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Instructions for use

The Trabecula and Its Related Structures*

By

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トラベキュレーとその関連構造*

由 本 正 英**

CONTENTS

Introduction

According to the International Glossary of Terms published by IAWA, a trabecula is defined as a rod-like or spool-shaped part of a cell wall which projects radially across the lumen.   During the course of an extensive survey on the formation and structure of compression wood cells in young trees of *Picea glauca*, we observed numerous rod- or spool-like trabeculae and several other types of structures traversing the lumen mostly radially.   Although the latter types are out of the definition of IAWA, subsequent investigations carried out to reveal their nature led us to a belief that trabeculae should be considered in a broad sense and the rod- or spool-type found in the definition is only one of the representatives of a category of structure, which includes trabeculae and is not defined at present, and that most of other types are not abnormal deviations but are rather intimately related to the rod- or spool-like one and should be regarded as other representatives of the structure, though a few types of them seem to belong another or other categories.   In the present paper they are called together "trabeculae and their related structures" irrespective of their nature.

Accompanying recent wide use of SEM in the study of wood anatomy, a considerable number of papers on trabeculae and their related structures have been published, nevertheless, they deal with mostly the rod- or spool-type and few observation was made on others by SEM.   On the other hand, detailed light microscopic observations on a variety of type are found in old German and Italian literature. As will be seen later, fine structural studies with the aid of SEM and other recent sensitive tools have covered only a fraction of a diverse variety of trabeculae and their related structures.   In the present paper several types of structures traversing the lumen mostly radially, including rod- and spool-like trabeculae, are studied using SEM (scanning electron microscopy), a SEM–UVM (ultraviolet microscopy) combination method, PLM (polarizing microscopy) and ordinary light microscopy.   Mutual relationships among different types and the causal mechanism of their formation are also discussed closely.

As stated above, diverse aspects of trabeculae and their related structures were investigated in detail by old German and Italian scientists.   However, it is a wonder that none of recent authors except WERKER and BAAS (1981) refer to these great contributions, and that standard reference texts on plant and wood anatomy except PANSHIN and DE ZEEUW (1980) mention only rod- and spool-like trabeculae (*e. g.*, ESAU 1965, TSOUMIS 1968, JANE 1970, FAHN 1982).   Since the old contributions seem to be forgotten, some of which have not lost up-to-date values and are thought to exceed the general understanding on these structures in the present day, it would

be appropriate to make a brief review on the subject.

Historical

I) *Contributions of German botanists in the last century*

The trabecula was first reported by SANIO (1863), as sometimes called as SANIO's trabecula. However, it is little known that the observation was made on macerated tracheids of a hardwood species *Hippophaë rhamnoides*. He stated that this "false endwall" (falsche Scheidewand) is thought to have a beam-like cylindrical body, because when turned 90 degrees round the long axis of the tracheid, it gave a round spot on the cell wall. After nine years, WINKLER (1872) observed similar structures in sections of *Araucaria brasiliensis*, and presented the fact that such bars occur sometimes as solitary ones, sometimes in a long file aligned at the same height through a number of cells. He stated that these structures are entirely analogous to those found by SANIO (1863). To my knowledge, it is the first report with drawings of trabeculae in cross, radial and tangential sections. Although he also illustrated a side view of a trabecula in a tangential section, he would have taken an endwall or a resin plate for the trabecula in this case. Later, SANIO (1873–1874) reported in a study of *Pinus silvestris* that trabeculae are of a cellulosic nature and originate in cambium from which they extend radially both outwards and inwards occasionally beyond many growth rings.

The occurrence of trabeculae was confirmed repeatedly by many workers in gymnosperms and angiosperms. DE BARY (1877) distinguished tracheary elements with beam-like structures as "Tracheae trabeculatae" from those with spiral thickenings and those with pits. However, this term was mainly used for a particular type of cell found on the edges of the primary vascular bundle of *Lycopodium* and those found in the transfusion tissue of the leaves of *Biota* (*Thuja*) and *Juniperus*, and he regarded the structure reported by SANIO as an unusual and abnormal one. He observed trabeculae in *Drymis winteri*. STRASBURGER (1891) also found trabeculae in many conifers. He believed an involvement of mechnical factors in their formation, and stated that this could be verified by applying a mechanical pressure to the tree trunk. The occurrence of trabeculae was also reported by RUSSOW (1882) and KNY (see MÜLLER 1890).

Two brilliant contributions made by MÜLLER (1890) and RAATZ (1892) are very extensive and still have not lost their up-to-date values. MÜLLER (1890) observed trabeculae and their related structures in 28 conifers and suggested the general occurrence of these structures in all the parts of the axial organs of all conifers. A similar content is found in STRASBURGER (1891). MÜLLER made a detailed review on the occurrence of bar-like structures in higher plants, and mentioned the pattern of the occurrence in xylem, especially the appearance and disappearance of a row of trabeculae in a radial file, and detailed anatomy of these structures. He recorded several types of structure differing from rod-like trabeculae, *i. e.*, disconnected, curved and plank-like ones with or without the confluency to the radial wall, and structures with irregular surfaces or protuberances. He noted

the presence of the so-called central core (Mittellinie) continuous to the middle lamella and the affinity between the surface layer of trabeculae and the inner most layer of the host cell. Müller also stated that trabeculae and their host cell wall show the same chemical reactions with phloroglucinol-HCl, zinc-chlor-iodide and H_2SO_4-aniline, and the same optical reactions under a polarizing microscope. He discussed several possible hypotheses as to the cause of their formation in detail and concluded that trabeculae originate from folds of the radial walls of the cambial cells. He stated that the fold of the radial wall is a common feature of coniferous woods and can easily be formed by the tip growth of the cambial cell, and that the folds would be altered into plank-like structures or trabeculae by the absorption of the basal part of the folds. In addition, he is the author of the name of SANIO's bar (Sanio'sche Balken).

Based on the observations on 14 conifers and 3 hardwoods, RAATZ (1892) published a similar but more voluminous paper with a number of drawings. He supposed that trabeculae and their related structures would also occur in all hardwood species, and mentioned the pattern of their occurrence in a radial file, development from the cambium, reactions with chemical reagents, and the distribution in a growth ring and in a cell. He reported a variety of type other than those found by MÜLLER, e. g., pit-including forms and several abnormal forms. He stressed the occurrence of all intermediates between the typical trabecula and a partial contact of the tangential walls within a cell and the developmental homology between these two types of structure, and ascribed the origin of trabeculae to the contact of the tangential walls. However, his chief interest lay in the initial theory on which he made detailed discussion in relation to the occurrence of the short row of trabeculae devoting more than a half of the paper.

The activity of old German botanists in the study of trabeculae, however, seems to have dropped thereafter, and to my knowledge, no subsequent papers were published by those peoples.

II) *Vinicultural researches in Italy and Germany*

The second rise of the activity is found to have begun by an Italian scientist L. PETRI in the early decade of the present century. Unfortunately, I cannot mention details of the Italian literature because of my ignorance of the language, however, according to German literature (see later), PETRI (1911, 1912 a, b) first observed "cordi endocellulari" (trabeculae) in vine infected by a disease called "arricciamento" in Italian, and regarded their occurrence as a characteristic feature of the disease. Since this disease caused a serious decrease in production and lacked in decisive diagnostic markers, it became an important problem whether the occurrence of trabeculae is a characteristic manifestation of the disease or not. However, MAMELI (1913, 1916 a, b) confirmed the occurrence of trabeculae even in healthy vines and other 19 dicotyledons (e. g., *Populus nigra*, *Acer tataricum* and *Castanea vesca*), and denied the causative relation between the occurrence of trabeculae and the infection of the disease.

PETRI (1912 c) also published a very voluminous paper dealing with histological

and cytological aspects of this structure. According to PETRI, the cambial cells equipped with the primordia of trabeculae generally differ from normal ones and have one or two nuclei which are surrounded by bright and clear haloes and are irregular in form sometimes showing disorganized chromatine. He found a body which is strongly stained by haematoxylin and situated near the nucleus of the cambial cell, and named it "corpo d'escrezione" (body of excretion), and thought trabeculae are formed from this body through its increase in diameter and the resultant contact with the plasma membranes lining the tangential walls. He found a stimulating effect of late frost on the formation of trabeculae. The occurrence of trabeculae in the pith, bark, leaves and epidermis of vines was also reported by PETRI (1913).

Whether the occurrence of trabeculae is a manifestation of the disease or not became a subject of discussion in Germany lagging about 20 years behind in Italy. The disease has been called "Reisigkrankheit" or "Krautern" in German. SCHNEIDERS (1934, 1937, 1938) thought that the formation of trabeculae is evoked only by infection, and claimed that there is a definite correlation between the severity of infection and the frequency of trabeculae. Although he found trabeculae in many other hardwood species (mostly fruit trees), a conifer and potato stems, he thought these plants were also infected. JÖHNSSEN (1933) drew a similar conclusion from grafting experiments. However, other investigators found trabeculae in not infected vines (KROEMER and MOOG 1936) and other plants (many fruit trees and other 18 species including conifers by KROEMER et al. 1936, 7 herbaceous plants, by BÄRNER 1937 b), and threw doubt on its diagnostic value (BODE 1938, MAIER 1939, MÜLLER-STOLL and BALBACH 1939, HEPP and THATE 1943).

Although their studies were very practical in contrast to botanists, they also made histological and cytological observations on trabeculae. SCHNEIDERS (1934, 1938) stated that trabeculae show lamellated structures after the treatment with swelling agents, and that the central core (Mittelfaden) and the lamellated structures are identical in structure and in chemical nature with the middle lamella and cell walls of the host cell respectively. He also noted the occurrence of trabeculae in petioles, young shoots and the axes of bunches of grapes in seriously infected vines imported from USA.

Since "Reisigkrankheit" has many features common with those found in virus diseases, BÄRNER (1937 a, b) made microscopic researches on plants of Solanaceae and Cucurbitaceae infested by viruses and healthy potatoes in order to check the possibility of this structure as an early diagnostic marker of virus diseases. Although he failed to find trabeculae in healthy potatoes, he could not found any positive correlation between the severity of the infection and the frequency of trabeculae, and denied the possibility. According to BÄRNER, trabeculae found in these herbaceous plants were quite similar to each other in structure, form, and optical nature between crossed nicols. He reported the occurrence of a disconnected and curved form in these plants.

From the observation on the development of trabeculae in the cambium of vines BODE (1938) concluded that the formation of trabeculae is a result of an

abnormal degeneration of cell division.   He also reported that the orientation of trabeculae always coincide with that of the spindle axis which is determined in each organ, *i. e.*, parallel to the surface in epidermis, random in parenchyma of bark, perpendicular to the long axis in xylem and bast, and parallel to the axis in pith.   He found trabeculae in several other woody species.

On the other hand, MÜLLER-STOLL and BALBACH (1939) studied morphology of trabeculae and recorded curved, branched and disconnected forms with or without mulberry-like ends or minuite protuberances.   Abnormalities in the quantity of cell wall deposition and in the shape of the central core were reported.   They also studied the distribution of trabeculae in cross sections taken along branches of *Vitis,* and stated that trabeculae were especially abundant in the basal part of branches.   Similar results were also obtained by SCHNEIDERS (1934, 1938), BÄRNER (1937 b), FUESS and SCHNEIDERS (1935), MAIER (1939), *etc.*

BALBACH (1939) studied chemical nature of trabeculae especially that of the central core, and reached a conclusion that the cell walls of trabeculae are composed of cellulosic lamellae, and that the central core is seemingly similar to but essentially different from the middle lamella and is mucilaginous or gummy in nature.   False trabeculae similar but different in the cause of their formation were also reported (BODE 1939, *c.f.,* KÜSTER 1925).

The occurrence of trabeculae has still been regarded as a feature of the disease. However, most investigators do not believe the diagnostic value of trabeculae, especially for European varieties (STELLWAAG 1948, 1953, STELLWAAG and LUSIS 1953, BRÜCKBAUER 1957, 1958, 1963, OCHS 1955, 1957, WILHELM and HOPP 1961), though SCHNEIDERS (1957–1958) still persists in his belief.   In addition, an atypical form of "Reisigkrankheit" has been reported recently.   The samples taken from the vines infected this form also showed a greater number of trabeculae than the normal, though not so closely studied (BRÜCKBAUER and RÜDEL 1976).

Later, MÜLLER-STOLL (1965) published a paper on trabeculae, aside from those in *Vitis.*   He collected wood samples from a number of regions in Europe and found the preferential occurrence of trabeculae in the samples from exposed sites of the Alps.   He also devoted a half of the paper to describe the morphology of trabeculae and the pattern of the occurrence in a light microscopic level.   Normal, curved, branched and disconnected forms with or without gaps were reported to occur in conifers and hardwoods as was the case of *Vitis.*   He also pointed out the differences in the average diameter of trabeculae, and in the length and frequency of the rows between conifers and hardwoods.   He noted an intimate relation between the occurrence of trabeculae and the histological abnormalities caused by late frost, and suggested the primary involvement of low temperature in the formation of trabeculae.

III) *English literature by botanists and wood anatomists*

On the other hand, English literature on trabeculae by botanists and wood anatomists had only been sporadically published in the former half of the present century.   In the literature of those times some authors used a term "bar of Sanio"

for crassulae (GERRY 1910, JEFFREY 1912, HALE 1923 a, c.f., GROOM and RUSHTON 1913, SIFTON 1915, BAILEY 1919), and this caused some confusion between these two different structures (e.g., KÜSTER 1925, SCHNEIDERS 1938, 1957-1958).   In spite of scrutiny of the literature, I failed to ascertain the first investigator who defined the term "trabecula".   SIFTON (1915) and BAILEY (1919) used this term without any comment.

