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리기가소나무 (Pinus rigida Miller) 枝材의 壓縮異常材, 對應材 및 側面材 特性에 관한 走査電子顯微鏡의 員 研究

要 約

한국에서의 리기가소나무 (Pinus rigida Miller, pitch pine) 枝材의 壓縮異常材의 特性에 관한 研究가 光學顯微鏡의 員 方法을 통하여 先 12)에 의하여 1972년에 發表되었다. 本 研究에서는 리기가소나무 枝材의 解剖學의 特性에 관한 후의 研究의 續報로써 壓縮異常材(compression wood), 對應材(opposite wood) 및 側面材(side wood)의 横斷面과 放射斷面의 組織학의 特性을 走査電子顯微鏡을 통하여 比較 연구한 바 언어진 結果를 要約하여 보인 다음과 같다.

1. 壓縮異常材에 있어서 春材로부터 秋材로의 假導管 移行은 僅限이며 假導管의 排列 및 크기 역시 거의 형태한 狀態을 나타내지만 對應材 및 側面材에 있어서는 假導管의 移行이 急하며 假導管의 排列 및 크기도 壓縮異常材의 假導管보다 不定이다. 또한 對應材의 年輪幅은 壓縮異常材 및 側面材의 年輪幅보다 더 좁으며 側面材의 横斷面과 放射組織은 壓縮異常材 및 對應材의 放射組織보다 더明確하다.

2. 壓縮異常材의 假導管 특히 春材 假導管이 둔각 傾向을 나타내는데 반하여 對應材 및 側面材의 假導管은 다소 많은 모양을 나타낸다. 그리고 細胞間隙(intercellular space), 螺旋腔(helical cavity) 및 螺旋裂(spiral check)이 壓縮異常材의 春材 및 秋材에 모두 존재하는데 반하여 對應材에 있어서는 春材 및 秋材 모두에 存在하지 않는다.

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3. The tracheids transition from earlywood to latetwood is very gradual and the tracheids are nearly regular in both arrangement and size in compression wood but this transition in opposite wood and side wood is abrupt and the tracheids in opposite wood and side wood are less regular than those in compression wood. Also, the annual ring width of opposite wood is narrower than that of compression wood or side wood and the rays revealed on cross surface of side wood are more distinct than compression wood and opposite wood rays.

2. The tracheids of compression wood show roundish trends especially in earlywood but those of opposite wood and side wood show some angular trends. And intercellular space, helical cavity, and spiral check are present in both earlywood and late wood of compression wood but not present in opposite wood and side wood irrespective of earlywood and late wood.

3. The wall thickness of latewood tracheid is similar to that of earlywood tracheid in compression wood whereas the wall thickness of latewood tracheid is by far thicker than that of earlywood tracheid in opposite wood and side wood and the $S_3$ layer of secondary wall is lack in compression wood tracheid unlike opposite wood and side wood tracheid.

4. The tracheids in compression wood are often distorted at their tips unlike those in opposite wood and side wood and the bordered pit in compression wood tracheid is located at the bottom of helical groove unlike that in opposite wood and side wood tracheid.

5. The bordered pits in radial wall of opposite wood and side wood tracheids are oval in shape but those of compression wood tracheids show some modified oval shape.
6. In earlywood of side wood, the small apertures of cross-field pits are roundish triangle to rectangle and the large one are fenestriiform through the coalition of two small ones. However, the small apertures of cross-field pits are upright oval and the large ones are procumbent oval shape in earlywood of opposite wood and the apertures of cross-field pits in compression wood are tilted bifacial convex lens shape in earlywood and slit in latewood because of the border on tracheid side.

Key word: branch of pitch pine, compression wood, opposite wood, side wood, scanning electron microscope.

Introduction

When an arboreal plant is deviated from its equilibrium position in space, radial growth is promoted on either under or upper part to support its own weight and the general term reaction wood is applied to the specialized type of wood that is produced on the wide area of eccentric cross surface in leaning stems or branches.

The reaction wood formed in gymnosperms is called compression wood because of its formation on compression-stress part of under side but the reaction wood in angiosperms is called tension wood because of its formation on tension-stress part of upper side in leaning stems or branches.

