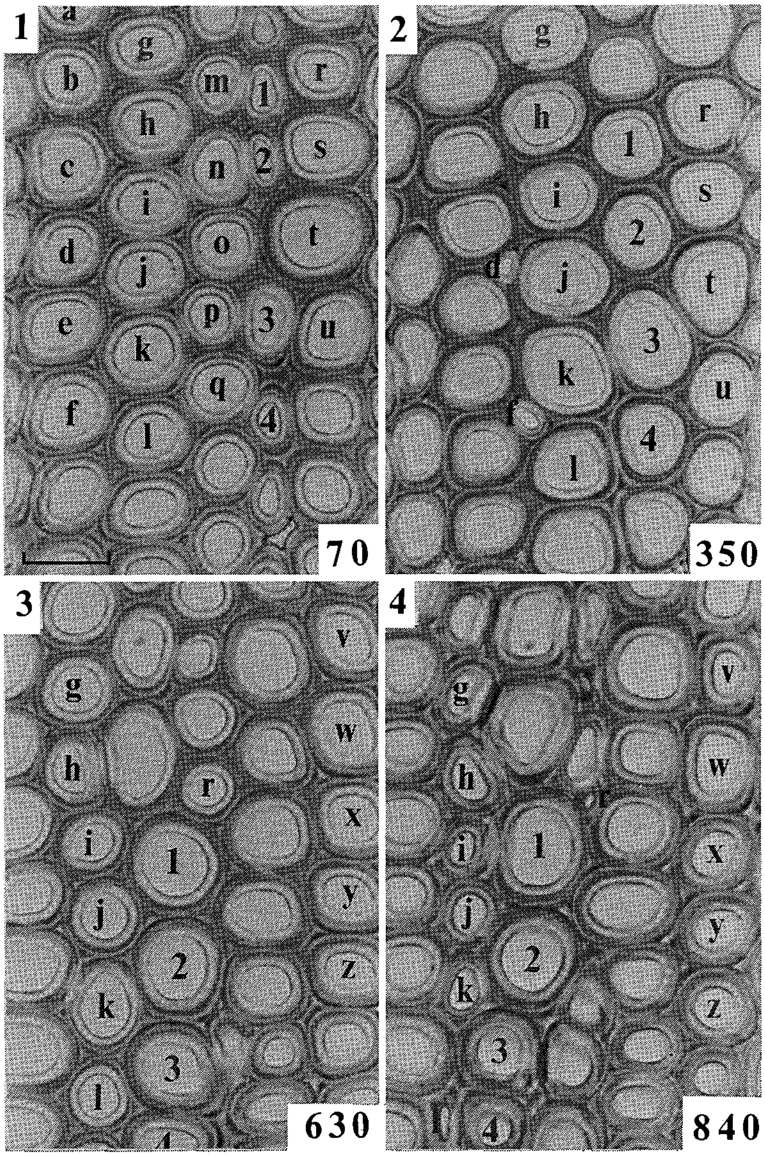


Fig. 6. Micrographs of transverse section of compression wood taken at about 300μm intervals along the length. The numerals in each micrograph indicate the distance, in micron, from the first occurrence of tracheid (1). Mark ; 25μm