To my knowledge, the first English report in which trabeculae are described, though to a limited extent, is GROOM and RUSHTON (1913).   They found trabeculae in some Indian pine woods, and noted that the bars seen in transverse section are hollow and mostly cylindrical, but close to the attachment to the tracheid wall the bar may deepen so that the contours of it and its cavity are vertically elongated.

After 10 years HALE (1923 b) found trabeculae in *Alnus oregona* traversing the lumen of a wood parenchyma cell as well as those of many tracheids, and thought that they may be of wide spread occurrence in angiosperms as well.   A similar content is found in RECORD (1934).   The latter author observed trabeculae in fibers of *Hernandia ovigera* and in some ray cells of *Aegiceras* sp.   Hale later stated (1935) that the typical form is a hollow rod of round cross section, though various degrees of distorted shape occur, and composed of similar materials to those of the walls of the cells of which they are a part.   He pointed out the fact that trabeculae often seem to be associated with certain structural abnormalities, such as bird's eye structures, abnormally large horizontal resin ducts, as well as with the presence of wounds where the cambium has been exposed to fungal infection.   From these circumstantial facts, he ascribed their origin to the filamentous fungus parasite in the cambium of growing trees and thought that trabeculae are formed by the deposition of wall materials on the filament, though the first author who implied the fungal origin is probably JEFFREY (1917).

Recently, an increasing number of fine structural studies using SEM and TEM have been published.   KEITH (1971) studied rod-like trabeculae in conifers using SEM, PLM, and ordinary microscopy, and with the aid of delignifying agents.   According to KEITH, a trabecula is not hollow but has a central core, and the substance of the core was removed by delignification.   The dominant direction of the orientation of cellulose was reported to be essentially parallel to the long axis of the trabecula.   He observed also some abnormal trabeculae.   Later, KEITH et al. (1978) gave a further report on trabeculae in conifers, in which they stated that the confluency of cell wall and a trabecula was verified.

The publications of BUTTERFIELD and MEYLAN on trabeculae were all made on hardwoods grown in New Zealand.   They observed by SEM a trabecula with a vestured pit in a vessel member of *Fuchsia excorticata* (MEYLAN and BUTTERFIELD 1973) and a file of trabeculae traversing a vessel member, fibers and axial parenchyma cells (BUTTERFIELD and MEYLAN 1979).   They also published a brief note on a trabecula found on a tangential surface of *Knightia excelsa* (BUTTERFIELD and MEYLAN 1972).   They pointed out a possibility that the formation of trabeculae results from a disordered periclinal division in the cambial initial or xylem mother

cells in such a manner that the cell plate fused with a side wall at some points produces a rod upon radial expansion (BUTTERFIELD and MEYLAN 1980).

Based on the observation on trabeculae in Japanese native hardwoods, OHTANI (1977) reported that the shape of trabeculae in hardwoods is similar to that reported in conifers, and that trabeculae are thin in the cells with wide lumen and thin walls, and thick in those with narrow lumen and thick cell walls. He found the trabeculae in ray cells as well as in vessel members and fiber tracheids.

KUČERA (1978) observed trabeculae in pith parenchyma cells in the neighborhood of the vascular nodules of *Taxus baccata*. The trabeculae are reported to be hollow. On the other hand, PARAMESWARAN (1979) made a TEM-observation on trabeculae in *Agathis alba* and came to a similar conclusion to that of KEITH et al. (1978) as to the confluency of trabecular structure.

WERKER and BAAS (1981) reported the trabeculae occurred in the secondary tissues of *Inula viscosa* and *Salvia fruticosa*. Trabeculae of plank-like form and those with bordered pits or various gaps were observed. They suggested that trabeculae are produced as a result of injuries.

YUMOTO and OHTANI (1981) studied rod-like trabeculae in compression wood tracheids with the aid of SEM, PLM, and a SEM-UVM combination method, and reached a conclusion that trabeculae are composed of the same layers with the wall of the host cell.

The present understanding of botanists and wood anatomists on the nature of the trabecula and its related structures is based mainly on the English literature. However, it can be said from the above review that the literature has dealt with only a few aspects of the trabecula and its related structures.

Materials and Methods

Materials were taken from the first to third internodes of vertical or artificially tilted young trees of *Picea glauca ca.* 1.7 to 2.0 m high, grown in the nursery of the Laboratory of Forest Tree Breeding in Nayoro, College Experiment Forests, Hokkaido University. These materials were originally collected for the studies on the formation and structure of compression wood cells, and were chiefly compression wood differing in the degree of development from very slight to fully developed. Normal wood cells were also included in many of these samples. Trabeculae and their related structures were relatively rich in number all over the samples, however, they were especially abundant in the transitional zone from artificially induced compression wood to normal wood (YUMOTO, to be published), and early-earlywood affected by late frost.

A light microscopic observation was made on 20-micron-thick sections stained with a genetian violet — orange G combination. These sections were originally prepared for the measurement of mitotic figures in the cambial zone (YUMOTO et al. 1982 a). Although gentian violet strongly stains weakly lignified parts of tissues, the violet does not stain well the cell walls of mature tracheids, and therefore, it was actually not suitable for the present study. However, since the occurrence of

trabeculae and their related structures was especially abundant in the early-earlywood (normal wood) of these gentian-violet-stained sections, they were used for the observation without preparing another set of sections stained suitably, *e.g.*, by safranine.

A SEM-observation of trabeculae on the radial surfaces was mostly made on specimens originally prepared by a SEM–UVM combination method (YUMOTO *et al.* 1982 b) for the studies of the structure of normal and compression wood cells (YUMOTO 1982, YUMOTO *et al.* 1982 b, 1983). Materials were embedded in a methacrylate resin mixture and after sectioning (1-micron-thick cross sections for UVM), their radial surfaces were finished on an ultramicrotome (LKB, Ultrotome III) and soaked in acetone or xylene to remove the embedding resin. After dried at room conditions, specimens were mounted on specimen stubs and coated with gold. If a trabecula is situated on the radial-transverse edge of the specimen and is cut longitudinally, a SEM-observation on the longitudinal cut surface of the trabecula can be matched with an UVM- and a PLM-observation on the corresponding cross section (*e.g.*, Photo 31 a–c). Thin sections were also immersed in the same organic solvents and photographed under an UV-microscope (Carl Zeiss, Type MPM–01) at a wavelength of 280 millimicrons using ordinary commercial films. PLM-photographs were also taken under this microscope. In addition, a small number of specimens were finished on a freezing microtome without embedding and prepared for a SEM-observation as usual.

To obtain the transverse view of trabeculae, tangential sections of 1-micron-thickness were cut from methacrylate embedded specimens and the remainders of the specimens were immediately immersed in the organic solvents and prepared for a SEM-observation in the same manner as stated above. Most of these specimens were severed from trees which were gravitationally stimulated at 45 degrees for 2 or 3 days in order to examine the effects of the short term stimulation on wood anatomy (YUMOTO *et al.* to be published). Although these specimens contain the transitional zone from compression to normal wood where the occurrence of trabeculae and their related structures was especially abundant, since no matched cross sections were prepared, the accurate position of the finished surface in the sequence of the transition could not be confirmed. By this method an observation of a cut surface of a trabecula by SEM can be matched with those by UVM and PLM on the corresponding tangential section. For the details of the technique readers refer YUMOTO *et al.* (1982 b).

Compression wood is a particular type of wood formed generally on the lower side of leaning stems or branches in most of gymnosperms. Its formation is thought to be a geotropic manifestation and to cause recovering of the displaced organ to its original position. The nature of compression wood is different from that of normal wood in many respects, and all intermediates can be found between normal and the most well-developed compression wood (YUMOTO *et al.* 1983). The presence of the severe compression wood is easily detected by its reddish color and life-less appearance, but the detection of mild and slight one is difficult without microscopic inspection. Most of anatomical particularities are found in axial tracheids. In well-developed compression wood they are round in cross section with the occurrence of inter-

cellular spaces, and have thicker cell walls. Their secondary wall lacks in the S3 layer, and the S2 layer has a characteristic system of radial cavities (spiral grooves). Compression wood contains more lignin than the normal and the excessive lignin is mainly found in the outer S2 layer. This layer is called the S2 (L) layer (CÔTÉ *et al.* 1968). For the details of the nature of compression wood readers refer recent reviews (*e.g.*, CÔTÉ and DAY 1965, WESTING 1965, 1968, CASPERSON 1965, WILSON and ARCHER 1977, TIMELL 1981).

Results and Discussion

I) General comments

Several types of structures which resemble or seem to be related to the rod- and spool-like structure (trabeculae as defined by IAWA) were observed. However, many of them do not assume a beam-like structure, and therefore, are not adequate to call trabeculae because the word trabecula means a little beam in Latin (STEARN 1973). Although the rod- or spool-like structure and most of others seem to have ontogenetically close relationships to each other, as will be seen, some show different nature in some respects, and presumably, a few types of structures described in the present paper belong to another or other categories. However, since detailed course of the formation of trabeculae and their related structures still has not been disclosed, it might be premature to conclude their relationships. There is also a possibility that a type of structure which will be described in the following sections, might actually consists of two or more ontogenetically different ones. Therefore, in the present paper no proposal to the terminology is made, and *the term trabecula is used only for a rod- and spool-like structure as defined by IAWA*, and other structures are classified for covenience into four basic types and two varieties. Brief definitions are as follows ;

  a) Basic types
    i) Trabecula ; a structure rod- or spool-like in form, nearly round in cross section.
    ii) Plate ; a structure plank-like in form, its cross section highly elliptic or elongated in the axial direction of the host cell.
    iii) Confluence ; a rod or plank confluent to a radial wall, its central core also confluent to the radial middle lamella.
    iv) Adhesion ; a wall-pinch-like structure, contact of the tangential walls in a cell.
    v) Tangential confluence ; a confluence oriented in the tangential direction.
  b) Varieties
    i) Pit-including form ; above types (except adhesions) with a pit-like structure.
    ii) Abnormal form ; above types deviating from the normal features.

In the present study two third of trabeculae and their related structures were found in compression wood differing in the degree of development. Compression wood is known to differ from normal wood in many respects (see note on page 213). However, from the present observation the fundamental structure of a basic type in compression wood seems not to differ from that found in normal wood

except for the reported differences in cell wall structure between these two types of wood. And, as will be stated later, there is a notable difference in the length of the row of trabeculae or their related structures, and are several patterns of their occurrence. The difference between normal and compression wood seems to exert no influence on the pattern of the occurrence. However, the dominant pattern is different between the above mentioned two trabecula-rich zones, *i. e.*, the transitional zone from compression to normal wood, and early-earlywood affected by late frost. Although it cannot thoroughly deny a possibility that there might be some structural differences between trabeculae or their related structures of different length of the row, or between those found in the samples of different dominant patterns, or between compression and normal wood, the following description will be made on the assumption that the fundamental structure of a basic type is not altered by these factors.

II) Basic types

i) *Trabeculae*

The trabecula denotes a structure rod- or spool-like in form traversing the cell lumen radially (Photos 1 to 27). Its cross section is round or slightly elliptic. Cell walls of this form may be fused with the radial wall of the host cell, but the central core is not confluent to the radial middle lamella. If so, it belongs to the confluence. Its surface is smooth. A trabecula with an irregular surface is regarded as abnormal. All intermediates can be found between this form and the plate or the adhesion of the tangential walls.

The trabecula is the most common structure traversing the cell lumen radially and most variable in structure. As stated above, the fundamental structure of trabeculae in compression wood is not different from that in normal wood, however, their appearances are noticeably altered accompanying the changes of the host cell wall. Trabeculae in compression wood have not been reported except for our brief note (YUMOTO and OHTANI 1981) to my knowledge. Although MÜLLER-STOLL (1965) illustrates rows of trabeculae in wood of *Pinus mugo* which seems to be compression wood, he does not mention whether the wood is compression wood or not. On the other hand, external morphology of trabeculae in normal wood has been relatively well documented. Therefore, in the present paper, attention will be focussed on the external feature of trabeculae in compression wood and the inner structure of this form both in normal and compression wood.

Photos 1 and 2 show typical trabeculae in normal and compression wood tracheid respectively. It should be noted that the inner most layer in the former is the S3 layer and that in the latter is the S2. Generally, trabeculae in well-developed compression wood have also spiral grooves as is the wall of the host cell. Minute compression failures are often seen on each rib between the grooves. However, spiral grooves on trabeculae are occasionally found to be only poorly developed even in the so-called typical compression wood as shown in Photo 3, which was taken on a specimen severed from the lower side of a tree inclined at 45 degrees. In such a case a compression failure, if present, is found to occur on

the whole trabecula. Photo 10 shows a trabecula in a compression wood tracheid formed by a 3-day stimulation at 45 degrees. In contrast to the host cell wall, no grooves can be seen on the trabecula. Thus, the degree of the development of spiral grooves on trabeculae is not necessarily comparable to that of the host cell, though that of the latter itself is variable to some extent (YUMOTO et al. 1983).

In mild and slight compression wood tracheids, no grooves can be found in both trabeculae and their host cell walls (Photo 4). However, at the base of trabeculae, grooves of presumably different nature were sometimes observed (Photo 11). Cracks resembling these grooves were observed by OHTANI (1977) in a vessel element of Acanthopanax sciadophylloides, and he regarded the crack as an artefact caused by drying during specimen preparation. However, the method used in the present study for SEM-observation causes little shrinkage during drying (YUMOTO et al. 1982 b), therefore, the grooves at the base of trabeculae in mild compression wood would not be artefacts.

The occurrence of intercellular spaces is also one of the common features of compression wood though it is unstable in nature (YUMOTO et al. 1983). The spaces were occasionally found at the base of trabeculae as shown in Photos 7 to 9. In extreme cases the spaces at both the bases fuse into a common room (Photo 9). The structure found in Photo 9 might seem not a trabecula but a part of host cell wall. However, since the opposite view gave a similar image, it is believed to be a trabecula, though a possibility remains that it might be a part of a confluence. RAATZ (1892) reported the occurrence of intercellular spaces at the base of the trabeculae in parenchyma cells of a resin canal tissue in Pinus silvestris. Although a row of trabeculae penetrating parenchyma cells of a resin canal tissue was observed (Photo 119), no intercellular spaces were seen there.