In gymnosperms, as a rule, well-developed compression wood on under part and suppressed opposite wood on upper part are related to the increased and decreased xylem production caused by the respective surplus and deficit of plant hormonal growth regulators such as naturally occurring auxin, indole-3-acetic acid (IAA) redistributed by the action of gravity.

This compression wood distinguished from its surrounding parts by dark color is present in members of Ginkgoales, Coniferales, and Taxales but not present in Cycadales and Gnetales among gymnosperms and even present in primitive angiosperms such as several species of Buxus whose wood contains both tracheid and vessel, namely Buxus japonica, Buxus microphylla, and Buxus sempervirens.

Although the narrow-ringed opposite wood on upper part, medium-ringed side wood, and wide-ringed compression wood on under part are present in leaning stems and branches of gymnosperms simultaneously, most studies have been concentrated on compression wood.

Therefore, this experiment was executed to examine the anatomical features on cross and radial surface of compression wood, opposite wood, and side wood formed in branch of pitch pine, Pinus rigida Miller, one of the most abundant conifer species planted in Korea.

Review of Literature

Compression wood has attracted many wood anatomists' interests since the first description in Picea abies (L.) Karst by German botanist Karl Gustav Sanio in 1860 (Fig. 1) by the review of Timell (1980).29

Anatomically compression wood differs in many respects from normal wood. In the researches of Core, Côté, and Day (1961),41 and Côté, Day, and Timell (1967),71 they reported that the abrupt transition from earlywood to latewood tracheid which is typical characteristic of normal wood in many species was not found in compression wood, where this transition was more gradual. And Cockrell

Fig. 1. Drawing of a tranverse section of branch compression wood in Picea abies. (Sanio, 1860)22
(1974), and Côté, Simson, and Timell (1966) reported the fact that the tracheids of compression wood are chiefly round except the first-formed earlywood in contrast to angular in normal wood viewed on cross surface.

By the reports of Onaka (1949), and Wardrop and Dadswell (1952), the tracheids in compression wood were often distorted at their tips and shorter than those of normal wood, i.e. only half as long, and these short tracheids in compression wood were a result of the high rate of anticlinal divisions in the cambial zone of the tissue.

Also, Timell (1981) reported that the majority of tracheids in compression wood had thicker walls and narrower lumens than in normal earlywood but the difference in these respects between compression and normal latewood was slight.

Another feature of compression wood is the presence of intercellular space, especially in earlywood. According to Phelps, Saniewski, Smolinski, Pieniazek, and McGinnes (1974) and Timell (1981), such spaces were both frequent and large in compression wood of Larix, Picea, and Pinus, but they seemed to reach their widest development in Pseudotsuga. Even though the intercellular space can be a useful diagnostic characteristic of compression wood, this space was also found in normal woods of some conifer species such as Juniperus and Cupressus by Core, Côté, and Day (1979), and McGinnes and Phelps (1972).

According to Butterfield and Meylan (1980) and Wardrop and Dadswell (1952), the facts were known that the $S_1$ layer in compression wood tracheid was considerably thicker than that in normal wood tracheid and the orientation of microfibrils in $S_1$ layer of compression wood tracheid was almost transverse, namely the angle from 80° to 90°. Also, the facts that the $S_2$ layer in compression wood tracheid differed from that in normal wood tracheid frequently having helical cavity, called spiral striation in the past, and the $S_2$ layer surface might appear faintly ribbed when viewed from the cell lumen were known by Côté, Kutscha, and Timell (1968) and Phelps, McGinnes, Smolinski, Saniewski, and Pieniazek (1977). By the reports of Timell (1978a, 1978b), however, some gymnosperms did not have all the anatomical modifications associated with typical compression wood, for instance, helical cavity was lack in the Taxales, Ginkgoales, and Araucariaceae and the compression wood of Taxus baccata had well-developed helical thickening instead of helical cavity. And the facts that this helical thickening on the lumen surface in some gymnosperms was present in both the normal wood and compression wood but generally absent in the compression wood tracheid of Douglas-fir (Pseudotsuga menziesii), that is, the almost transverse thickening typical of the normal wood tracheid in Douglas-fir was replaced by helical rib in the compression wood tracheid and spiral (helical) check was formed along the weakest proportion of the $S_2$ layer, which usually means helical cavity, by the subjection of mechanical or drying stress in compression wood were also reported by Timell (1978a, 1978b).

