



Title	An Observation of the Trabeculae in Some Dicotyledonous Woods Using Scanning Electron Microscopy
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Citation	北海道大學農學部 演習林研究報告, 34(1), 69-77
Issue Date	1977-03
Doc URL	http://hdl.handle.net/2115/20974
Type	bulletin (article)
File Information	34(1)_P69-77.pdf



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An Observation of the Trabeculae in Some Dicotyledonous Woods Using Scanning Electron Microscopy*

By

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走査型電子顕微鏡による数種双子葉植物の
木部のトラベキュラーの観察*

大谷 諄**

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Introduction

According to the International Glossary of Terms published by the International Association of Wood Anatomists, a trabecula is "a rod-like or spool-shaped part of a cell wall which projects radially across the lumen." In some standard reference books on wood anatomy, however, the descriptions of trabeculae are confined to the longitudinal tracheids in softwoods and there are no descriptions on trabeculae in hardwoods (e. g. PANSIN and DE ZEEUW, 1970; JANE, 1970). Although Hale (1951) has described that trabeculae frequently occur in both hardwoods and softwoods (most often reported in the latter), the details have not yet been described. In recent years, BUTTERFIELD and MEYLAN (1972), and MEYLAN and BUTTERFIELD (1973 a) observed trabeculae in the vessel members of an angiosperm, *Knightia excelsa*, with the aid of a SEM and noted the similarities between these and the trabeculae observed in the various gymnosperm woods examined by KEITH (1971). So far as the author knows, there is no information on trabeculae in dicotyledonous woods except for the brief obser-

* Received July 31, 1976.

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vations by RECORD (1934), BUTTERFIELD and MEYLAN (1972), and MEYLAN and BUTTERFIELD (1973 a, b). In particular, observations on trabeculae in Japanese dicotyledonous woods have not yet been reported.

During a recent study on vessel wall sculpturing (such as pits, perforation plates, warts, spiral thickenings...) of Japanese dicotyledonous woods (212 species, 120 genera, 52 families) using the SEM, the author found trabeculae in some dicotyledonous woods. To obtain more detailed information on the trabeculae, further observations were made on many samples from these species and the results are presented here.

Materials and Methods

The following 6 species were used in this study:

- Kamatsuka, *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAFF
Nanakamado, *Sorbus commixta* HEDL.
Mayumi, *Euonymus sieboldianus* BLUME
Koshônoki, *Daphne kiusiana* MIQUEL
Koshiabura, *Acanthopanax sciadophylloides* FRANCH. et SAVAT.
Ezoniwatoko, *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA

Wood samples of the above species were collected from living trees or obtained from the wood collection of the Department of Forest Products, Hokkaido University. Specimens were finished to the shape of $7 \times 7 \times 2$ (mm) from the sapwood of the collected samples using a new razor blade and dried at room conditions. They were then mounted on specimen stubs with electric conductive paste. The longitudinal radial and tangential surfaces to be observed were coated with gold or carbon-gold in a high vacuum. SEM examination was carried out at 15 kV with a JSM-2 microscope.

In addition to SEM examination, radial sections containing trabeculae were examined with the aid of a polarizing microscope to observe the microfibrillar orientation in the cell wall of the trabeculae.

Results

Trabeculae were found only in the vessel elements of *Pourthiaea villosa*, *Sorbus commixta* and *Daphne kiusiana*, while they were found in both vessel elements and fiber tracheids of *Euonymus sieboldianus* and *Acanthopanax sciadophylloides*. In *Sambucus sieboldiana*, they were found not only in both vessel elements and fiber tracheids but also in the ray parenchyma cells.