The microfibrils of the S3 layer of a trabecula run along the long axis of the trabecula as shown in Photo 1. Since the orientation of the microfibrils in the S2 layer of compression wood tracheids is known to be parallel to that of spiral grooves (CASPERSON 1959), it is concluded that the microfibrils in the S2 layer of the trabecula in Photo 2 run also nearly in parallel to its long axis. The orientation in the S2 layer of a trabecula in normal wood cannot be known from external features. Although the angle of the microfibrils in the S2 layer in compression wood tracheids is reported greater than in normal wood (WARDROP and DADSWELL 1950, MATSUMOTO 1957), the materials examined in the present study showed no appreciable difference in the angle between normal and compression wood (YUMOTO et al. 1982 b, 1983). Therefore, the orientation of the microfibrils in the S2 layer of trabeculae in normal wood tracheids such as that shown in Photo 1 is supposed to be also similar to that in compression wood shown in Photo 2. Namely, the microfibrils of the S2 layer in the middle of trabeculae run nearly in parallel to their long axes. A similar conclusion is found in MÜLLER (1890), KEITH (1971) and OHTANI (1977).

However, this is not the case for relatively thick trabeculae. Photo 4 shows a pair of thick trabeculae in mild compression wood. They might be slightly

elliptic in cross section, *i. e.*, intermediates to the plate.   The microfibrilar orientation in the middle of the trabeculae is helical along their long axes.   As will be shown later, the microfibrils in the S2 layer of the plate is also helically arranged being parallel to that of the host cell wall.   It can be said, therefore, that the orientation in the middle of trabeculae is nearly parallel only in a thin trabecula, and that as the width increases, it becomes helical to correspond with that of the host cell wall.

As repeatedly reported, a trabecula shows an increase in diameter towards its ends to the tangential walls.   The increase generally does not occur evenly round the circumference of the trabecula but occurs in the direction parallel to the orientation of microfibrils in the S2 layer of the host cell.   This is clearly shown in compression wood tracheids because of their lack in the S3 layer (Photos 3, 10 and 11).   The microfibrils are divided into two bundles of opposite directions near the base of the trabeculae, and at first, run more or less divergently and finally are merged with those of the S2 layer of the host cell wall.   Since such a pattern of microfibrilar arrangement causes a shortage of the microfibril deposition on the site being off the course of the microfibrils running from trabeculae, two depressions of the cell wall are made at a base of a trabecula (arrow in Photo 10).   This would account for the formation of the "root-like projections" (KEITH 1971, OHTANI 1977).   A "neck" found at the right base of the trabecula in Photo 1 (arrow) would be formed by the same cause.   The alteration of the course of the microfibrils from the host cell wall to a trabecula or *vice versa* is clearly shown in Photo 7.

Although OHTANI (1977) reported the orientation of such projections is parallel to the long axis of the host cell, and a similar content is also found in GROOM and RUSHTON (1913), in the present study such projections were not in parallel to the long axis but helical corresponding to the microfibrilar orientation of the S2 layer. This disagreement would come from the difference in the nature of the materials examined.   Namely, in the former case the materials were collected from mature wood in which the angle of microfibrils in the S2 layer is known smaller than in juvenile ones examined in the latter (ZOBEL *et al.* 1959).

The orientation of the microfibrils in the S1 layer could not be disclosed well in the present study.   Judging from the fact that cross sections of trabeculae show little birefringence between crossed nicols (Photos 12 c and 13 c), it is supposed to be nearly parallel to the long axis of trabeculae at their middle portion.   An UVM- and PLM-photograph of a longitudinal section of trabeculae in well-developed compression wood are shown in Photos 22 a, b.   Although they are not cut exactly along the central axis of the row, the S1 layer is seen at the bases of trabeculae (arrow) showing lower UV-absorption and higher birefringence.

Photos 5 and 6 show longitudinal cut surfaces of relatively thick trabeuclae in mild and well-developed compression wood tracheids respectively.   The layers which seem to correspond with the middle lamella (thick arrow), the S1 (thin arrow) and the S2 layer (double arrow) can be seen in different texture.

Photos 12 a–c and 13 a–c show cross sections of trabeculae (tangential sections of the samples) in normal and mild compression wood tracheids respectively ; photos a by SEM, b by UVM and c by PLM. In the center of the trabecula a spot with more or less strong UV-absorption is found. It has been called Zentralfaden, Axenfaden (in German) or central core (KEITH 1971). The central core usually shows slightly lower UV-absorption than the middle lamella, and the walls around the core have a similar thickness and a similar strength of UV-absorption to those of the host cell walls.

The wall of trabeculae in compression wood tracheids consists of zones of different strength of UV-absorption (Photo 13 b). The inner zone adjacent to the core has far lower absorption than the core. Since the S1 layer of compression wood tracheids is known to have less lignin than the middle lamella and the outer S2 layer (CÔTÉ et al. 1968, YUMOTO et al. 1983), this zone would correspond to the S1 layer. Surrounding this region, strong UV-absorption decreasing towards the cell lumen is seen. This distribution pattern of UV-absorption coincides with that found in the S2 layer of compression wood tracheids (WOOD and GORING 1971, FUKAZAWA 1974, YUMOTO et al. 1983), and therefore, the zone would be the S2 layer.

The central core is, however, variable in the strength and the distribution pattern of UV-absorption as well as in form. It sometimes shows strong absorption comparable to that of the middle lamella (Photo 14) especially when the core is thick. In some cases almost no absorption can be found at the mid portion of the central core (Photo 15), and on rare occasions, the core is difficult to recognize (Photo 16). However, this does not mean the absence of the core. Namely, Photo 23 shows the matched cut surface of the trabecula seen in Photo 16. The part which is thought to correspond to the central core can be recognized as a shallow depression, and is not a hollow cavity but filled with some substances. The core shown in Photo 17 is shifted from the central position. Such a case is rarely found. Trabeculae with elongated central cores are illustrated in Photos 18 to 20. Usually, the elongation occurs in the axial direction of the host cell, however, on rare occasions, it orients nearly at right angles to the axis (Photo 20). Since the outlines of the trabeculae shown in Photos 18 and 19 are slightly elliptic, they are thought to be intermediates to the plate. Photo 24 shows the matched cut surface of the trabecula seen in Photo 18. The elongated central core is clearly shown in different texture. The core often assumes a more or less irregular shape near the base of trabeculae as seen in Photo 21.

Photos 25 a, b and 26 a, b show thick trabeculae in well-developed compression wood tracheids. The central core of the former assumes an elongated shape orient-ing at right angles to the direction of microfibrils. Occasionally, the core contains intercellular spaces as shown in Photos 26 a, b. Although the length of the space along the axis of this trabecula cannot be inferred from the photograph, it would be a similar structure to that shown in Photo 9. The cores found in well-developed compression wood tracheids are often thick or show a certain degree of irregularity.

In these photographs the presence of the S1 layer around the core and that of spiral grooves are clearly illustrated. The grooves in the cell wall of compression wood tracheids are known to reach the S2 (L) layer (CÔTÉ *et al.* 1968). The photographs demonstrate that this is also the case in the wall of trabeculae.

Occasionally, the wall of a trabecula is found to be fused with a radial wall of the host cell. As stated above, the central core of the trabecula should not be confluent to the radial middle lamella. In such a case, however, it is practically impossible to confirm this from an observation on the radial surface, and this can only be solved by the observation on the cross section of the structure. Since a structure shown in Photos 27 a, b has a central core separating from the radial middle lamella, the structure is judged to be a trabecula.

From the facts obtained in the present study, it is concluded that the wall of trabeculae consists of the same layers with those of the host cell. However, the central core showed a slightly different nature from the middle lamella, namely, it usually has more or less weaker UV-absorption. The supply of lignin precursors would be in short for the core. The smaller dimension of the core may be responsible for the lower absorption.

The wall and the central core of trabeculae have been thought to be identical with or to be similar to the wall and the middle lamella respectively by many workers (*e. g.*, MÜLLER 1890, RAATZ 1892, SCHNEIDERS 1934, 1938, KEITH 1971, OHTANI 1977, KEITH *et al.* 1978) except for BALBACH (1939). He concluded that the wall of trabeculae is little lignified, and that the central core does not contain lignin and is gummy in nature from detailed observations on fresh materials of *Vitis*. The reason which led him to such a different conclusion remains to be solved.

A relation between the diameter of a trabecula and the wall thickness and width of the host cell was suggested by OHTANI (1977) in hardwood species. BUTTERFIELD and MEYLAN (1979) reported also a linear relation of the diameter of trabeculae to the host cell wall thickness. However, beyond the general agreement that trabeculae are thin in earlywood and thick in latewood (MÜLLER 1890, RAATZ 1892, RECORD 1934), it is not necessarily so, and MÜLLER-STOLL and BALBACH (1939) and MÜLLER-STOLL (1965) denied any correlation between the width of trabeculae and the wall thickness of the host cell. From the present observation (Photos 12 b, 13 b, 14 to 21 and 25 b to 27 b) it can be said that the width depends not only on the thickness of the host cell wall but also on that of the central core, unless the trabecula is abnormal (see Abnormal forms), and that the above mentioned relation suggested by OHTANI (1977) and BUTTERFIELD and MEYLAN (1979) is available only when the core is relatively thin as compared with the total thickness of the trabecula.

ii) *Plates*

The plate denotes a structure plank- or plate-like in form traversing the cell lumen radially (Photos 28 to 36). It differs from the trabecula only in that it is not round but considerably or highly elliptic in cross section. This form is the

most common and definite structure other than the trabecula. The width or height of the plate varies widely, and the plate sometimes develops into an extraordinarily wide form as shown in Photo 104. All intermediates were found between the plate and the trabecula or adhesion. In most cases, plates are found as a solitary or twin form, however, they occasionally constitute a very long row (Photo 104). A long row of trabeculae often begins with a plate, decreasing its width to alter into rod-shaped trabeculae (Photos 105 and 106).

Photos 28 and 29 show the typical form in a normal and two transitional tracheids between normal and compression wood respectively. The inner most layer in the former is the S3 and that in the latter is the S2. The orientations of both the layers on plates are apparently parallel to those of the respective layers seen on the host cell wall. However, near the margins of the plates the microfibrils of the S2 layer run in a more or less similar way to that found in rod-like trabeculae making depressions at their bases (arrows). In narrow ones such as shown in Photo 32, the orientation of the S2 layer is a little greater than that of the host cell. In compression wood the degree of development of spiral grooves on the plate is similar to that found on the host cell wall. As already mentioned, the materials examined in the present study showed no significant difference in the microfibrilar angle between normal and compression wood, and therefore, the orientation in the S2 layer of plates in normal wood (e. g., Photo 28) can be thought to be similar to that found in compression wood (e. g., Photos 29, 32 and 33).

Photos 30 a–c show transverse views (a by SEM, b by UVM and c by PLM) of a plate (tangential views of the host cell). Apparently, the plate has no continuity to the radial wall. UV-absorption and the birefringence of the plate are similar to those of the walls of the host and neighboring cells. The central core of the plate does not assume a fine filament-like structure as in trabeculae but a thin plate, which seems identical to the middle lamella. The occurrence of such a form of the central core strongly stands against the fungal theory proposed by JEFFREY (1917) and HALE (1935) as to the origin of trabeculae. In the cross section of plates the central core sometimes widens at its ends as reported by RAATZ (1892). Longitudinal views of a plate (transverse views of the host cell) are shown in Photos 31 a–c. Here also no difference can be found between the plate and the host cell wall in the strength and distribution pattern of UV-absorption, birefringence and the texture of the cut surface. If the matched SEM-photograph were not available, we could not realize that it is not a cell wall between two adjacent tracheids but a plate-like structure interposed in the tracheid. Since the plate is situated in the transitional zone from normal to compression wood, the tracheids at right show strong and characteristic UV-absorption typical in this zone (YUMOTO et al. 1982 b).

Photo 32 illustrates a narrow plate on which minute compression failures are seen orienting nearly perpendicular to the direction of each rib as is the case of trabeculae (Photo 2). The plates seen in Photo 33 are the widest of those observed by SEM during the present study. Photo 34 shows a cross section of a plate in a well-developed compression wood tracheid. The texture of the cut surface is

similar to those of the host and neighboring tracheids as in normal wood (Photo 30 a). The distribution pattern of UV-absorption of this plate was also similar. The central core of this plate shows a slight sigmoid curve. The core of such a shape was also found in plates in normal wood tracheids. Photo 35 represents twin plates found in the transitional zone from compression to normal wood. A similar case is illustrated in Photos 36 a, b. These tracheids show particular features of this transitional zone (YUMOTO, to be published). They have characteristics of both normal and compression wood tracheids, i. e., the presence of the S3 layer, lack of the S2 (L) layer, slight roundness in cross section and the occurrence of intercellular spaces.

From these facts it is strongly suggested that plates are composed of the same layers with those of the host tracheids as is the case of trabeculae. The occurrence of all intermediates between trabeculae and plates would imply that these two types belong to the same category. The affinity between trabeculae and other types will be closely discussed in General discussion.