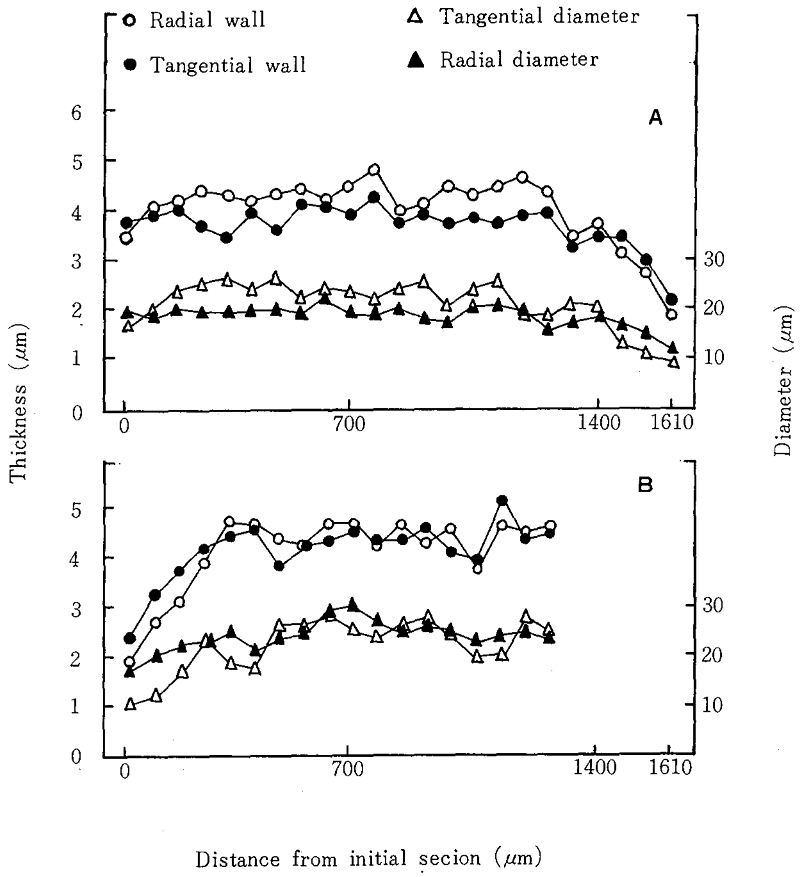


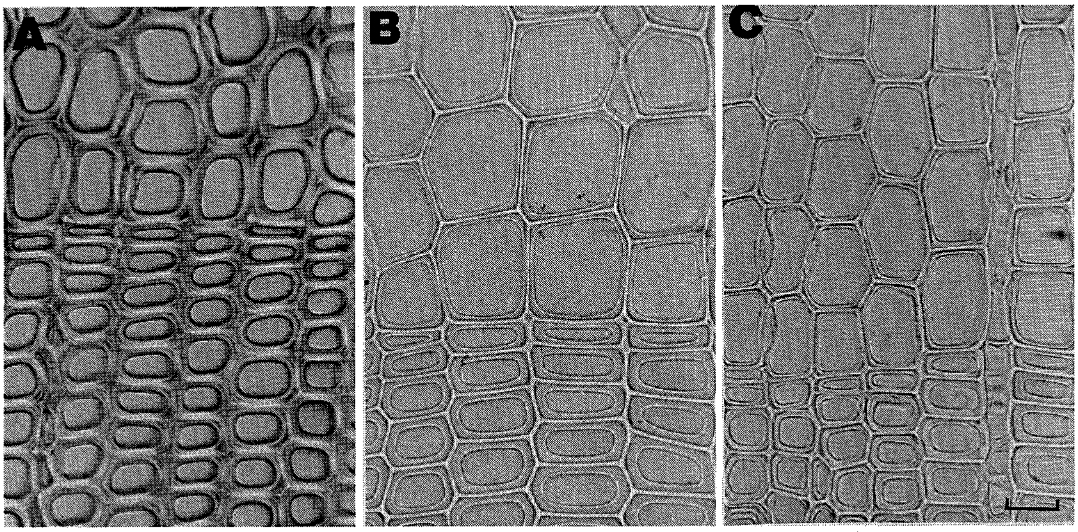
Fig. 7. Variations in tracheid diameter and wall thickness along the length of compression wood tracheid.
A; Tracheid (i) B; Tracheid (1)

observed perfectly by this method. As many oblique-cutted tracheids were observed, another method should be considered to investigate the closer variation on this point.

Okumura et al. studied similarly on the normal wood tracheids in *Pinus densiflora* Sied. et zucc.[21] They showed that in late wood tracheids, tangential diameter was larger in the mid-region of the tracheid than radial one, and only tangential one decreased towards the cell tips, and also only radial wall thickness decreased similarly, and consequently the so-called tapering end wall was formed towards the cell tips.