It was often observed in radial planes of *Euonymus sieboldianus*, *Acanthopanax sciadophylloides* and *Sambucus sieboldiana* that the trabeculae ran radially through the lumina of several cells containing vessel elements and fiber tracheids (photos 1 and 2). In many cases, however, trabeculae were not always arranged in straight line, as shown in photos 3, 4 and 5. In photo 3 (*Acanthopanax sciadophylloides*),

deviations, which occur in the alignment of trabeculae from cell to cell, take place mainly in the vertical plane. Trabeculae in the three vessel elements shown at the right in this photo do not traverse the lumina at a right angle to the longitudinal tangential walls. In photo 4 (*Sambucus sieboldiana*), deviations occur mainly in the horizontal plane. Although a trabecula is not found in the portion (labelled V) of the vessel element remaining at the center in this photo, it may be present in the fiber tracheid (labelled F) existing behind the vessel element, because deviations occur in the horizontal plane. Although the trabecula traverses the lumen at right angles to the tangential wall in each of two adjacent vessel elements at the left in photos 3 and 4, deviations in the alignment of trabeculae are found at the bases contacting the tangential walls between the lumina of the adjacent vessel elements (photo 5).

In addition to the trabeculae running radially through the lumina of several cells, it was also found in all the species observed that solitary trabeculae traversed the lumina of single vessel elements or single fiber tracheids. Photo 6 shows a solitary trabecula traversing the lumen of a single fiber tracheid in *Acanthopanax sciadophylloides*.

In photos 7-10 the trabeculae in the vessel elements, fiber tracheids and ray parenchyma cells observed in the present study are cylindrical, barlike, or spool-shaped structures extending radially across the lumina of the cells from one tangential wall to the other. This corresponds well to the description in regard to trabeculae in longitudinal coniferous tracheids (PANSIN and DE ZEEUW, 1970). They show an increase in diameter toward their bases contacting the tangential wall. Portions of the trabecula, except the bases, are round in a cross section (arrow) as shown in photo 11 (*Sambucus sieboldiana*). The cylindrical portion of the trabeculae, except the bases, is generally found in vessel elements and ray parenchyma cells as well as fiber tracheids, except in the narrow lumina of them as shown in photo 8. The diameter of the trabeculae varies considerably. Regardless of the species observed, the diameter of the trabeculae (in the cylindrical portion) in the vessel elements ranged from 1.0 μ to 2.3 μ , while that (in middle portion) in fiber tracheids ranged from 1.5 μ to 3.9 μ . As a rule, therefore, the diameter of the trabeculae in the vessel elements is smaller than that in the fiber tracheids. This fact is clearly shown in the trabeculae extending across the lumina of the vessel elements and fiber tracheids in photos 1, 4 and 8.

Although trabeculae show an increase in diameter toward their bases, the diameter does not always symmetrically increase at the bases. Such examples are shown in photos 12-16. In photos 12 (*Sambucus sieboldiana*) and 13 (*Sorbus commixta*), an increase in diameter at the bases is more remarkable in the longitudinal direction than in the tangential. In photos 14, 15 and 16, illustrating trabeculae in the vessel elements of *Pourthiaea villosa*, *Euonymus sieboldianus* and *Daphne kiusiana* respectively, the symmetry of the base is broken by the spiral thickenings (arrows in these photos) in the vessel wall. Root-like projections consisting of the spiral thickenings at the base disappear gradually toward the middle

portion of the trabecula.

Trabeculae of abnormal (distorted) shape in longitudinal coniferous tracheids have already been reported by KEITH (1971). Abnormal trabeculae were also observed in both vessel elements and fiber tracheids of *Acanthopanax sciadophylloides* and *Sambucus sieboldiana*. Photos 17 and 18 show trabeculae of abnormal shape in a fiber tracheid and a vessel element of *Acanthopanax sciadophylloides*, respectively.