The plate has not been reported in recent papers except for KEITH et al. (1978) and WERKER and BAAS (1981) (FUJIKAWA and TAKAOKA independently observed plates in Abies sachalinensis; personal communications). WERKER and BAAS reported the occurrence of the plate in the wood of Inula viscosa. Although MÜLLER (1890) and RAATZ (1892) illustrated very wide plates, the occurrence of this type has not been mentioned in the studies on Vitis (e. g., MÜLLER-STOLL and BALBACH 1939, BALBACH 1939). Probably, this came from the fact that their observations were largely made on cross sections in which plates give a similar image to that of trabeculae. The formation of plates cannot thought to be evoked by the longitudinal extension of trabeculae because of the limited longitudinal growth during the differentiation in gymnosperms.

iii) Confluences

The confluence denotes a rod- or plank-like structure confluent to a radial wall of the host cell (Photos 37–40). The confluence is not a mere fold of cell wall but has a central core. The central core of the confluence is connected with the radial middle lamella along its entire length. Narrow confluences can be distinguished from folds of cell wall or fused trabeculae only by an observation on their cross sections (c.f., Photos 27 a, b). It should be noted that in SEM-observation on radial surfaces the presence of an underlying ray tracheid occasionally gives an impression as if there were a confluence. The width of the confluence or the length from the radial wall varies considerably. The occurrence of this form was not rare. The confluence was, in most cases, found as solitary but twin or long files were occasionally observed. A pit-like structure (see later) is often found at the tip of the confluence.

Photos 37 and 38 show the typical form of the confluence in compression wood tracheids (the former is situated in the transitional zone from normal to compression wood). The orientations of the microfibrils in the S2 layer of these confluences are the same with those of the host cells except near the tips or margins of the

confluences as is the case of plates.   This would be also the case in the confluence in normal wood tracheids.   Cross sections of confluences (tangential sections of the host cells) clearly show that they are not simply attached to the parent radial wall but are essentially fused to it (Photos 39 a–c and 40 a–c).   Apparently, the central cores of the confluences are confluent to the middle lamella.   The texture of the cut surface, strength and distribution pattern of UV-absorption and the bire-fringence are quite similar to those of their host and neighboring cells as is the case of the plate.   From these facts it can be said that they are also composed of the same wall layers with those of the host cells, and that their structure is the same with that of plates except for the confluency to the radial wall.   In Photos 39 a–c the tip of the confluence is somewhat round in accordance with the widened central core.   MÜLLER (1890) observed a similar case.   Occasionally, the confluence is found to be bent back (Photos 40 a–c).

Although the occurrence of confluences is reported by MÜLLER (1890) and RAATZ (1892), it is not mentioned not only in recent works but also in the vini-cultural literature.   This structure might have been considered to have no relation to trabeculae.   In the case of vinicultural literature this would also come from the fact that their observations were mostly made on cross sections of the samples as is the case of plates.

From the observation on macerated tracheids there seem two different types of confluence, i. e., the true confluence and the tangential branching of tracheids (YUMOTO, unpublished).   The intervened double wall between the tangential branches of such a tracheid assumes a similar appearance to the confluence.   The tangential branching of tracheids is reported to be formed by the tip growth of the neigh-boring initials in the cambium by some authors (NEEFF 1922, WŁOCH 1976).   Long filies of confluences might belong to such a category.   On the other hand, the true confluence gives an impression as if it were formed by an abortive pseudo-transverse cell division.   The origin of this and other types will be discussed in General discussion.

iv) *Adhesions*

The adhesion denotes a wall-pinch-like structure, or a contact of both the tan-gential walls within a cell (Photos 41 to 48).   The central core of the adhesion can be said to be shortened and widened into the middle lamella between the tracheids situated immediately on the pith and cambial side of the host cell.   Adhesions are usually found at one of the tangential sides of a tracheid, though they can occur in the middle of the host cell (when observed in cross section) leaving two canal-like lumens on both the tangential sides of the adhesion.   All intermediates can be found between the adhesion and the trabecula, plate or confluence.   If an adhesion is streched radially, they become one of these basic types.   Although adhesions generally occur in solitary form, they were occasionally found in a twin form (Photo 44), or often occur in two or more adjacent tracheids slightly deviated in height (Photo 45).   In the early-earlywood affected by late frost they were especially abundant and often found intermingled with other types (Photo 111).

Photos 41 and 42 show typical adhesions found in normal wood tracheids. If the adhesion in Photo 42 were planed more deeply, it would give a similar appearance to that shown in Photo 41. Photo 43 illustrates a stretched adhesion. Since a depression is seen (arrow), it may be an intermediate to the confluence.

Photo 44 illustrates a twin form in well-developed compression wood. The middle lamella between the tracheids at right and left, *i. e.*, the "central core" of the adhesions, is very thick giving a different texture from the secondary walls. Such a "row" of adhesions was also reported by RAATZ (1892). Three adhesions occurring in the close vicinity are illustrated in Photo 45. Adhesions often occur making such a loose group.

Photos 46 to 48 a, b show adhesions on the tangential surface. In Photo 46 a trabecula is seen immediately adjacent to the adhesion. A similar case was illustrated by RAATZ (1892). An adhesion in contact with a ray is shown in Photo 47. The one seen in Photos 48 a, b is believed to be an intermediate to the confluence because of the presence of an invaginated part (arrow). In Photo 48 b a thick mass of the middle lamella or the central core is clearly shown. Thus the adhesion is a wall-pinch-like structure, and there would be no objection to the view that it is a part of the host cell wall.

RAATZ (1892) also observed all intermediates between adhesions and trabeculae, and claimed that trabeculae are formed from adhesions by stretching. Although MÜLLER (1890) did not distinguished the adhesion, some of the folds of the radial wall he described (Figs. 8 and 9 in Taf. XIV) are apparently identical to the adhesion. Adhesions have not been reported by other authors to my knowledge. Probably, they have been, even if observed, regarded merely as an abnormal feature.

v) *Tangential confluences*

All the structures mentioned above traverse the cell lumen radially. However, confluences orienting in the tangential direction were found (Photos 49 to 56). Tangential trabeculae or tangential plates have not been observed. There seem to be no structural differences between radial and tangential confluences except their orientation. They were all found near or at the tip of tracheids. A row of tangential confluences, which is expected, if any, to be found in tangential sections, was not observed. The tangential confluence often included a pit-like structure as is the case of the radial confluence.

Photo 49 illustrates a tangential confluence found near the tip of a mild compression wood tracheid. It should be noted that the surface seen is not the tangential but the radial. It highly resembles radial confluences. A similar one with a pit-like structure in a normal wood tracheid is shown in Photo 50 and its enlargement in the next photograph. As will be seen, this pit-like structure is quite similar to those found in the radial confluence. A possibility that this structure might be a tangential "trabecula" was denied by the observation on the same sample rotated in a 180-degree arc on the specimen holder. Photo 52 illustrates a tangential confluence in a well-developed compression wood tracheid. A similar

confluence with a pit-like structure is shown in Photo 53. In contrast to the confluences shown in Photos 49 and 50, they give an impression that they were developed from folds of cell wall formed by some physical forces. Occasionally, the tangential confluence is found at the tip of the tracheid (Photo 54).

Tangential confluences were also found in ray tracheids (Photos 55 and 56). This confluence closely resembles the radial confluences with pit-like structures shown in Photos 59 a-c and 60 a-c. The occurrence of radially oriented trabeculae in ray cells were reported by OHTANI (1977) and WERKER and BAAS (1981) using SEM.

Since the SEM–UVM combination method was not applied for the observation on the tangential confluence, its behavior under an UVM and the relation between the behavior and its three-demensional structure were not disclosed. However, from the facts presented above it can be concluded that it is also a part of the host cell wall.

Tangential confluences have little been reported, at least, in relation to tra-beculae. However, RAATZ (1892) mentioned the occurrence of folds near the tip of tracheids (*i. e.*, tangential confluences), some of which had bordered pit-like structures. In addition, SCHULZ (1882) observed tangentially oriented bars in the tracheids immediately adjacent to rays in the wood of some pine species. However, according to RAATZ (1892), he probably took resin plates for trabeculae. A similar bar orieted in the tangential direction was reported as a trabecula by WINKLER (1872). Since this bar is drawn to be attached to a ray, it could really be also a resin plate. PENHALLOW (1907) stated that the dark resin plates closely resemble SANIO's bands, for which they might very readily be mistaken upon casual observation.

Other than these short tangential confluences found at or near the tip of tracheids, considerably long ones in the middle of tracheids were also observed light microscopically (Photos 128 to 130). Trabeculae (Photo 129 arrow), adhesions (Photo 128 arrow) or confluences (Photo 130 arrow) were found associated with these long tangential confluences. These structures give an impression that they are somewhat different from the above stated short tangential confluences in nature, and it seems rather adequate to call them the "radial branchings" of tracheids.

III) Varieties

i) *Pit-including form*

The pit-including form denotes a trabecula, plate, confluence or tangential confluence with a pit-like structure (Photos 57 to 70). The pit-including form is mostly the confluence. No trabecula with a pit-like structure was observed during the present study, though it was reported by RAATZ (1892), MEYLAN and BUTTERFIELD (1973) and WERKER and BAAS (1981). The pit-like structure was found at the margin of plates or at the tip of confluences. The size of the pit-like structure considerably varies from small slits to big gaps. The pit-including form is usually found as solitary. However, this form can constitute a row as shown in Photos 63, 64 and 117. All intermediates between malformed bordered pits and the typical pit-like structures were found.

Photos 57 and 58 show confluences with a big pit-like structure and a small slit-like one respectively. In the latter a half of a thick trabecula is also seen on this side of the pit-including confluence. Cross sections of the pit-including forms (tangential sections of tracheids) attached to the cross field in normal and mild compression wood tracheids are illustrated in Photos 59 a–c and 60 a–c. The form and the lignin distribution pattern highly resemble those of the bordered pits. A pit-membrane-like structure is also seen between the "borders". A torus-like thickening is often found at the middle of the outer margin of the membrane (Photos 60 b arrow, 66 and 69). The torus-like structure shows no appreciable UV-absorption in accordance with the fact that lignification of tori had not occurred in the specimens examined in the present study.

A plate with a pit-like structure is shown in Photo 61. This is an isolated instance of the pit-including plate during the present observation. Occasionally, pit-including form is found near the tip of tracheids (Photo 62). Twin forms in normal and well-developed compression wood are shown in Photos 63 and 64 respectively. The opposite view (observation on the same structure rotated in a 180-degree arc on the specimen holder) of the right one in the latter photograph is given in Photo 70, and that of the left one was rather a deformed bordered pit similar to that shown in Photo 65. Intermediates between these two are represented in Photos 66 to 69.

Whether these pit-like structures are really ontogenetically homologous to the bordered pits has been a matter of controversy. RAATZ (1892) observed this form and thought that the structure is in fact the bordered pit. He found also a small split-like structure in a rod-like trabecula and stated that this is identical to the pit found in the end wall of strand tracheids. MÜLLER-STOLL (1965) noted trabeculae with splits in *Picea abies* and doubted RAATZ's interpretation that the split is a trace of the bordered pit of the end wall of strand tracheids. He also observed branched trabeculae in *Picea abies* and regarded them as extreme cases of the splitting. However, judging from Abb. 12 in his paper, he possibly observed similar pit-including forms to those seen in the present study, though lines corresponding to the pit-membrane-like structure are not illustrated in his figures. Branched trabeculae are also reported in *Vitis* (MÜLLER-STOLL and BALBACH 1939).

More recently, MEYLAN and BUTTERFIELD (1973) reported a trabecula with a vestured-pit-like structure in a vessel member of *Fuchsia excorticata*. Since vestures around the pit aperture are well demonstrated in their figures, the trabecula is thought to have unequivocally a vestured pit. Although WERKER and BAAS (1981) reported the occurrence of trabeculae with pit-like structures, they did not discuss whether the gaps are really pits or not.

In the present study it was shown that the pit-like structure has a similar structure to the bordered pits, and that its behavior under an UVM also quite resemble that of the bordered pits. From this and the occurrence of all intermediates from malformed bordered pits to the pit-like structures in question, it is concluded that the pit-like structures are in fact homologous to the bordered pits.

The pit-including form observed in the present investigation has only one opening. The pit aperture is transformed into a more or less slit-like opening, and the pit membrane is cut into a half and turned 90 degrees round the cut surface. However, RAATZ (1892) illustrated a wide confluence with 4 bordered pit pairs found in *Araucaria imbricata*, each of which assumes normal bordered pits and opens to both sides of the confluence. WERKER and BAAS (1981) also found plates with well-developed bordered pits in those within vessel members in *Inula viscosa*.

ii) *Abnormal forms*

Abnormal form denotes the trabecula, plate, confluence, or tangential confluence deviating from the normal in some features. Whether a structure is regarded as abnormal or not depends on the degree of the deviation. Several kinds of abnormality can be distinguished, *i. e.*, abnormalities in shape, those in cell wall deposition and those in the shape of the central core. Although compression failures are sometimes found on the surface of trabeculae and their related structures (Photos 2, 3, 32 and 38), this feature is not listed as abnormality in the present study.

A plenty of abnormal forms were observed by light microscopy and SEM. Since features of abnormalities cannot be well demonstrated by ordinary light microscopy, attention will be focussed on the SEM- and UVM-observation.

Photo 71 shows a curved trabecula in a mild compression wood tracheid. This is a solitary instance of continuous (not disconnected) trabeculae curved in the horizontal plane. However, in vessel members of *Vitis* (MÜLLER-STOLL and BALBACH 1939) curved trabeculae were reported to occur abundantly especially in side shoots where they exceeded normal forms in number, and MÜLLER-STOLL (1965) reported that trabeculae in *Sorbus aucuparia* were mostly curved in the vessel members but straight in wood fibers. He thought the abundant occurrence of curved trabeculae in vessel members would be a result of the drastic dimensional change during the differentiation. Since the dimensional change is limited in conifers, this may explain the scanty occurrence of curved trabeculae in the materials examined in the present study, though MÜLLER-STOLL (1965) reported their occurrence in *Picea abies*. According to MÜLLER-STOLL and BALBACH (1939), the curvature usually occurs in the horizontal plane (Photo 71). However, it occasionally curves longitudinally as shown in Photo 72. The curvature is not thought to be an artefact brought about during the specimen preparation. If certain forces had been applied to trabeculae after they matured, they would have been broken as shown in Photo 73. Curved trabeculae were also reported by other investigators (*e. g.*, MÜLLER 1890, SCHNEIDERS 1938, BÄRNER 1937 b, BALBACH 1939).