Compression wood tracheid differed from the late wood tracheid of normal wood in variation of tracheid dimension along the length. In compression wood tracheid, not only radial but also tangential thickness decreased similarly towards the cell tips. It is probable that because of the rounded transverse shape characteristic of compression wood tracheids, the tapering pattern differs from that of normal late wood one. It cannot be decided at present which of these is a perferential type in compression wood tracheids. Further examination on this point will be needed, relating to the transitional changes between normal and compression wood.

Subsequently, peripheral variations in transverse shape and wall thickness of tracheids formed in the zone of an annuall ring boundary are shown in Fig. 8 and 9, respectively. Timell, who studied the nature of opposite wood and the early spring wood in certain species, reported that the early wood tracheids were square in outline and more reqularly arranged than in normal wood, and stated that normal coniferous wood might be regarded as an intermediate between opposite wood and compression wood.[18), 19)]



Eig. 8. Peripheral variation of tracheid shape viewed in transverse section in the outermost annual ring boundary of the 4th disk. A ; Compression side B ; Lateral side C ; Opposite side Mark ; 20μm

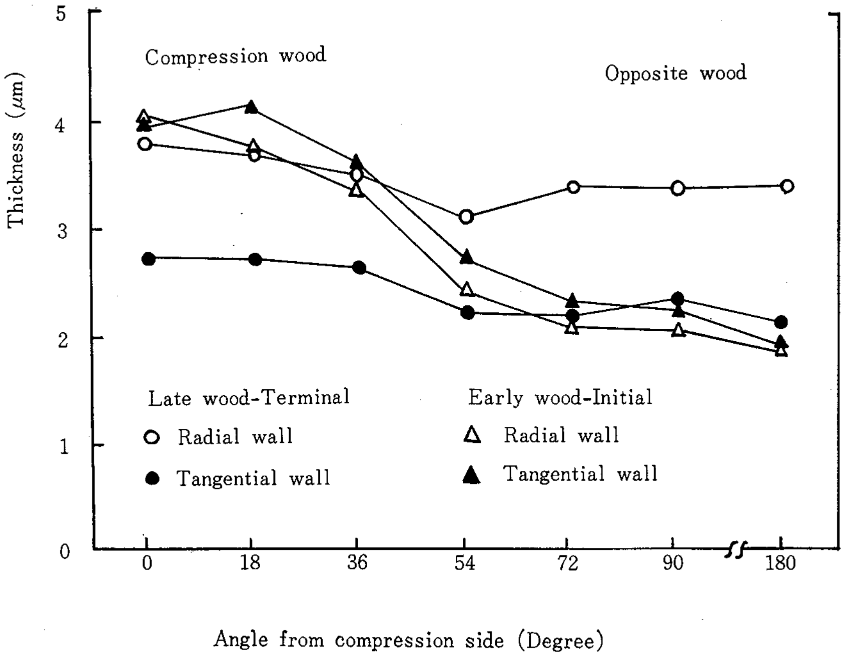


Fig. 9. Peripheral variation of cell wall thickness in the outermost annual ring boundary of the 4th disk.

It is evidently in Fig. 8 that in japanese black pine, the early wood tracheids in opposite wood show the rectangular shape but the side wood tracheids are square in outline rather than those of opposite wood. First-formed tracheids have the slightly rounded appearance as compared with those in side wood and opposite wood. As seen in Fig. 9, the wall thickness of initial tracheids varied conspicuously from compression wood to opposite wood. In compression wood, the wall thickness of those was slightly thicker than that of terminal tracheids and it gradually decreased towards opposite wood. In opposite wood, on the contrary, that of terminal tracheids was thicker than that of initial tracheids.

These facts reveal that the stimulus of compression wood formation has already been received by the differentiating xylem tracheids below the inclined stem at the beggining of the growing season. It is supposed that the early spring wood tracheids in compression wood side are transitional tracheids between compression wood and normal wood. A closer examination of such tracheids might indicate the difference of compression wood forming stimulus to some extent.