According to Côté (1977), the $S_2$ layer was the inner layer of the secondary wall since the $S_3$ layer was absent in compression wood tracheid. Compression wood tracheid had not only helical thickening but also warty layer lined the inner surface of the $S_2$ layer despite the absence of $S_3$ layer was also known by the report of Core, Côté, and Day (1961).

The microfibril angle of $S_2$ layer in compression wood tracheid is larger than that in normal wood tracheid. Whereas $S_2$ microfibril angle of 10° to 20° can be expected in normal wood tracheid, the angle in compression wood tracheid approached 45° as typical but 30° to 50° microfibril angle was most common according to Desch and Dimwoodie (1981) and Panshin and de Zeeuw (1980). However, values from 16° to 71°-78° have been reported by Timell (1981) and Cockrell (1974).

The bordered pit connecting the longitudinal tracheid was located at the bottom of helical groove in compression wood and the cross-field pit in compression wood could not be used for diagnostic purpose as that in normal wood were reported by Timell (1981) and Onaka (1949) respectively.

On the other hand, the anatomical studies on opposite wood and side wood are fewer than those
of compression wood.

The opposite wood formed in the narrow radius diametrically across from the compression wood differs from normal wood. Though the annual ring width and percentage of latewood were usually variable as in the report of Lee and Eom (1984),¹³ and Timell (1973),²⁶ Park (1983, 1984a, 1984b)¹⁷,¹⁸,¹⁹ reported that the annual ring width and percentage of latewood in opposite wood were smaller than those in compression wood or side wood. The facts that $S_2$ layer of opposite wood tracheid was thicker than in normal wood tracheid and $S_3$ layer was frequently buckled in the latewood of opposite wood were also reported by Timell (1973).²⁶

Timell (1981)³⁰ reported the side wood was of normal wood in contrast to special tissue of compression wood and opposite wood.

**Materials and Methods**

The disc of branch wood for observation of anatomical features on compression wood, opposite wood, and side wood was prepared from the first branch of *Pinus rigida* Miller that grows on flat land in campus of College of Agriculture, Seoul National University, Suwon, on May 11, 1984 (Fig. 2).

Regular hexadrons, 1 x 1 x 1 cubic centimeter, of compression wood, opposite wood, and side wood were collected from the under, upper, and side part of the disc, respectively.

After the hexadrons were removed from the disc, they were immediately boiled with 30% ethyl alcohol at 80°C-90°C for 3 hours in stainless steel autoclave by direct heating on an electric heater for softening and microtomed to sections of ca. 80μm thick on cross and radial surface through sliding microtome.

The sections were immediately dehydrated in a series of 30, 40, 50, and 60% ethyl alcohol for 30 minutes each and reserved in 70% ethyl alcohol until they were prepared for viewing through scanning electron microscope.

Prior to mounting for observation, these sections were subdivided to area of 5 x 5 millimeters and dehydrated further in a series of 80, 90, 95%, and absolute ethyl alcohol, and absolute isooamyl acetate for 30 minutes each. The sectioning and dehydration were carried out as in the method of Sass (1958).²³

Then these dehydrated sections were contained in aluminum tube having many small pores for free penetration of liquefied carbon dioxide gas and transferred into specimen chamber of critical point dryer made by Ladd Research Industries.

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**Fig. 2.** Diagrammatic picture on the position of tested disc from branch wood (a) and photograph on cross surface of the disc revealing compression wood, opposite wood, and side wood (b).
After the sections contained in the tube were confined in the specimen chamber, the liquefied carbon dioxide gas was filled and sustained in specimen chamber for 30 minutes at 63.279kg/cm² (900 psi) for freezing of sections and then heated until the temperature 41°C and pressure 98.434kg/cm² (1400 psi). The heating was stopped at this point for cooling and the gas was drained slowly from specimen chamber.

These dried sections were immediately mounted on top of copper specimen stubs, with the aid of double face vinyl tape and then coated with gold in thickness of 200 Å to prevent primary reflected electrons in FINE COAT ION SPUTTER JFC-1100 at 1.2 KV and 10mA for 4 minutes.