Disconnection is one of the most common abnormalities (Photos 72 to 75, and 77). Disconnected forms seem to be relatively rich in number in long rows of trabeculae. Disconnected plates have not been observed. Generally, a disconnected form consists of two stub-like structures projecting from both the tangential walls facing to one another, and the tips of the stubs are equipped with irregular protuberances. However, sometimes one of the stubs is missed and instead a small

cavity is seen as shown in Photo 75.   Disconnected forms have been reported by many earlier workers by light microscopy (e. g., MÜLLER 1890, RAATZ 1892, MÜLLER-STOLL and BALBACH 1939, MÜLLER-STOLL 1965).   They thought that the disconnection would occur during the phase of surface extension of the host cell.

Abnormal trabeculae caused by insufficient or irregular cell wall deposition are illustrated in Photos 76 to 82.   This kind of abnormality was found mostly in trabeculae.   Photo 76 shows a case in which wall materials are deposited round the more or less whole central core.   However, such a case is relatively rare and in most cases partly no material is deposited showing a central-core-like filament. The surfaces of such forms have deformed (Photo 77) or spiny protuberances (Photos 79 to 81), or minute pores (Photo 78).   This type of abnormal trabecula can be formed in the close vicinity of normal ones as shown in Photo 79.   The orientation of the microfibrils in the S2 layer of these trabeculae is difficult to recognize.   Similar abnormal forms were reported by KEITH (1971) using SEM and PLM, and judging from his PLM-photograph, the orientation seems to be also irregular.   Photo 82 shows an extreme case in which a very small quantity of wall material is deposited only round the mid portion of the central-core-like filament. This abnormal trabecula composed a row with other three abnormal ones (Photos 78 and 81).   The thin central-core-like filament emerges from and come into a hollow or cavity.   Such cavities are generally observed when little wall material is deposited near the base of trabeculae as shown in Photos 78 to 82.   In Photos 79 to 82 the central-core-like filaments are broken.   This implies a fragile nature of the filaments, though whether the breaking had occurred during the specimen preparation or not was not ascertained.

A transverse section of a similar abnormal trabecula in a mild compression wood tracheid is shown in Photos 87 a, b.   In the matched UV-photograph a dark spot in the center of its cross section (central core), a ring of lower absorption around the core (S1 layer) and outer dark ring of the S2 layer are recognizable.   In contrast to the normal trabeculae shown in Photos 12 to 21, 25 and 26, the wall of this trabecula is quite thinner than that of the host cell.   From this UV-photograph the dark spot is measured to have a diameter of less than 0.5 micron, and therefore, the thin thread of ca. 0.4 micron in diameter seen in SEM-photograph is thought to be the central core itself.   The core seems to be composed of several thin units, though such a unit was not observed in other cases. The cross section of a similar abnormal form is also seen in Photos 98 a, b.

Photos 83 to 85 show an abortive trabecula and plate.   The host cell seems to have been dead in the early stage of cell wall formation.   The amorphous material on the middle of the bar would be the debris of cell contents.   Since almost no secondary wall was formed as shown in Photo 84, which is also supported by the shape of the bordered pits seen in Photo 83, the central cores of trabeculae and plates would take such shapes respectively.   Both increase their width towards the tangential walls.   A structure with irregular wall deposition is illustrated in Photo 86.   It is probably a confluence, though might be a mere fold

of the cell wall. Various abnormal forms which thought to be caused by the partial or irregular wall deposition have been reported using light microscopy (MÜLLER 1890, RAATZ 1892, MÜLLER-STOLL and BALBACH 1939, BALBACH 1939, MÜLLER-STOLL 1965).

In the abnormal forms above mentioned the diameter of the central core does not seem to differ so markedly from the normal, however, it often develops into an abnormal thickness and/or shape. Generally, thick trabeculae have thick central core, even if the trabecula is normal (Photos 13 b, 14, 18, and 19). The central core of extremely thick trabeculae are often abnormal in form as shown in Photos 88 a–c. This trabecula is thought to be an intermediate to plates or confluences. The intensity of UV-absorption of such a thick central core is always the same with that of the middle lamella. The thickness of the secondary wall varies round the circumference of the core.

Abnormalities of the central core were often observed also in plates and confluences. Photos 89 a–c show a confluence with an abnormally thick central core. Here, the central core assumes thick mass showing the same intensity of UV-absorption and the same texture of the cut surface with those of the middle lamella. Similar abnormal confluences were also reported by MÜLLER (1890) and RAATZ (1892).

Other than the structures above described, each of which is recognizable as one of the basic types, more complicated cases were recorded. In Photo 90 some of the structures can be recognized as abnormal trabeculae (Photo 90 arrow, and 93) or plates (Photo 91) but others (Photo 92) are amorphous and difficult to classify into the basic types. The host is seemingly two but actually an anastomosed tracheid. Similar or related cases were also observed by light microscopy, and are shown in Photos 123 to 127. Plates and amorphous structures stretching over the seemingly two tracheids are seen in Photo 124 and 126, and Photo 125 respectively. Since the occurrence of this type of abnormality seems to be intimately associated with the formation of trabeculae, it will be mentioned later again.

In addition to the SEM- and UVM-observation, many abnormal trabeculae were also found by light microscopy. A barrel-like form with an uneven surface, two club-shaped stubs extending from a common double wall, a disconnected form with spiny projections and a rod-like one with a small cavity, etc. were observed. A few examples are shown in Photos 120 to 122. Since external structure of abnormal forms cannot be closely studied by ordinary light microscopy, no further description will be made here.

IV) Patterns of the occurrence

In the materials examined in the present study, the occurrence of trabeculae and their related structures was relatively abundant on the whole. However, they were especially rich in number in two regions of the xylem as stated above, *i. e.*, early-earlywood affected by late frost and in the transitional zone from compression to normal wood formed by the interruption of the geotropic stimulation. The pattern of the occurrence differed between these two regions. In the former adhe-

sions were abundantly found and long rows of trabeculae were not rare. On the other hand, in the latter the occurrence of the adhesion was not so abundant, and trabeculae were frequently observed in a short row or solitary form. Confluences were also rich in number. In the transitional zone from normal to compression wood, the occurrence of trabeculae and their related structures was also relatively abundant.

In most of standard textbooks on wood anatomy photographs of long rows of trabeculae are illustrated, however, short-row and solitary trabeculae have been reported repeatedly since the first observation of trabeculae in sections (WINKLER 1872). MÜLLER (1890) classified "Sanio'sche Balken" into three types, *i. e.*, trabeculae in row, twin trabeculae and solitary ones. In the present study latter two were especially abundant, and plates and confluences were found to occur mostly in a short row or a single form with a few exceptions. The length of a row is thought to depend on the position at which its primordium is originated; if it originates in the cambial initial, a long row of trabeculae extending from the cambium towards both the phloem and xylem would continue to be formed until the initial matures or the primordium is eliminated for some reasons; if it originates in a xylem mother cell, a short row or a solitary trabecula would be formed only in the xylem.

In a row of trabeculae each unit often shifts tangentially or vertically to some extent (Photos 106 and 108), as reported by many workers (MÜLLER 1890, RAATZ 1892, MÜLLER-STOLL and BALBACH 1939, MÜLLER-STOLL 1965, KEITH 1971, OHTANI 1977). The shift is thought to be brought about by the growth of the host cell or by the spatial adjustment among cells during the differentiation. This would explain relatively scanty occurrence of long rows in hardwoods (RAATZ 1892, MÜLLER-STOLL 1965). The orientation of a unit in a row has been reported to often deviate obliquely in the vertical plane (MÜLLER 1890) and in horizontal plane (MÜLLER-STOLL and BALBACH 1939, MÜLLER-STOLL 1965). However, in the present study, only one abnormal trabecula showed the deviation in the horizontal plane (Photo 76).

A long row of trabeculae often begins with a plate as shown in Photos 105 and 106, and as reported by MÜLLER (1890) and RAATZ (1982), though plates occasionally occur also in the middle of the row (Photo 107). Two long rows of plates are illustrated in Photo 104. Since the section is cut slightly obliquely to the radial longitudinal plane, the exact length of these rows could not be ascertained. However, the neighboring sections, though not exactly serial, proved that the rows are more than twice the length of those shown in Photo 104. The occurrence of such a long row of plates was very rare.

Occasionally, a few rows of trabeculae run in parallel to each other being close together. Photo 99 shows three rows of trabeculae in typical compression wood running in parallel; one emerges from the radial wall (right to left), one is almost embedded (thick arrow) and the other is almost planed off leaving its fragments (fine arrows). A similar case in normal wood is shown in Photo 108. Such

a pattern of the occurrence was also reported by Müller (1890), Raatz (1892), Schneiders (1938), Bärner (1937 b), Gärtel (1954), and Werker and Baas (1981). In Photo 99 one of the rows emerges from the radial wall towards the cambial side (left). In another case a row was found to disappear into the radial wall towards the same direction. Müller (1890) reported a similar case to the latter, but Raatz (1892) claimed exclusive occurrence of the former disputing Müller's observation. In the region where the longitudinal orientation of tracheids is not perpendicular to the orientation of rays, when observed in a radial section, trabeculae does not run at right angles to the longitudinal wall of the host cells but run in parallel to that of rays (Photo 110).

Other than short rows of trabeculae, those composed of a few different types were often found. SEM-photographs of such cases are shown in Photos 94 to 96, in which twin forms comprising a trabecula and a pit-including confluence (Photo 94) or a plate (Photo 95), and a short confluence (might be a mere fold of cell wall) and an adhesion (Photo 96) are seen. A light microscopic observation provided further instances. In Photo 114 five plates differing in width and an adhesion make a common row. A row composed of two trabeculae and two plates (Photo 115), a row of a pit-including confluence and two plates (Photo 116), a row of a trabecula and two or one pit-including confluence (Photos 117 and 118), and many other cases were observed. Raatz (1892) also illustrated similar heterogeneous rows.

Short rows and solitary forms were found frequently to occur making a loose group. Müller (1890) made a similar observation especially in *Araucaria brasiliana (brasiliensis)*. Photos 100 to 102 show such a pattern of the occurrence by SEM. In Photo 100 five trabeculae and three confluences are seen in solitary or twin form. Photo 101 shows a similar case in which two trabeculae, a plate and an adhesion are found in a limited area. In Photo 102 rows of abnormal forms which are also shown in Photos 78 to 82, and two adhesions are illustrated. Light microscopy is more suitable to show this type of occurrence. Photo 111 illustrates abundant occurrence of adhesions in early-earlywood affected by late frost (arrow). Although such a feature is common in this zone, it is not restricted there and occasionally found in not affected regions (Photo 112). While, in Photo 113 many plates, some of which are very wide, are seen instead of adhesions. Such massed occurrence of the plate was not common.

A few different types except tangential confluences were often found in the close vicinity in a tracheid. In Photos 98 a, b a rod-like trabecula, a plate and an abnormal trabecula are seen. Such a pattern of the occurrence was not rare and suggests that they did not occur haphazard but were formed through a common cause. Butterfield and Meylan (1979) reported several unusual trabeculae occurred close together in a vessel member of *Fuchsia excorticata*. A similar pattern of the occurrence is known also in *Vitis* (Bode 1938, Müller-Stoll and Balbach 1939).

Several trabeculae or related structures except tangential confluences were

sometimes observed in a cell leaving relatively narrow space (not in the close vicinity as those shown above). Photo 109 shows four pairs of plates aligned in two tracheids leaving almost the same intervals. Similar cases were reported by MÜLLER (1890) and RAATZ (1892), and TAKAOKA observed in *Abies sachalinensis* six rows of trabeculae arranged in almost the same intervals giving a ladder-like appearance traversing the lumina of four tracheids (personal communication).

Many solitary or short-row trabeculae and their related structures except tangential confluences were often found to occur sporadically aligned in the radial direction with intervals of a considerable distance through a number of tracheids. An example is shown in Photo 103, in which five trabeculae, two plates, two adhesions, and a confluence are aligned in a solitary form or making short rows. This implies a genetical tendency of a particular cambial initial liable to form the primordium of trabeculae. MÜLLER-STOLL and BALBACH (1939) suggested a similar genetical difference of the cambial initial based on the study of the distribution of trabeculae in cross sections obtained along branches of *Vitis*.

Trabeculae and their related structures were occasionally found associated with the anastomosis (Photos 90 to 93 and 123 to 127) and branching of tracheids (Photos 128 to 130). In the former case amorphous structures are also observed (Photos 92 and 125). The branching of tracheids seems to occur in relation to frost injuries, but in the case of the anastomosis surrounding tracheids and other part of the host cell showed entirely normal features. In either case the host cell seems to have failed to complete cell plate formation. Since the occurrence of such cases were rare, it might be abnormal in nature, however, as will be stated, abnormal cell division seems to have an intimate relation to the occurrence of trabeculae and their related structures.

Close by trabeculae and their related structures except tangential confluences, abnormal tangential pits were often formed (Photos 97, 100, 111 to 113 and 127). They have a similar size to the radial bordered pits, and are apparently different from the tangential pits found near the growth ring boundary which are smaller in diameter (LAMING and TER WELLE 1971, KORAN 1977). According to GREGUSS (1955), in *Picea glauca* tangential pitting is present in all longitudinal tracheids throughout the growth layer. In fact during the present study, small tangential pits were occasionally found even in the middle of the growth ring. However, the tangential pits in question is large in size, and the formation of such tangential pits seems to have a causal relation to that of trabeculae and their related structures.