3.3 Cell wall structures of tracheids in an annual ring boundary

Micrographs, taken with polarized light, of the last 3 annual ring boundaries are shown in Fig. 10. The lack of S_3 was detected from the early spring wood tracheids of the 6th annual ring in which compression wood was formed abundantly, but the S_3 layer was present in the ring number 7 and 8. Figure 11 shows the outermost annual ring boundary of disk 4. The lack of S_3 was detected from the initial tracheids. As compared with the micrograph (C) in Fig. 10, the difference of the compression wood severity was recognized evidently.

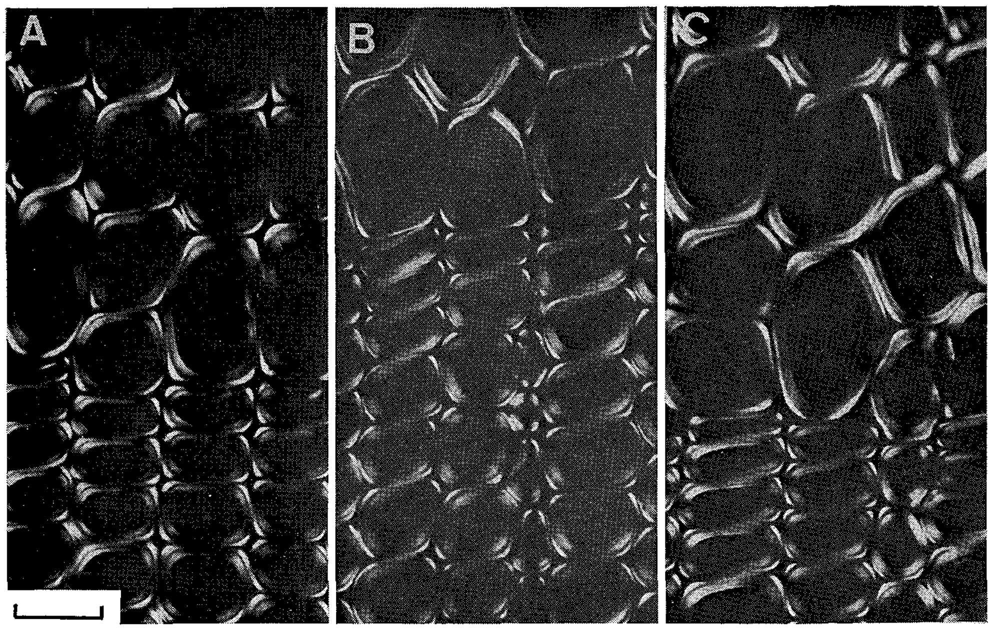
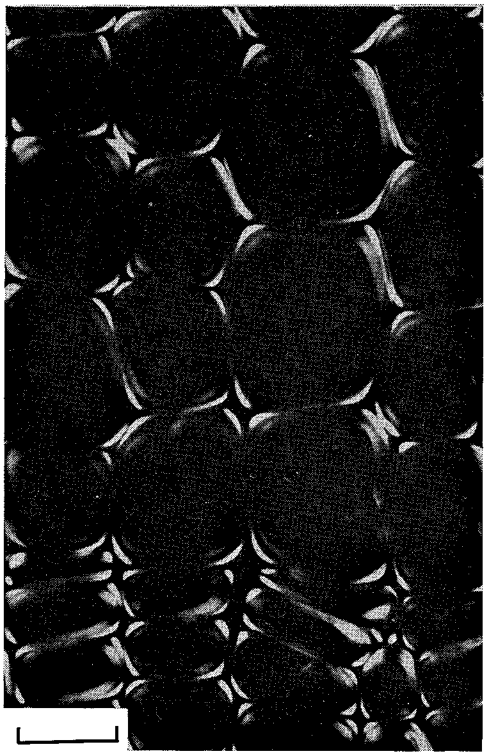


fig. 10. Polarizing micrographs of annual ring boundary of compression wood in disk 2. A; 6th annual ring boundary B; 7th annual ring boundary C; 8th annual ring boundary Mark; 20um

Also from the helical striation of radial sections, when viewed in the polarizing microscope, the compression wood severity could be compared, as shown in Fig. 12. No helical striation was recognized in the initial tracheids of the outermost annual ring of disk 1, but in those of disk 3 and 5 helical striations were detected distinctly.