After the coated sections on copper stubs were placed in the holder of JSM-T300 scanning microscope, various anatomical features on cross and radial surface of compression wood, opposite wood, and side wood were examined and photographed with Polaroid at 15KV in Cancer Research Institute, College of Medicine, Seoul National University, Seoul. The drying, coating, and examination in scanning electron microscope were carried out as in the procedure by Berlyn and Miksche (1976). ¹

The observed anatomical features in this study were the tracheid transition from earlywood to latewood within an annual ring, rays, tracheid shape, intercellular space, spiral check and helical cavity, wall thickness and composition of tracheid on cross surface and the tip shape of tracheid, bordered pit on tracheid wall, and cross-field pits on radial surface with the proper magnification from 100 to 10,000 according to observation items in order to compare and discuss anatomical features among compression wood, opposite wood, and side wood.

**Result and Discussion**

A study on the anatomical features of pitch pine (*Pinus rigida* Miller) branch wood in Korea was reported by Lee in 1972.¹² In his paper, tracheid length, width, and thickness without distinction of compression wood, opposite wood, and side wood were completely analyzed through photomicroscopic method and concluded that the length and width of branch wood tracheids were shorter and narrower than those of stem wood.

As a study on anatomical features in branch wood of *Pinus rigida* Miller grown in Korea, compression wood, opposite wood, and side wood are selected and treated for the purpose of comparing them in this study.

By observation, the tracheid transition from earlywood to latewood is very gradual and the tracheids are nearly regular in both arrangement and size in compression wood (Fig. 3). But this transition in opposite wood and side wood is abrupt and also the tracheids of opposite wood and side wood are less regular in both arrangement and size than those of compression wood (Figs. 4 and 5). On the other hand, the annual ring width of opposite wood is narrower than that of compression wood or side wood and the rays revealed on cross surface of side wood are more distinct than compression and opposite wood rays (Figs. 3, 4, and 5).

The gradual transition of compression wood tracheids was reported by Core, Cšštš, and Day (1961)⁴ and the regular arrangement and size of compression wood tracheids are similar to Timell's report (1978b, 1983).²⁸,³¹ Also, the facts that the
annual ring width and percentage of latewood in opposite wood are smaller than those in compression wood or side wood were reported by Park (1983, 1984a, 1984b, 17,18,19).

When viewed on cross surface, the tracheids of compression wood show roundish trends especially in earlywood (Figs. 6 and 7) but those of opposite

Fig. 4. Cross surface of opposite wood illustrating one annual ring. Scanning electron micrograph (bar = 100μm).

Fig. 6. Cross surface of earlywood in compression wood. Scanning electron micrograph (bar = 10μm).

Fig. 5. Cross surface of side wood illustrating one annual ring. Scanning electron micrograph (bar = 100μm).

Fig. 7. Cross surface of latewood in compression wood. Scanning electron micrograph (bar = 10μm).
wood and side wood are some angular (Figs. 8, 9, 10, and 11) as shown by Cockrell (1974), Coté, Simpson, and Timell (1966), Lee and Eom (1984), and Timell (1978a, 1978b, 1983) and intercellular space, helical cavity, and spiral check are present in both earlywood and latewood of compression wood (Figs. 6, 7, and 19) but nor present in opposite wood or side wood irrespective of early-
wood and latewood (Figs. 8, 9, 10, and 11). By the report of Timell (1981), the intercellular spaces were both frequent and large in compression wood of *Larix, Picea, Pinus,* and *Pseudotsuga* and the spiral check were described as a different feature from helical cavities in that the spiral checks are caused by mechanical or drying stress along the weakest proportion of helical cavity.

**Fig. 8.** Cross surface of earlywood in opposite wood. Scanning electron micrograph (bar = 10 μm).

**Fig. 10.** Cross surface of earlywood in side wood. Scanning electron micrograph (bar = 10 μm).

**Fig. 9.** Cross surface of latewood in opposite wood. Scanning electron micrograph (bar = 10 μm).

**Fig. 11.** Cross surface of latewood in side wood. Scanning electron micrograph (bar = 10 μm).
The odd features which attract interests were the presence of border on intercellular spaces in *Juniperus virginiana* L. as shown by Lee and Eom (1984),13 and McGinnes and Phelps (1972)14 and the presence of intercellular spaces even in normal wood of *Juniperus virginiana* L. as shown by Butterfield and Meylan (1980),2 Core Côté, and Day (1979),5 and McGinnes and Phelps (1972).14