General discussion

I) Mutual relationships among trabeculae and their related structures

In the strict sense the mutual relationships can only be verified by studying the cause of their formation. Apparently, this lies beyond the sphere of the present study. However, the cause can be speculated from the facts presented in this and other studies, and the relationships could be substantiated indirectly by some different ways. The one is based on the concept that if all intermediates

are found between two seemingly different types, these two would be identical in their nature. Although this idea is a basic concept of morphology, it could not deny thoroughly a possibility of confusing ontogenetically different ones. Another comes from the assumption that if two types occur together in the close vicinity, they would be arisen through the same cause, if not haphazard. When several different types are aligned constituting a common row, it can be permitted to assume that they are formed from the same origin, and therefore, fall under the same category. The structural affinity between different types may also strengthen their relationship.

Pit-including and abnormal forms are thought to be varieties of basic types, *i. e.*, trabeculae, plates, confluences, adhesions and tangential confluences. The structure of the pit-including form seems not to differ from those without the pit other than the occurrence of the pit-like structure. Abnormal forms are variable in structural features. However, those shown in Photos 71 to 83 and 87 a, b apparently belong to trabeculae, those in Photos 86 and 89 a–c are malformed confluences, and those in Photos 85 and 88 a–c are plates or thick trabeculae. Therefore, whether the pit-like structure and/or abnormalities are present or not is a foreign matter to the relationship.

The mutual relationship between trabeculae and plates is apparent, because all intermediates have been found between these two types, and also because these two types often constitute a common row (Photos 95, 105 to 107 and 115). Plates often occur in a tracheid together with other types in the close vicinity (Photo 98 a, b). The fact that the central core of trabeculae has a variable strength of UV-absorption might seem to stand against the structural affinity with the plate in which the core ordinarily shows strong absorption comparable to that of the middle lamella. However, it would be rather due to the smaller dimension of the core of trabeculae, because thick cores generally have strong UV-absorption.

Confluences also occur in the close vicinity to trabeculae in a tracheid (Photo 46, RAATZ 1892), and make a common row with trabeculae (Photos 94, 117 and 118) or plates (Photo 116). MÜLLER (1890) reported the preferential occurrence of confluences at the top of the row of trabeculae. The central core and the walls of confluences are quite similar to those of plates in the texture of the cut surface, in the strength and distribution pattern of UV-absorption, and in the birefringence. Every intermediate can be found between confluences and adhesions (Photos 43, 48 a, b and 111 to 113). It should be noted here that confluences are probably ontogenetically different from branching of tracheids which has been reported to be formed by the tip growth of the neighboring cambial initials (NEEFF 1922, WŁOCH 1976). The cause of the formation of trabeculae and their related structures will be discussed closely in the following section.

Among adhesions, trabeculae, plates and confluences there are also all intermediate structures, which made RAATZ to propose his contact theory. Adhesions can make a common row with trabeculae or plates (Photos 112 to 114) and occur together with all other basic types except tangential confluences (Photos 101 to 103,

109, 111 to 113 and 127). Occasionally, an adhesion or adhesions lead a row of trabeculae. RAATZ (1892) illustrated a similar case.

Tangential confluences also show similarities to other types in wall structure and often include pit-like structures. However, they were found exclusively at or near the tip of tracheids and did not occur in the close vicinity to other basic types. The row of tangential confluences, which is, if any, expected to be found in the tangential section have not been observed. On the other hand, the long tangential confluence or the radial branching found in the middle of tracheids (Photos 128 to 130) are in many cases associated with the occurrence of adhesions (Photo 128), trabeculae (Photo 129) or confluences (Photo 130). This structure seems to be different from the tangential confluences found at or near the tip of tracheids and has many features common with the anastomoses of tracheids (Photos 90 to 93 and 123 to 127).

From above discussion, it is apparent that there are all intermediate structures among trabeculae, plates, confluences and adhesions, and that they often occur close together or in a common row. Therefore, these types are believed to have intimate ontogenetical relations to each other and to fall within a common category. In the further discussion, they will be referred to trabeculae and their "homologous" structures. On the other hand, the behavior of the tangential confluence is different from other types in many respects, and therefore, there is a good possibility that it belongs to another category. However, if it is formed by a similar cause or causes to those of trabeculae and their homologous structures, it should be thought that this type of structure also falls within the same category. The relationship between the tangential branching of tracheids and the confluence also hangs on the cause or causes of their formation, and the radial branching and anastomosis of tracheids seems to have an intimate causal relation to trabeculae and their homologous structures.

II) Cause of the formation of trabeculae and their related structures

1) *Tangential confluences and branchings of tracheids*

As stated above, tangential confluences show a different nature from trabeculae and their homologous structures in many respects. They were found exclusively at or near the tip of tracheids. The tip of tracheids is known apt to be distorted or bifurcated during the development especially in compression wood (MÜNCH 1940, WARDROP and DADSWELL 1952). Since the bifurcation occurs in the radial direction, the resultant confluence found at the base of the bifurcation is oriented in the tangential direction. The form of some tangential confluences such as those shown in Photos 52 and 53 suggests the involvement of certain mechanical forces. Therefore, these tangential confluences can be thought to be formed by the tip growth during the differentiation of the host tracheids. RAATZ (1892) also observed similar tangential confluences and ascribed their formation to the tip growth of the tracheid.

However, those illustrated in Photos 49, 50 and 54 show no trace of the involvement of mechanical forces and have quite similar structural features to the

radial confluences. Since the occurrence of such tangential confluences was rare in the present study, little information is available for consideration, and therefore, the cause of their formation and the relationship to trabeculae and their homologous strutures cannot be concluded.

The long tangential confluence in the middle of tracheids or the radial branching has similar features to the anastomosis of tracheids. The anastomosis might be a result of the lysis of the cell wall situated between originally two tracheids brought about by an activity of certain pathogenes. However, this seem not plausible, since no trace of the activity was observed in the surrounding cells and the remainder of the host cell. The anastomosis is rather well explained by an abortive cell division. This idea is also available for the radial branching. As will be mentioned later, the formation of similar branched tracheids was reported to be a result of incomplete cell plate formation (ZALASKY 1975 a, 1975 b).

On the other hand, the tangential branching which gives a similar appearance and might have a causal relation to the confluence was reported to be formed by the tip growth of the neighboring initials in the cambium (NEEFF 1922, WŁOCH 1976). The occurrence of intervened rays or tracheids between the branches they observed proves this possibility. WŁOCH (1976) thought that the folding of tracheids (i. e., confluences) would occur through the elimination of the intervened cells. However, this seems not available for the confluences found in the present study, since in no case such a previously intervened cell was observed. Therefore, the confluence is believed to have little relationship to the tangential branching formed by the tip growth of the neighbouring initials, though it might be possible that initials with the primordia of the confluence develop into branched ones in the course of their growth in the cambium.

2) *Trabeculae and their homologous structures*

i) *Hypotheses hitherto proposed*

Concerning the formation of trabeculae and their homologous structures, many hypotheses or theories have been proposed since the last century. Following factors have been thought as direct or indirect causes of the formation.

  1) Folds of the radial walls (i. e., confluences) (MÜLLER 1890)
  2) Contacts of the tangential walls (i. e., adhesions) (RAATZ 1892)
  3) Excretion bodies (X-bodies) (PETRI 1912 c)
  4) Fungal infection (JEFFREY 1917, HALE 1935)
  5) Infection of certain diseases (SCHNEIDERS 1934, 1938)
  6) Degenerated mitoses (BODE 1938)
  7) Low temperature (MÜLLER-STOLL 1965)
  8) Injuries (WERKER and BAAS 1981)

A brief review of these hypotheses is given in Historical.

The first two are based on the observation of matured cells. MÜLLER's fold hypothesis can be said to come from the structural affinity between trabeculae, plates and "folds" (see later). He thought that a type of "fold" (i. e., confluence) is different from plates only in that the former is fused with the radial wall, and

that if a plate reduces its height or width, it becomes identical with a trabecula. RAATZ's contact theory is based on the occurrence of all intermediate structures among trabeculae, plates and adhesions. He thought the formation of the partial contact of the tangential walls in a cell (*i. e.*, adhesion) could be brought about by some essentially different factors. Although RAATZ disputed MÜLLER's fold hypothesis, some of the "folds" in the tangential section illustrated by MÜLLER (Figs. 8 and 9 in Taf. XIV) are apparently identical to the adhesions reproted by RAATZ (Fig. 4 in Taf. XXVIII). Therefore, these two hypotheses are not essentially different but quite similar to one another The intimate structural and ontogenetical relation among trabeculae and their homologous structures was clearly demonstrated in the present study. However, there seems no reason to think trabeculae and its homologous structures are developed from confluences or adhesions, and it seems also possible that confluences and adhesions are on the same level with other types and formed by one or some common causes.

PETRI's theory is based on detailed observations of the cambial cells, however, the excretion bodies are at present regarded as X-bodies (*e. g.*, SCHNEIDERS 1957–1958), and if this is the case, it is difficult to believe that the primordia of trabeculae are originated from excretion bodies, because X-bodies are known to consist largely of virus particles (BAWDEN 1964). BODE's theory is based on a similar microscopic observation on the cambial cells. However, he failed to find the excretion bodies and reached an essentially different conclusion. As is the case of PETRI, it is practically quite difficult to disclose the course of the primordium formation in the cambial cells, because the formation cannot be observed sequentially on the sections from fixed materials.

The well known fungal theory proposed by HALE is based on only a few circumstantial facts as reviewed in Historical (JEFFREY only stated simply that the formation of trabeculae is probably due to the activity of parasitic fungi). This theory was probably arisen from a superficial resemblance between trabeculae and fungal hyphae and lacks in any experimental evidence. Although the fungal theory has been introduced in almost all the standard textbooks, following cases are difficult to explain by this theory; the exclusive radial orientation of trabeculae, the occurrence of wide plates, confluences and adhesions, and their preferential occurrence in the transitional zone from compression to normal wood. During the present study, furthermore, no trace of the fungal activity was observed. However, as will be mentioned, it might be possible that the proliferation of trabeculae is stimulated by a chemical agent or agents secreted from fungal parasites or produced through a complicated host-parasite interaction.

The concept that plants which contain trabeculae are all infected by certain diseases claimed by SCHNEIDERS lies beyond the verification, because it is impossible to prove the complete absence of trabeculae in a given plant, and also because whether a given plant is infected by an unspecified latent disease or not cannot be confirmed. At present no viniculturist agrees with this concept as stated in Historical.

The fact that the proliferation of trabeculae in *Vitis* infected by "Reisigkrank-heit" is stimulated by low temperature has been noted by many viniculturists (*e. g.*, PETRI 1912 c, JÖHNSSEN 1933, FUESS and SCHNEIDERS 1935). Involvement of unspecified climatic factors was already implied by RAATZ (1892) about a century ago. However, it is not clear whether low temperature itself elicits the prolifera-tion or frost injury caused by low temperature does it. WERKER and BAAS (1981) thought all injuries including that caused by low temperature enhance the forma-tion of trabeculae. However, why the proliferation of trabeculae occurs by low temperature or injuries is not stated by the authors.

ii) *Circumstantial evidence and a possibility of abnormal cell division as a cause*

As pointed by HALE (1935), trabeculae often seem to be associated with some structural abnormalities including wounds, and the proliferation of trabeculae is also known to be caused by the infection of certain diseases (*e. g.*, SCHNEIDERS 1934, 1938) and by the exposure to low temperature (MÜLLER-STOLL 1965, *c.f.*, JÖHNSSEN 1933, FUESS and SCHNEIDERS 1935). In the present study trabeculae and their homologous structures were apparently abundant in the transitional zone from compression to normal wood (and also relatively abundant in the zone from normal to compression wood) as well as in early-earlywood affected by late frost. The abundant occurrence was also observed in sections cut from a portion of "hazel" growth (ZIEGLER and MERZ 1961) in *Picea sitchensis* (YUMOTO *et al.* unpublished). The hypothesis should explain why they are abundant there. And, it should also explain the characteristic patterns of their occurrence, association with the anasto-mosis and radial branching of tracheids, and the preferential occurrence of the tangential pits near the trabecula and its homologous structures.

As stated above, a particular initial seems liable to form trabeculae and their homologous structures (Photo 103). A similar genetical tendency of the cambial initial was also reported by MÜLLER-STOLL and BALBACH in *Vitis* (1939). A study on the relative position of trabeculae and their homologous structures in macerated tracheids (YUMOTO unpublished) disclosed the fact that although they can be found in any position within a tracheid as stated by MÜLLER (1890), RAATZ (1892), MÜLLER-STOLL and BALBACH (1939), *etc.*, most of them are preferentially situated at the just middle of the tracheids. These facts strongly suggest that trabeculae and their homologous structures are not formed by direct external factors such as fungal hyphae, but formed by a certain internal factor or factors within the cell. Since nuclei are known to show a similar distribution pattern in tracheids (BAILEY 1920), it can be thought that the formation of trabeculae and their homo-logous structures may be associated with a certain activity or activities of nuclei.

The fact that the proliferation can be caused by many different factors sug-gests that their involvement is of secondary nature. Probably, one or some cytologi-cal events which are brought about by the above mentioned factors will evoke the proliferation. Unfortunately, developmental studies of trabeculae have only been made by PETRI (1912 c) and BODE (1938) many years ago by light microscopy.

The latter author attributed the formation of trabeculae to the abnormal degenera-
tion of mitosis in the cambium.   A possibility of the disordered periclinal division
as a cause of trabecular formation was also noted by BUTTERFIELD and MEYLAN
(1980).   In this respect PETRI's observation that the cambial cell with the primor-
dium of trabeculae sometimes has two nuclei is of special interest, since such a con-
dition is thought to be brought about by an abortive or insufficient cytokinesis.
This idea is also supported by the association of the trabecula and its homologous
structures with the anastomosis and branching of tracheids which are thought to
be formed by abortive cell divisions or insufficient cytokinesis.