Eig. 11. Polarizing micrograph of the 8th annual ring boundary of compression wood in disk 4. Mark ; 20μm

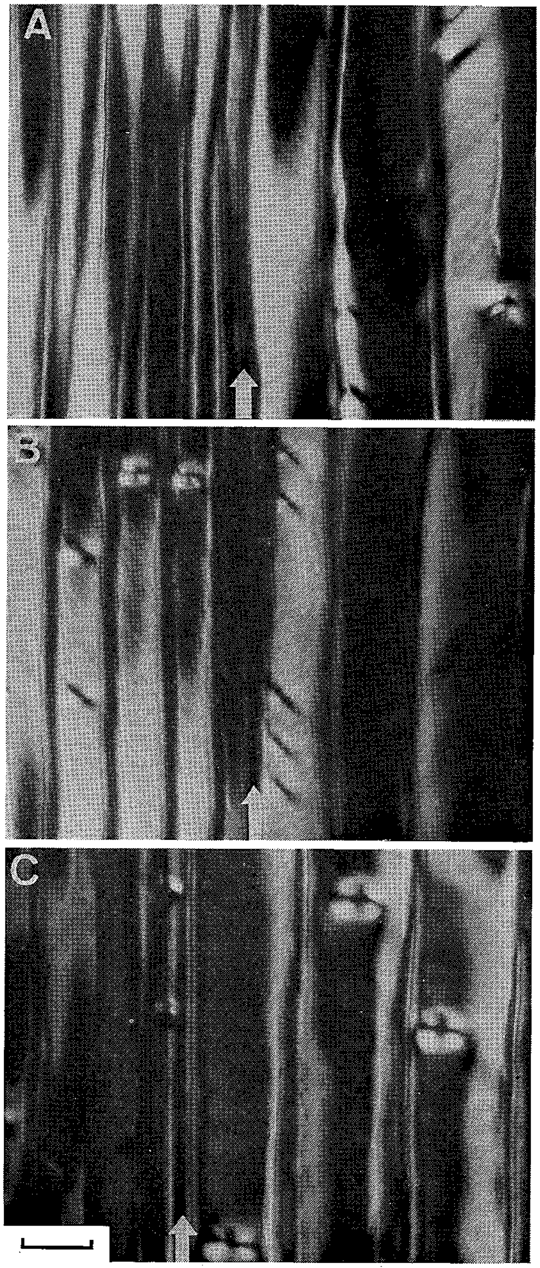
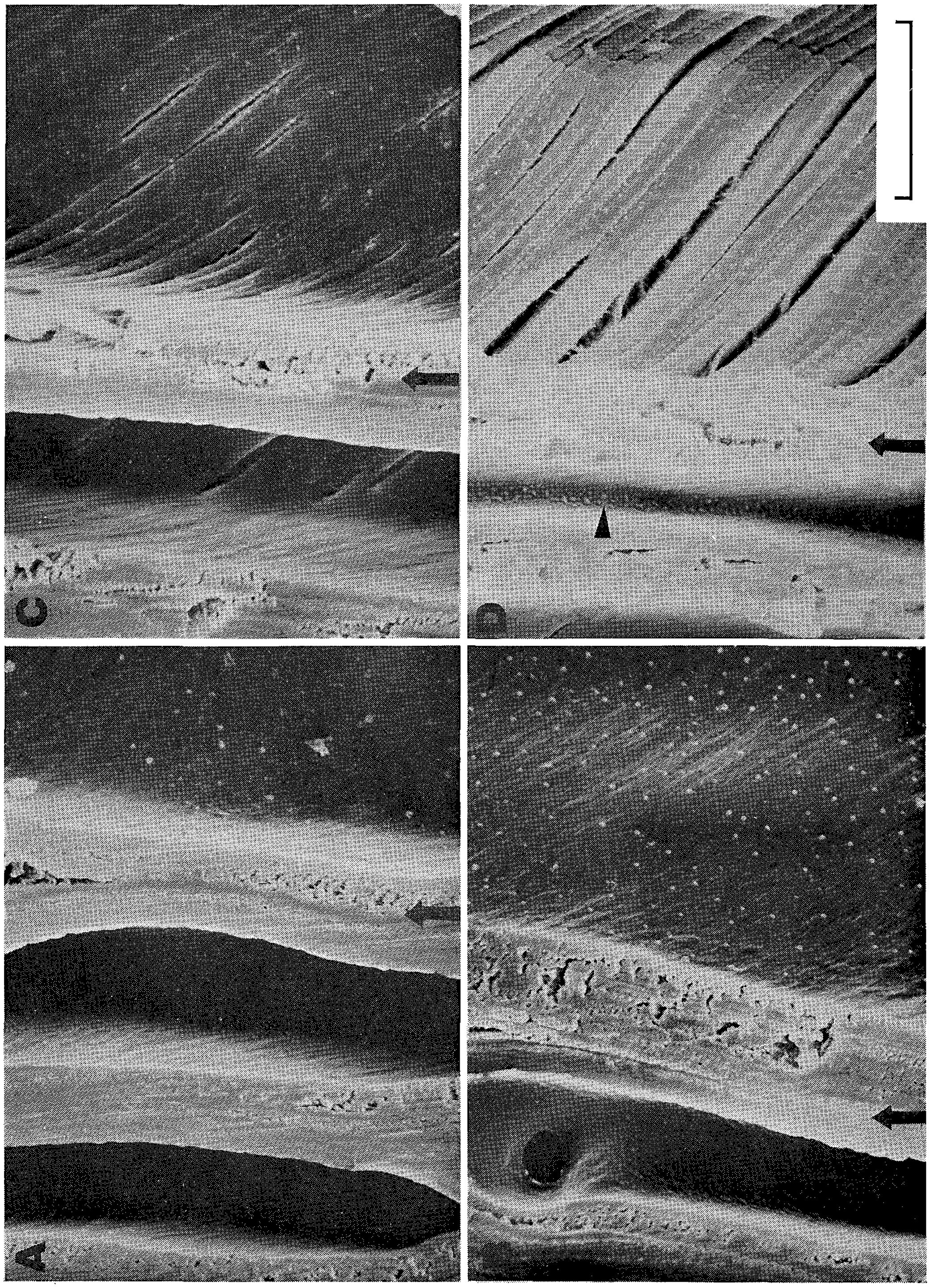