It was found in many trabeculae observed that the surface of trabeculae facing the lumen had a smooth continuity with the inner surface of the tangential wall at the bases (photos 12, 15, 16 and 18). In photo 19 (*Acanthopanax sciadophylloides*), cracks (arrows in this photo), which presumably occur during the specimen preparation, can be seen at the base of the trabecula. It is assumed that the direction of these cracks corresponds to the orientation of the microfibrils at the base in some thickness of the cell wall from the surface. This fact must be evidently supported by the orientation of the microfibrils at the base shown in photo 20 (*Acanthopanax sciadophylloides*). In a fiber tracheid at the right in photo 20, a major portion of the trabecula at this side is removed and the internal structure is exposed. Both arrows in this photo show the orientation of microfibrils running parallel to one another in the secondary wall at the base of the trabecula. Photos 21 and 22 show trabeculae, cut almost parallel with their long axis, in a vessel element and a fiber tracheid of *Euonymus sieboldianus*, respectively. Planes cut through the central core of trabeculae at the bases are shown at the right in photo 21 and at the left in photo 22. At the bases of trabeculae shown in these photos the intercellular layer in the tangential wall is connected with the central core of the trabeculae and the secondary wall in the tangential wall shows a structural continuity with that of the trabeculae. Furthermore, striations running parallel to the long axis of the trabecula can be seen in the cylindrical portion of trabeculae in these photos. This fact was also confirmed in the trabeculae in vessel elements and fiber tracheids of *Acanthopanax sciadophylloides* and *Sambucus sieboldiana*. Two layers (labelled A and B) in the secondary wall of a trabecula are found in photo 23 showing a portion of a trabecula in a vessel element of *Sambucus sieboldiana*. Striations in the layer (labelled B in this photo) show the orientation of a steep helix (Z) to the long axis of the trabecula.

In addition to SEM observations as described above, radial sections containing intact trabeculae in the vessel elements and fiber tracheids of *Euonymus sieboldianus*, *Acanthopanax sciadophylloides* and *Sambucus sieboldiana* were examined under the crossed nicols of a polarizing microscope. It was confirmed that extinction in the cylindrical portion of the trabeculae except the bases occurred under the crossed nicols when the polarizer was parallel to the long axis of the trabeculae.

Discussion and Conclusions

The selection of the species used in this study is based on the fact that occurrence of trabeculae was found in these species during the above-mentioned prelimi-

nary observations. Therefore, it cannot be said that the occurrence of trabeculae is more remarkable in the species observed in this study compared with that in the other. Even in *Sambucus sieboldiana*, in which occurrence of trabeculae was the most marked among the species observed, it often happened that trabeculae could not be detected within a specimen of the species. This fact suggests that trabeculae are irregularly distributed and that the frequency of their occurrence is very low in the wood tissue.

Although trabeculae were found not only in the vessel elements and fiber tracheids but also in the ray parenchyma cells in the present study, trabeculae in ray parenchyma cells could not be detected except in the examples shown in photos 9 and 10. Within the limits of this study, therefore, it is concluded that the occurrence of trabeculae in ray parenchyma cells is very rare compared with that in both vessel elements and fiber tracheids.

It has been considered that the origin of trabeculae is traceable to the cambium where they form as a delicate filament of wall substance across a fusiform initial, and that a secondary wall is laid down on this filament after the cell division, at the same time and in the same manner as wall thickening is progressing in the cell (PANSIN and DE ZEEUW, 1970). According to this, several cells with trabeculae running continuously in radial direction originate in the same fusiform initial. On the other hand, it is well known that the arrangement of cells surrounding the differentiating vessel is notably disturbed by expansion of the vessel at the stage of the enlargement of cells in dicotyledonous woods (ESAU, 1965). Therefore, it is reasonable to assume that deviations in alignment of trabeculae in the horizontal plane observed frequently in the present study are caused by cellular adjustments in relation to vessel differentiation. This view is also supported by the fact that frequency and degree of deviations, especially in the horizontal plane, are more remarkable in dicotyledonous woods compared with that in softwoods.

Trabeculae observed in the present study varied in shape considerably. This is closely related to the lumen diameter and the wall thickness of the cell in which a trabecula occurs, not to species and kind of cells. That is, trabeculae are thin cylindrical, slightly enlarged toward the bases contacting the tangential wall in the cells with large lumina and thin wall, while they are thick spool-shaped in the cells with narrow lumina and thick wall.