Ubiquitous nature of trabeculae, *e. g.*, in leaves, petioles, pith and bark (PETRI
1913, SCHNEIDERS 1934, 1938), implies the formation of trabeculae would be as-
sociated with an activity or activities of the cell common to all these organs and
tissues.   Cell division is one of the common activities of the meristematic tissues.
As stated earlier, BODE (1938) reported that the orientation of trabeculae in a
tissue is parallel to that of the spindle axis which is determined in the tissue.
This also supports the possibility of abnormal cell division as a cause of trabecular
formation.   He did not mention the occurrence of pseudo-transverse or anticlinal
division in the cambium, however, it also occurs there.   Some of the tangential
confluences which are not thought to be caused by the tip growth of the host
tracheids (Photos 49, 50 and 54) might be formed in relation to this type of cell
division.   The formation of confluences also could be explained by abortive
pseudo-transverse divisions, as noted in a previous section.

Thus, circumstantial evidence strongly indicates certain causal relations between
abnormal cell divisions and the formation of trabeculae and most of their related
structures.   The possibility of abnormal cell division as a cause will be further
strengthened in the following section.

iii) *Explanation of existing hypotheses by abnormal cell division*

As stated above, the proliferation of trabeculae has been reported to be evoked
by the infection of certain diseases and low temperature, or associated with wounds
and fungal galls or cankers.   Four of the above listed hypotheses are based upon
these facts.   However, it seems not so difficult to explain the stimulating effects
of these factors by abnormal cell division.

According to MÜLLER-STOLL (1965), a treatment of temperature at 0°C (night
temperature, duration of 3 weeks) on saplings of *Vitis* grown up from cuttings
induced a marked proliferation of trabeculae, its value reaching *ca.* 450 per cm^2 of
section.   It should be noted here that at this temperature no plant tissues can be
frozen.   Namely, freezing or the resultant injury is not necessary for the trabecular
formation, and the proliferation can be caused only by chilling.   Mitosis is known
to be disturbed by the application of low but nonfreezing temperatures (GRIF 1967)
as well as that of very low ones.

Cytological studies on artificial application of cold on the cambium have been
made by ZALASKY (1975 b, 1975 c).   He reported that the occurrence of abnormal
cell divisions and a variety of changes in chromosome structure which lead to the

establishment of a chimeral condition were induced by the application of low tem-
perature. The chimeral tissue is characterized by deformed cells often with incom-
plete cell plates (*i. e.*, radially branched tracheids) and irregular cell wall deposition,
some of which have similar structures to the confluences observed in the present
study. Furthermore, he noted the occurrence of trabeculate structures (ZALASKY
1975 b).

ZALASKY also studied anatomical features of some abnormal tissues such as galls
and rough-bark caused by the infestation of fungi (ZALASKY 1973, 1975 a, 1976).
Interestingly, the structure of these abnormal tissues has many features common
with those formed by frost. Similar structural abnormalities including those which
are thought to be caused by abnormal cell divisions were also reported by other
workers in galls, tumor and wounded tissues (JACKSON and PARKER 1958, PETERSON
1960, WICKER 1970, RICKEY *et al.* 1974, MOORE 1978, SMITH 1980), and in hazel
growth (ZIEGLER and MERZ 1961). The structural similarity found among these
tissues suggests the existence of a common cause responsible for their formation.
WŁOCH (1981) also reported the occurrence of abnormal cytokinesis in the cambium
of tumor-affected tissues. Therefore, there is a good possibility that disturbed
cell division occurs in these tissues in general as is the case of the cold-induced
abnormal tissues. Thus, it could be thought that in all the tissues reported to be
associated with the occurrence of trabeculae, abnormal cell division occurs, which
is, on the one hand, responsible for the trabecular formation and, on the other
hand, causes the formation of the abnormal structural features stated above.

It should be noted that WŁOCH (1976) observed an elongated hole of a
tracheid (*i. e.*, plate) in tumor-affected *Picea abies* and suggested a possibility of the
tip growth of a neighboring cambial initial as a cause of its formation. However,
WŁOCH's idea does not explain many facts associated with the occurrence of
trabeculae and their homologous structures, *i. e.*, the pattern shown in Photo
109, association with the anastomosis and radial branching of tracheids and their
preferential occurrence in the just middle of the tracheids (YUMOTO unpublished).
I believe that there must be the involvement of certain biological processes in the
formation of a structure in a plant tissue, and that trabeculae and their homologous
structures could not be formed directly by such a mechanical force.

Thus, most of above listed hypotheses can be explained to a considerable
extent in terms of the disturbance of normal cell division. This hypothesis may also
explain the preferential occurrence of trabeculae in the transitional zone from com-
pression to normal wood. Geotropic stimulation enhances cell division in the cambial
cells (YUMOTO *et al.* 1982 a). It can be thought that the cell division, which is
evoked by the geotropic stimulation and begins immediately before the interruption
of the stimulation, is not completed well because of drastic physiological changes
brought about by the interruption. Their occurrence is also relatively abundant
in the transitional zone from normal to compression wood. It is a little awkward
to explain, because the tracheids with the trabeculae in this zone is thought to
have been situated, at the beginning of the stimulation, *i. e.*, stem displacement, in

the early stage of the surface extension (YUMOTO *et al.* 1982 a, 1982 b) at which no cell division is believed to occur in axial elements.   However, on the contrary, such an adverse situation might cause abnormal cell divisions.

Trabeculae and their homologous structures can be formed in entirely normal tissues other than rather particular tissues memtioned above.   This fact might seem to stand against the possibility of abnormal cell division as a cause.   However, the occurrence of abnormal cell division is believed to be not so seldom in plant tissues as frequently assumed.   As well known, natural polyploidy, aneuploidy and other chromosomal alterations are common in angiosperms and also reported in conifers (KIELLANDER 1950, MERGEN 1958, OWENS 1967, CHING and DOERKSEN 1971).

As stated earlier, the abnormal large tangential pits often occur in the close vicinity of trabeculae and their homologous structures.   The occurrence of abnormal tangential pits is reported in the tissues of frost cankers and tumors (ZALASKY 1975 a, 1975 c, RICKEY *et al.* 1974), and in hazel growth (ZIEGLER and MERZ 1961, *c.f.*, BOSSHARD 1975).   SATO and ISHIDA (1982) also observed similar large tangential pits in a strand tracheid adjacent to a resin canal.   The occurrence of the abnormal tangential pits seems to be a common feature in the abnormal tissues in which trabeculae and their homologous structures are rich in number.   Probably, both the formation of trabeculae and that of the abnormal tangential pits are elicited by a common cause, however, it is difficult to believe in a certain direct causal relation between trabecular and tangential pit formation.

A clue for the question why low temperature and infestation of fungi or other pathogenes cause abnormal cell divisions and structural abnormalities of cells can be sought in the recent progress in cell biology.   As well known, micro-tubules which take many important roles in cell division, cell wall formation and determination of cell shape (HEPLER and PALEVITZ 1974, PICKETT-HEAPS 1974, GUNNING and HARDHAM 1982) are temperature sensitive.   Therefore, if microtubules are partly destroyed or their system is disorganized by a cold treatment, abnormal cell divisions, irregular cell-wall deposition and deformed cell shapes are expected to occur easily, all of which were, as stated above, observed in cold- and frost-affected tissues.   Namely, a cold treatment can be thought to evoke the formation of trabeculae and their homologous structures as well as that of the abnormal structural features mediating disorganization of microtubule system.

However, there is another possibility.   A variety of physiological alterations are known to be caused by injuries and infection of virus, bacteria and fungi (*e. g.*, STROBEL and MATHRE 1970) as well as by chilling treatments (GRAHAM and PATTERSON 1982).   Spindle activity and cytokinesis can be inhibited by various agents (DYER 1976).   The polypoid formation and the inhibition of mitosis caused by the infection of bacteria were reported by several authors (WIPF and COOPER 1940, JAKOWSKA 1949, CEBRAT *et al.* 1972).   Therefore, it might be also possible that some of physiological alterations caused by injuries, infection or chilling disturb normal cell divisions by producing certain chemical agents.

It should be noted here that it is not necessary to suppose a direct causal

relation between the abnormal cell division thus caused and trabecular formation. It seems rather reasonable to think that abnormal cell division caused by low temperature or infections elicits genetical alterations of the cambial cell, through which the initial receives a tendency liable to fail in cell division, and thus, to form trabeculae and their homologous structures. As stated in an earlier section, such a genetical tendency is found in the present study (Photo 103) and was reported by MÜLLER-STOLL and BALBACH (1939). The abundant occurrence of trabeculae and their homologous structures in hazel growth also supports this possibility, since a rather perpetuating nature of this abnormal growth is difficult to ascribe to a persistent stimulation of external factors.

How trabeculae and their homologous structures are resulted from abnormal cell divisions remains to be solved. Probably, the primordium of trabeculae is formed through ill-controlled fusion of fragmosomes to a tangential wall during cell plate formation. However, there might be the participation of an abortive pseudo-transverse division in the formation of confluences, and the relation between the formation of the trabecula or its homologous structures and that of the anastomosis or branching of tracheids is not clear. For the solution of the subject further evidence is needed, especially the occurrence of abnormal cell divisions in the trabecula-rich zones.

Conclusions

From the above discussion it can be said that the trabecula, plate, confluence and adhesion have an intimate ontogenetical relationships to each other, and that they also have a causal relation to the anastomosis and radial branching of tracheids. All of them are believed to be formed by the disturbance of normal cell division. On the other hand, at least, some of the tangential confluences are probably onto-genetically different, namely their formation is caused by the tip growth of the host cell during the differentiation. However, whether this is also the case for other tangential confluences remains to be solved. The relationship between the confluence and the tangential branching of tracheids which is reported to be formed by the tip growth of the neighboring initials in the cambium is not plausible.

Consequently, the trabecula and its related structures are regarded as a type of abnormal structure which is formed by ill-controlled biological processes. This means the formation of these structures is not genetically determined. In this point they are essentially different from other wall sculptures such as pits, perforation plates and spiral thickenings; their formation is thought to be genetically determined. This concept leads to further conclusions that they would have no function in plant tissues, and that there is no answer to the question why they are formed.

The hypothesis that trabeculae and their homologous structures are formed by the disturbance of cell division is highly speculative and lacks in critical evidence. However, this hypothesis is believed to be far more plausible than the fungal theory and to be testable. It is hoped, at first, to study the cytology of trabecular

formation induced by a treatment of low temperature. The application of anti-mitotic agents could provide a definitive answer to the validity of this hypothesis. And, whether the formation of trabeculae is actually mediated by certain disorganization of microtubule system or not could be verified by the application of anti-microtubule agents or, to the contrary, microtubule stabilizers.

Summary

External and internal structure, and the pattern of the occurrence of trabeculae and their related structures were described. The related structures denote those which resemble or are believed to have certain relations to rod- and spool-like trabeculae but are out of the definition of IAWA. Ontogenetical homology between trabeculae and most of the related structures was confirmed. The cause of their formation was closely discussed. The literature concerning the trabecula and its related structures was nearly completely reviewed.

1) Observations were made on young trees of *Picea glauca* with the aid of SEM, UVM, PLM, and a SEM–UVM combination method. The materials examined comprise both normal and compression wood, and were originally collected for the studies of the formation and structure of compression wood cells.

2) The trabecula and its related structures were classified for convenience into five basic types (trabeculae, plates, confluences, adhesions and tangential confluences) and two varieties (pit-including and abnormal forms).

i) The trabecula is a structure of rod- or spool-like form oriented radially. Its central core is separated from the radial middle lamella. Trabeculae were the most common structure among the basic types and were rich in variation.

The microfibrils of the S3 layer on trabeculae run along the long axis of trabeculae. The orientation of the microfibrils in the S2 layer in the middle of thin trabeculae was nearly in parallel to the long axis, however, in relatively thick ones it was helical along the axis. At the base of trabeculae microfibrils in the S2 layer were divided into two bundles of opposite directions which are parallel to that of the equivalent layer of the host cell wall. This made root-like projections at the bases of a trabecula. The central core of trabeculae generally showed a slightly lower UV-absorption than the middle lamella, though it was variable in the strength and the distribution pattern of UV-absorption as well as in form.

In well-developed compression wood, trabeculae had spiral grooves as is the host cell wall, though their degree of development was not necessarily the same with that of the host cell wall. Occasionally, intercellular spaces occurred at the bases of trabeculae and in extreme cases the spaces of both the bases were fused into a common room.

The width of a trabecula was found to be related not only to the thickness of the host cell walls but also to that of the central core, unless the trabecula is abnormal.

ii) The plate is a structure plank- or plate-like in form oriented radially. It differs from the trabecula only in that its cross section is not round but considerably

or highly elliptic. The width of plates was variable. A long row of trabeculae was often found to begin with a plate. All intermediate structures were found between trabeculae and plates.

The orientations of microfibrils in the S2 and S3 layer were similar to those of the host cell wall except at the margin of plates. The texture of cut surfaces, and the strength and distribution pattern of UV-absorption of plates were similar to those of the host cell wall.

iii) The confluence denotes a rod- or plank-like structure confluent to a radial wall of the host cell. The central core of the confluence is also connected with the radial middle lamella.

All characteristics of confluences were identical with those of plates except for the confluency to the radial wall. They often included pit-like structures.

iv) The adhesion is a wall-pinch-like structure formed between both the tangential walls of a cell. The "central core" of this structure is modified into the middle lamella between the tracheids situated immediately on the outer and inner side of the host cell. There were all intermediate structures between trabeculae, plates, confluences and adhesions.

v) The tangential confluence is the confluence oriented in the tangential direction. It occurred at or near the tip of a tracheid and often included a pit-like structure.

vi) Pit-including form is the trabecula, plate, confluence or tangential confluence with a pit-like structure. Most of pit-including form were confluences. This pit-like structure had a pit-membrane- and a torus-like structure which showed a similar nature to pit-membrane and torus of the bordered pit under an UV-microscope. All intermediate structures were found between this pit-like structure and the bordered pit. The structure was thought to be actually homologous to the bordered pit.

vii) Abnormal form denotes above stated types which show some deviation from the normal features is some respects. Whether a structure is regarded as abnormal or not depends on the degree of the deviation. There were found several types of abnormality, *i. e.*, abnormalities in shape, those in cell wall deposition and those in the shape of the central core.