On the other hand, the wall thickness of latewood tracheid is similar to that of earlywood tracheid in compression wood (Figs. 6,7, and 12) in contrast to the fact that the wall thickness of latewood tracheid is by far thicker than that of earlywood tracheid in opposite wood and side wood (Figs. 8,9,10, and 11). The majority of tracheid in compression wood have thicker walls than in earlywood tracheid of normal wood but the difference in these respects between latewood tracheid of normal wood and compression wood is slight was also confirmed by the report of Timell (1981).30

On the structure of tracheid walls, the S3 layer is lack in compression wood unlike opposite wood and side wood (Figs. 13, 14, and 15) as described in the report of Core, Côté, and Day (1961),4 Côté, Simson, and Timell (1966),6 Côté, Kutscha, and Timell (1968),6 Côté (1977),9 and Timell (1978b, 1981, 1983).29,30,31 According to Timell (1973),26 the S2 layer of opposite wood tracheid was thicker than in normal wood tracheid and the S3 layer was frequently buckeled in the latewood tracheid of opposite wood.

When viewed on radial surface, the tracheids in compression wood are often distorted at their tips unlike those of opposite wood and side wood (Figs. 16, 17, and 18). According to Oñaixa (1949),15 Timell (1981),30 and Wardrop and Dadswell (1952),33 these distortion of compression wood tracheid tip was caused by the sliding of
P: primary wall, S₁, S₂, S₃: S₁, S₂, and S₃ layer secondary wall.

Fig. 15. Cross surface of earlywood tracheid in side wood illustrating the presence of S₃ layer. Scanning electron micrograph (bar = 1 μm).

T: tracheid, RT: ray tracheid

Fig. 17. The tracheid in side wood viewed on radial surface. Scanning electron micrograph (bar = 10 μm).

T: tracheid

Fig. 16. The distorted tracheid at tip in compression wood viewed on radial surface. Scanning electron micrograph (bar = 10 μm).

intrusive growth of trachieds. The facts that ray tracheids are present on upper margin of the ray and the bordered pit of longitudinal tracheid is modified to silt-like shape are also observed in side wood (Fig. 17).

The bordered pit in compression wood tracheid is located at the bottom of groove unlike that in opposite wood and side wood and helical cavities as well as spiral checks are present on the S₂ layer of compression wood tracheid when viewed from the cell lumen (Figs. 19, 20, and 21) as shown by Butterfield and Meylan (1980), ² Cockrell (1974), ³ Core, Côté, and Day (1961), ⁴ Côté, Simson, and Timell (1966), ⁵ Phelps, Saniewski, Smolinski, Pieniazek, and McGinnes (1974), ⁶ Timell (1978a, ¹¹, ¹⁹78b, ¹⁹83), ⁷, ⁸, ⁹ and Yama-
guchi, Itoh, and Shimaji (1980). ¹⁰

Schizogenous origin of spiral check which
Fig. 19. Radial surface of compression wood tracheid. Scanning electron micrograph (bar = 10 μm).

Fig. 20. Radial surface of opposite wood tracheid. Scanning electron micrograph (bar = 10 μm).

Fig. 21. Radial surface of side wood tracheid. Scanning electron micrograph (bar = 10 μm).

Fig. 22. Radial surface of compression wood tracheid illustrating schizogenous spiral checks. Scanning electron micrograph (bar = 10 μm).

BP: bordered pit
SC: spiral check
HC: helical cavity
TO: torus

seemed to split along the weakest proportion of helical cavity by either drying or mechanical stress are often observed in compression wood tracheid but not observed in opposite wood and side wood tracheid (Figs. 22, 23, and 24) was also reported by Timell (1983). 31

The bordered pits in radial wall of opposite wood and side wood tracheid are oval in shape (Figs. 24 and 26) but the bordered pits in radial wall of compression wood tracheid are somewhat different from those in opposite wood and side wood tracheid in that they frequently reveal some modified oval shape (Figs. 22 and 25).

The torus and margo are also observed in bordered pit and the white ring is considered to be initial pit border which has concentric microfibrillar
orientation (Figs. 24 and 26) as shown by Harada and Côté (1967).11)

Also in radial surface, the common wall area between ray parenchyma and longitudinal tracheid is called cross-field and the pit in this area as most important in wood identification. However, Onaka (1949)15 reported that pit of cross-field in compression wood could not be used for diagnostic

Fig. 23. Radial surface of opposite wood tracheid illustrating no spiral check. Scanning electron micrograph (bar = 10 μm).