It was confirmed in both vessel elements and fiber tracheids of *Euonymus sieboldianus*, *Acanthopanax sciadophylloides* and *Sambucus sieboldiana* that a trabecula consisted of a central core and a shell of cell wall substance enclosing it. This corresponds to the description of trabeculae in longitudinal coniferous tracheids given by KEITH (1971). It is clear that the central cores of trabeculae are connected with the intercellular layer of the tangential wall (photos 21 and 22) and the cell wall enclosing the core has a structural continuity with the tangential wall (photos 12, 19, 20, 21, 22 and 23). From photos 21, 22 and 23, it is assumed that the cell wall enclosing the central core of the trabecula consists of several concentric layers and microfibrillar orientation in them is parallel or steeply helical to the

long axis of the trabecula in the cylindrical portion except at the bases. Furthermore, polarizing [microscopic observations on trabeculae in vessel elements and fiber tracheids of *Euonymus sieboldianus*, *Acanthopanax sciadophylloides* and *Sambucus sieboldiana* suggest that the dominant direction of microfibrillar orientation in the cell wall of trabeculae is parallel to the long axis of the trabeculae except the bases. This view is also supported by the occasional occurrence of compression dislocations in trabeculae as shown in photo 5 (arrow). It was found from the SEM and polarizing microscope examination that microfibrillar orientation of the cell wall at the bases of trabeculae was different from that of the cylindrical portion, although the details could not be determined in the present study.

Acknowledgement: The author wishes to thank Dr. Shigeo ISHIDA for his valuable comments on the manuscript.

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要 約

本邦産双子葉植物6種(カマツカ, ナナカマド, マユミ, コショウノキ, コシアブラ, エゾニワトコ)の2次木部におけるトラベキュレーの形態を走査型電子顕微鏡(JSM-2型)によって観察した。得られた結果を要約すれば次の通りである。

1. トラベキュレーは、カマツカ, ナナカマド, コショウノキでは道管要素のみに、マユミ, コシアブラでは道管要素と繊維状仮道管に認められた。また、トラベキュレーは、エゾニワトコでは道管要素, 繊維状仮道管のみならず放射柔細胞にも認められた。しかし、放射柔細胞におけるトラベキュレーの出現は、道管要素, 繊維状仮道管におけるそれにくらべて極めて少なかった。

2. トラベキュラーは、数細胞の内腔を半径方向に横切って連続して存在している場合 (Photo 1, 2) と、一道管要素および繊維状仮道管の内腔を半径方向に横切って孤立して存在している場合 (Photo 6) が認められた。前者の場合、トラベキュラーは半径方向に一直線に連続していないことがしばしば観察された (Photo 3, 4, 5)。
3. 本研究で観察されたトラベキュラーの形は、すでに報告されている針葉樹材仮道管におけるものとおおむね同じであった。トラベキュラーの形はかなり変化にとむが、その形の変化はトラベキュラーが存在する細胞の内腔径と細胞壁厚に密接な関係がある。すなわち、トラベキュラーは、大きな内腔と薄壁を有する細胞 (道管要素, 繊維状仮道管, 直立細胞) では接線壁に接している両端部の方へ徐々にその直径が大きくなる細い円筒形をしているが (Photo 7~15) 狭い内腔と厚壁を有する細胞 (繊維状仮道管) では太い糸巻状をしている (Photo 1, 8)。
4. 特異な、やや奇形的なトラベキュラーが、コシアブラ、エゾニワトコの道管要素および繊維状仮道管に認められた。それらの例は Photo 17, 18 に示されている。
5. マユミ、コシアブラ、エゾニワトコの道管要素および繊維状仮道管に認められたトラベキュラーは、トラベキュラーの長軸に対して平行に、その中心を貫通している Central core と、それをとりかこんでいる細胞壁とから成りたっている。Central core は接線壁の細胞間層と連絡していて (Photo 21, 22)、それをとりかこんでいるトラベキュラーの細胞壁は接線壁と構造上連続していること (Photo 19~23) が認められた。走査型電子顕微鏡および偏光顕微鏡による観察結果をもとにして、トラベキュラーの細胞壁におけるミクロフィブリルの主配向は、その両端付近を除いてトラベキュラーの長軸方向に対してほぼ平行であることが推定される。