Fig. 12. Polarizing micrographs in radial section of the outermost annual ring boundary of compression wood. Arrows indicate annual ring boundaries. A ; Disk 5 B ; Disk 3 C ; Disk 1 Mark ; 20μm



Eig. 13. Scanning electron micrographs in radial section of the outermost annual ring boundary of compression wood. Long arrows indicate annual ring boundaries and a short arrow indicates one terminal tracheid.

A ; Disk 1 B ; Dik 2 C;Disk 3 D ; Disk 4 Mark ; 10μm

Furthermore, cell wall checks in the inner surface of tracheid was examined by scanning electron microscope using radial sections. As shown in Fig. 13 and 14, the transitional sculptures between normal wood and compression wood tracheids could be observed. In the first-formed tracheids, as seen in micrograph (A), no helical cavities were formed but they were recognized distinctly in micrograph (D).

Terminal tracheids without helical cavities were frequently observed, as indicated by a short arrow in micrograph (D). From an examination of cell wall structures of terminal tracheids, therefore, compression wood severity cannot be judged exactly.

These results reveal that the difference of compression wood severity was present among the transitional tracheids. It is evidently that the compression wood forming stimulus varied within the inclined stem in the righting process.

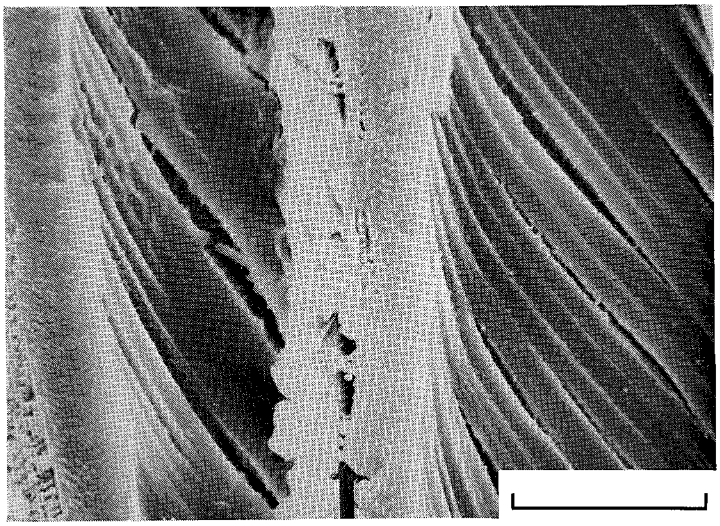


Fig. 14. Scanning electron micrograph in radial section of the 7th annual ring boundary of compression wood in disk 3. An arrow indicates an annual ring boundary. Compare the photo C in Fig. 13. Mark ; 10μm

Fukazawa suggested that the depth, the frequency of occurrence and the angle of helical cavities might be an indicator to classify the compression wood severity.[8] And also, from the transitional modifications of several anatomical features, Harris classified in 4 wood type of normal, mild, intermediate, sever and stated that the early wood was affected less than the late wood, particularly in mild wood.[22] Park et al., studied structure of branch wood in Akamatsu (*Pinus densiflora* Sieb. et Zucc.), reported the presence of the S_2 layer without spiral checks.[20]

Because of such complicated modifications of compression wood tracheids, it is difficult to make accurate estimations of the compression wood severity by visual observations. It should be examined whether the compression wood severity can be indicated by numerals, for example as an actual depth of helical cavity.

3.4 Occurrence of intercellular spaces

The occurrence of intercellular spaces was examined in transverse sections. Average number of tracheids up to the first occurrence of intercellular space was measured along 10 radial files in an annual ring. The result is shown in Fig. 15.

No intercellular space was present in the zone of every annual ring boundary. The first intercellular space occurred late as increasing annual rings in the same disk. And also, an examination of annual rings formed at the same growing season shows that no distinct difference in occurrence of intercellular spaces of the 6th annual ring was observed, and that in the ring number 7 and 8, however, the difference was evident in vertical positions within stem.

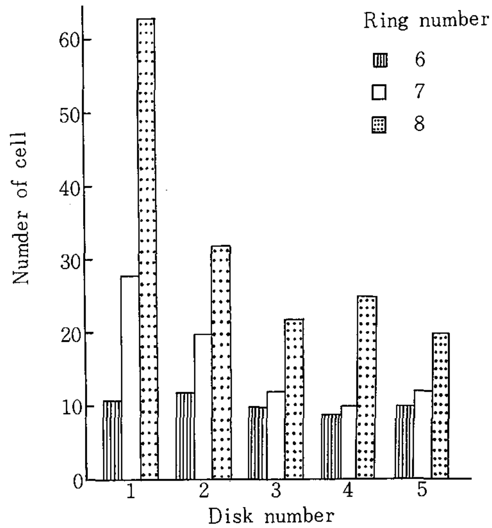


Fig. 15 The first occurrence of intercellular space.

This agrees with the result that no intercellular space was found in the zone of an annual ring boundary.[19] as it is considered that intercellular spaces might be plugged by lignin, as suggested by Fujita et al.,[12] we are investigating to furnish more evidence on this point. At any rate, if the compression wood forming stimulus affects the occurrence of intercellular spaces, the beggining of the occurrence of intercellular spaces in the early spring wood might be an indicator to estimate the compression wood severity.

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