Fig. 24. Radial surface of side wood tracheid illustrating no check. Scanning electron micrograph (bar = 10 μm).

BP: bordered pit

Fig. 25. Radial surface of compression wood tracheid having some modified oval shaped pit aperture. Scanning electron micrograph (bar = 10 μm).

BP: bordered pit, IPB: initial pit border

Fig. 26. Radial surface of opposite wood tracheid having oval shaped pit aperture. Scanning electron micrograph (bar = 10 μm).

TO: tours, MR: margo
BP: bordered pit
IPB: initial pit border

purpose as that in normal wood.

In earlywood of side wood, the small apertures of crossfield pits are roundish triangle to rectangle and the large ones are fenestriform through the coalition of two small one (Fig. 27).

In earlywood of opposite wood, the small apertures of cross-field pits are upright oval and the large ones are procumbent oval in shape (Fig. 28).
CFP: cross-field pit

Fig. 27. Radial surface of earlywood in side wood illustrating cross-field pit. Scanning electron micrograph (bar = 10 μm).

On the other hand, the apertures of cross-field pits in compression wood are tilted bifacial convex lens shape in earlywood and slit shape in latewood because of the border on tracheid side (Figs. 29 and 30). Apertures of cross-field pits in compression wood were narrower and steeper than those of opposite wood was reported by Lee and Eom (1984)\textsuperscript{13} as well.

CFP: cross-field pit

Fig. 29. Radial surface of earlywood in compression wood illustrating cross-field pit. Scanning electron micrograph (bar = 10 μm).

The epithelial cells which surround the resin canal are filled with the lump of resin and the orifice of resin canal is in the development of thin-wall-like tylosoid are observed in side wood (Fig. 31).

Time\textsuperscript{lin} (1972, 1981)\textsuperscript{25,30} found that the epithelial cells lining the horizontal resin canals to be similar in normal wood and compression wood of several species.
RC: resin canal, RE: resin, TY: tylosoid, EC: epithelial cell, T: tracheid

Fig. 31. Cross surface of vertical resin canal surrounded by epithelial cells. Scanning electron micrograph (bar = 100 \(\mu\)m).

Conclusion

In this study, the compression wood, opposite wood, and side wood formed in the branch of pitch pine, *Pinus rigida* Miller were selected and treated for the purpose of comparing their anatomical features on cross and radial surface through scanning electron microscope and the obtained results were as follows:

1. The tracheid transition from earlywood to latewood is very gradual and the tracheids are nearly regular in both arrangement and size in compression wood but this transition in opposite wood and side wood is abrupt and the tracheids in opposite wood and side wood are less regular than those in compression wood. Also, the annual ring width of opposite wood is narrower than that of compression wood or side wood and the rays revealed on cross surface of side wood are more distinct than compression wood and opposite wood rays.

2. The tracheids of compression wood show roundish trends especially in earlywood but those of opposite wood and side wood show some angular trends. And intercellular space, helical cavity, and spiral check are present in both earlywood and latewood of compression wood but not present in opposite wood and side wood irrespective of earlywood and latewood.

3. The wall thickness of latewood tracheid is similar to that of earlywood tracheid in compression wood where as the wall thickness of latewood tracheid is by far thicker than that of earlywood tracheid in opposite wood and side wood and the S3 layer of secondary wall is lack in compression wood tracheid unlike opposite wood and side wood tracheid.

4. The tracheids in compression wood are often distorted at their tips unlike those in opposite wood and side wood and the bordered pit in compression wood tracheid is located at the bottom of helical groove unlike that in opposite wood and side wood tracheid.

5. The bordered pits in radial wall of opposite wood and side wood tracheids are oval in shape but those of compression wood tracheids show some modified oval shape.

6. In earlywood of side wood, the small apertures of cross-field pits are roundish triangle to rectangle and the large ones are fenestriform through the coalition of two small ones. However, the small apertures of cross-field pits are upright oval and the large ones are procumbent oval shape in earlywood of opposite wood and the apertures of cross-field pits in compression wood are tilted bifacial convex lens shape in earlywood and slit shape in latewood because of the border on trached side.

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Literature Cited