Explanation of photographs

- Photo 1.** *Euonymus sieboldianus* BLUME Radial surface showing line of trabeculae running radially through the lumina of vessel elements and fiber tracheids. Arrows show trabeculae incorporating radial walls of fiber tracheids.
- Photo 2.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA Radial surface showing line of trabeculae running radially through the lumina of vessel elements and a fiber tracheid.
- Photo 3.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. Radial surface showing line of trabeculae running radially through the lumina of vessel elements. Deviations in the alignment of trabeculae from vessel to vessel take place in the vertical plane.
- Photo 4.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA Radial surface showing line of trabeculae running radially through the lumina of vessel elements and a fiber tracheid. Deviations in the alignment of trabeculae from cell to cell take place in the horizontal plane. V=Portion of vessel element. F=Fiber tracheid.
- Photo 5.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA An enlarged view of a part of photo 4. Although trabeculae traverse the lumina at a right angle to the tangential wall, deviations in the alignment of trabeculae are found at their bases contacting the tangential walls between adjacent vessel elements.
- Photo 6.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. Radial surface showing a solitary trabecula traversing lumen of a single fiber tracheid.
- Photo 7.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. A trabecula in a vessel element exposed by a tangential cut.
- Photo 8.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA A spool-shaped trabecula in a fiber tracheid lying between adjacent vessel elements having trabeculae.
- Photo 9.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA Radial surface showing trabeculae in upright ray cells. T=Trabecula.
- Photo 10.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA An enlarged view of a part of photo 9. A trabecula in an upright ray cell.
- Photo 11.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA A trabecula in a vessel element exposed by a tangential cut. Arrow shows cross section of cylindrical portion of a trabecula.
- Photo 12.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA An enlarged view of the base of the trabecula shown in photo 11.
- Photo 13.** *Sorbus commixta* HEDL. A trabecula in a vessel element.
- Photo 14.** *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAFF Portion of a trabecula in a vessel element. Arrows show spiral thickenings at the base of a trabecula.
- Photo 15.** *Euonymus sieboldianus* BLUME Portion of a trabecula in a vessel element. Arrows show spiral thickenings at the base of a trabecula.

- Photo 16.** *Daphne kiusiana* MIQUEL A trabecula in a vessel element. Arrows show spiral thickenings at the base of a trabecula.
- Photo 17.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. An abnormal trabecula in a fiber tracheid.
- Photo 18.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. An enlarged view of a part of photo 3. Portion of an abnormal trabecula in a vessel element.
- Photo 19.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. Portion of a trabecula in a vessel element. Arrows show cracks at the base of a trabecula.
- Photo 20.** *Acanthopanax sciadophylloides* FRANCH. et SAVAT. Bases of trabeculae in adjacent fiber tracheids. Arrows show microfibrillar orientation running parallel to one another in a layer of secondary wall at the base of a trabecula.
- Photo 21.** *Euonymus sieboldianus* BLUME A trabecula in a vessel element cutting almost in parallel with its long axis. Striations running parallel to the long axis of the trabecula are found in the cylindrical portion except the base. I=Intercellular layer. ST=Spiral thickening.
- Photo 22.** *Euonymus sieboldianus* BLUME A trabecula in a fiber tracheid cutting almost in parallel with its long axis. Striations running parallel to the long axis of the trabecula are found in the cylindrical portion except the bases. Central core of the trabecula is connected with the intercellular layer of the tangential wall (at the left in this photo). I=Intercellular layer. C=Central core.
- Photo 23.** *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA Portion of a trabecula in a vessel element. Each of two layers labelled A and B is connected with different layer in the tangential wall. Striations of steep helix (Z) are found in the layer labelled B. I=Intercellular layer.