3) Trabeculae and their related structures (except tangential confluences) occurred in a long or short row, or solitary. The length of a row would depend on the position of the primordium in the cambial zone. The direction of a long row was not necessarily perpendicular to the long axes of the host tracheids but was always in parallel to the orientation of rays.

Trabeculae and their related structures (except tangential confluences) were especially abundant in early-earlywood affected by late frost and in the transitional zone from artificially induced compression to normal wood (and also relatively abundant in the zone from normal to compression wood). In the former the occurrence of adhesions and long rows of trabeculae was abundant. While in the latter, confluences were rich in number and long rows were rare.

They were often found to occur making a loose group. Occasionally, a few rows of trabeculae occurred in the close vicinity running in parallel to each other. Heterogeneous rows composed of a few different types were also found. Different types occasionally occurred together in the close vicinity in a cell.

Several trabeculae and their related structures (except tangential confluences) were often found to be sporadically aligned in the radial direction in short rows or solitarily with intervals of a considerable distance.

Occasionally, trabeculae and their related structures except tangential confluences occurred associated with the radial branching and anastomosis of tracheids which are believed to be formed by an abnormal cell division.

Abnormal tangential pits were often found close by trabeculae and their related structures (except tangential confluences).

4) Mutual relationships among trabeculae, plates, confluences and adhesions was inferred from following facts ; they can occur together in the close vicinity to each other and often made a common row ; the occurrence of all intermediate structures among these types. On the other hand, the tangential confluence did not occur together with above mentioned types, and had no intermediates to them and therefore, there is a good possibility that it belong to a different category.

5) From these and other facts, and also from the literature, the cause of the formation of trabeculae and their related structures was discussed in detail. Aside from the tangential confluence, it was believed to be intimately associated with a certain activity or activities of the nucleus. A possibility of abnormal cell division as a primary cause of the trabecular formation was presented, which covers nearly all the hypotheses hitherto proposed.

Acknowledgments

References

1) BAILEY, I. W. (1919): Structure, development, and distribution of so-called rims or bars of Sanio. *Bot. Gaz.* **67** : 449–468.

2) BAILEY, I. W. (1920): The formation of the cell plate in the cambium of the higher plants. *Proc. N.A.S.* **6** : 197–200.

3) BALBACH, H. (1939): Untersuchungen über die Reisigkrankheit der Weinrebe. II. Der stoffliche Aufbau der Zellstäbe, mit besonderer Berücksichtigung des Zentralfadens. *Wein u. Rebe* **21** : 318–340.

4) BÄRNER, J. (1937 a): "Intrazellulare Stäbe" bei viruskranken Tabak- und Kartoffelpflanzen.

Nachrichtenblatt für den deutschen Pflanzenschutzdienst **4**: 33-34.

5) BÄRNER, J. (1937 b): "Intrazellulare Stäbe" bei viruskranken Solanaceen nnd Cucurbitaceen. *Angew. Bot.* **19**: 553-561.

6) DE BARY, A. (1877): *Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne.* Verlag von Wilhelm Engelmann, Leipzig.

7) BAWDEN, F. C. (1964): *Plant viruses and virus diseases.* 4th Ed., Ronald Press Co., N.Y.

8) BODE, H. R. (1938): Über die Entwicklungsgeschichte der intracellulären Stäbe im Cambium: Ein Beitrag zum Problem der Reisigkrankheit des Weinstocks. *Gartenbauwiss.* **11**: 272-288.

9) BODE, H. R. (1939): Über "unechte" intracelluläre Stabbildung in sekundären Zuwachszonen einiger Pflanzen. *Gartenbauwiss.* **12**: 399-405.

10) BOSSHARD, H. H. (1975): *Holzkunde,* Bd 3, *Aspekte der Holzbearbeitung und Holzverwertung.* Birkhäuser Verlag, Basel and Stuttgart.

11) BRÜCKBAUER, H. (1957): Untersuchungen zur Frage der Übertragbarkeit der Reisigkrankheit der Rebe durch Pfropfung. *Mitt. Klosterneuburg, Ser. A, Rebe u. Wein* **7**: 171-188.

12) BRÜCKBAUER, H. (1958): Stand unserer Kenntnisse über die virösen Abbauerscheinungen an Reben. *Weinberg u. Keller* **5**: 386-396.

13) BRÜCKBAUER, H. (1963): Ergebnisse fünfjähriger Untersuchungen über die Viruskrankheiten der Rebe und die Folgerungen für die Praxis. *Weinberg u. Keller* **10**: 247-264.

14) BRÜCKBAUER, H. and M. RÜDEL (1976): Untersuchungen über eine "atypische" Form der Reisigkrankheit bei der Rebesorte Silvaner. *Weinberg u. Keller* **23**: 53-79.

15) BUTTERFIELD, B. G. and B. A. MEYLAN (1972): Trabeculae in a hardwood. *IAWA. Bull.* **1972/1**: 3-9.

16) BUTTERFIELD, B. G. and B. A. MEYLAN (1979): Observations of trabeculae in New Zealand hardwoods. *Wood Sci. Technol.* **13**: 59-65.

17) BUTTERFIELD, B. G. and B. A. MEYLAN (1980): *Three-dimentional structure of wood.* 2nd. Ed., Chapman and Hall, London.

18) CASPERSON, G. (1959): Mikroskopischer und submikroskopischer Zellwandaufbau beim Druckholz. *Faserforsch. u. Textiltech.* **10**: 536-541.

19) CASPERSON, G. (1965): Zur Anatomie des Reaktionsholzes. *Svensk Papperstidn.* **68**: 534-544.

20) CEBRAT, J., K. CZERWIŃSKA and K. BOHDANOWICZ-MUREK (1972): introductory studies of bacterial effects on the course of mitosis in adventitious roots of *Allium cepa* L. *Acta Soc. Bot. Polon.* **41**: 205-216.

21) CHING, K. K. and A. DOERKSEN (1971): A natural chimera of Douglas-fir. *Silvae Gen.* **20**: 209-210.

22) CÔTÉ, W. A. Jr. and A. C. DAY (1965): Anatomy and ultrastructure of reaction wood. *In*: CÔTÉ, W. A. Jr., Ed., *Cellular ultrastructure of woody plants.* Cyracuse Univ. Press, Syracuse, N.Y. 391-418.

23) CÔTÉ, W. A. Jr., A. C. DAY and T. E. TIMELL (1968): Studies on compression wood. VII. Distribution of lignin in normal and compression wood of tamarack [*Larix laricina* (DU ROI) K. KOCH]. *Wood Sci. Technol.* **2**: 13-37.

24) DYER, A. F. (1976): Modifications and errors of mitotic cell division in relation to differentiation. *In*: M. M. YEOMAN, Ed., *Cell division in higher plants.* Academic Press, N.Y., 199-249.

25) ESAU, K. (1965): *Plant anatomy.* 2nd Ed., John Wiley & Sons, N.Y.

26) FAHN, A. (1982): *Plant anatomy.* 3rd Ed., Pergamon Press, Oxford.

27) FUESS, J. and E. SCHNEIDERS (1935): Über Wirkungen und Schäden der Maifröste 1934 an Kober 5 BB-Reben. *Gartenbauwiss.* **9**: 353-363.

28) FUKAZAWA, K. (1974): The distribution of lignin in compression- and lateral-wood of *Abies sachalinensis* using ultraviolet microscopy. *Res. Bull. College Exp. For., Hokkaido Univ.* **31**: 87–114.

29) GÄRTEL, W. (1954): Panaschüren bei Reben. *Weinberg u. Keller* **1**: 137–145.

30) GERRY, E. (1910): The distribution of the "bars of Sanio" in the Coniferales. *Ann. Bot.* **24**: 119–123.

31) GRAHAM, D. and B. D. PATTERSON (1982): Responses of plants to low, nonfreezing temperatures: Proteins, metabolism, and acclimation. *Ann. Rev. Plant Physiol.* **33**: 347–372.

32) GRIF, V. G. (1967): Effect of low temperature on mitosis in plants. *In*: A. S. TROSHIN, Ed., *The cell and environmental temperature.* Pergamon Press, Oxford, 64–65.

33) GREGUSS, P. (1955): *Xylotomische Bestimmung der heute lebenden Gymnospermen.* Akad. Kiado, Budapest (not seen, cited in LAMING and TER WELLE 1971).

34) GROOM, P. and W. RUSHTON (1913): The structure of the wood of east Indian species of *Pinus. J. Linn. Soc., Bot.* **41**: 457–490.

35) GUNNING, B. E. S. and A. R. HARDHAM (1982): Microtubules. *Ann. Rev. Plant Physiol.* **33**: 651–698.

36) HALE, J. D. (1923 a): The bars or rims of Sanio. *Bot. Gaz.* **76**: 241–256.

37) HALE, J. D. (1923 b): Trabeculae of Sanio in angiosperms. *Science* **57**: 718.

38) HALE, J. D. (1935): The structure of wood. *In*: T. A. McELHANNEY and associates Ed., *Canadian woods: Their properties and uses.* Forest Products Laboratories of Canada, Ottawa. 56–99.

39) HEPLER, P. K. and B. A. PALEVITZ (1974): Microtubules and microfilaments. *Ann. Rev. Plant Physiol.* **25**: 309–362.

40) HEPP, I. A. and R. THATE (1943): Der Einfluss verschiedener reisigkranker Unterlagssorten auf Entwicklung und Ertrag von Pfropfreben. *Wein u. Rebe* **25**: 82–89.

41) JACKSON, L. W. R. and J. N. PARKER (1958): Anatomy of fusiform rust galls on loblolly pine. *Phytopathol.* **48**: 637–640.

42) JAKOWSKA, S. (1949): Effects of *Bacterium tumefaciens* on *Allium cepa. Phytopathol.* **39**: 683–705.

43) JANE, F. W. (1970): *The structure of wood.* 2nd Ed., Adam & Charles Black, London.

44) JEFFREY, E. C. (1912): The history, comparative anatomy and evolution of the Araucarioxylon type. *Proc. Amer. Acad.* **48**: 531–571.

45) JEFFREY, E. C. (1917): *The anatomy of woody plants.* Univ. Chicago Press, Chicago.

46) JÖHNSSEN, A. (1933): Ueber die Reisigkrankheit der Rebe. *D. Weinbau* **12**: 221–223, 238–240, 249–252, 265–267.

47) KEITH, C. T. (1971): Observations on the anatomy and fine structure of the trabeculae of Sanio. *IAWA. Bull.* **1971/3**: 3–11.

48) KEITH, C. T., S. E. GODKIN, G. A. GROZDITS and G. CHAURET (1978): Further observations on the anatomy and fine structure of the trabeculae of Sanio. Proc. Joint Meeting Str. Sec. Bot. Soc. American and Pan American Group of IAWA., Blacksburg, Virginia, *IAWA. Bull.* **1978/2 & 3**: 47.

49) KIELLANDER, C. L. (1950): Polyploidy in *Picea abies. Hereditas* **36**: 513–516.

50) KORAN, Z. (1977): Tangential pitting in black spruce tracheids. *Wood Sci. Technol.* **11**: 115–123.

51) KROEMER, K. and H. MOOG (1936): Bericht über die Tätigkeit der Wissenschaftlichen Abteilung der Rebenveredlungsstation Geisenheim a. Rh. *Landw. Jahrb.* **82**: 684–685.

52) KROEMER, K., H. MOOG and G. TROOST (1936): Bericht über die Tätigkeit der Wissenschaftlichen Abteilung der Rebenveredlungsstation Geisenheim a. Rh. im Jahre 1935. *Landw. Jahrb.* **83**: 851–852.

53) KUČERA, L. J. (1978): Vascular nodules in the pith of yew (*Taxus baccata* L.). *IAWA. Bull.* 1978/4: 81–85.

54) KÜSTER, E. (1925): *Pathologische Pflanzenanatomie.* 3. Aufl., Gustav Fischer, Jena.

55) LAMING, P. B. and B. J. H. TER WELLE (1971): Anomalous tangential pitting in *Picea abies* KARST. (European spruce). *IAWA. Bull.* 1971/4: 3–8.

56) MAIER, W. (1939): Die Häufigkeit der Zellstäbe in den Internodien der Triebe reisigkranker Reben. *Wein u. Rebe* 21: 240–250.

57) MAMELI, E. (1913): Sulla presenza dei cordoni endocellulari nelle viti sane e in quelle affètte da "roncet". Nota prelimiare della dott. *Atti dell'Accademia Nazionale dei Lincei: Classe di Scienze Fisiche, Matematiche e Naturali*; Rendiconti 5, 22: 879–883.

58) MAMELI, E. (1916 a): Risposta alla nota del Dottor Petri: "Sul significato patologico dei cordoni endocellulari nei tessuti della vite". *Atti dell'Instituto Botanico dell'Universita di Pavia*, Serie II, 16: 41–45.

59) MAMELI, E. (1916 b): Sulla presenza dei cordoni endocellulari nei tessuti della vite e di altre dicotiledoni. *Atti dell'Istituto Botanico dell'Universita di Pavia*, Serie II, 16: 47–65.

60) MATSUMOTO, T. (1957): Studies on the compression wood. V. The relation of the slope angle of the fibrils to shrinkage of the leaning hiba timber. *Iwate Univ., Fac. Agr. Sci. Bull.* 3: 190–193 (in Japanese with English summary).

61) MERGEN, F. (1958): Natural polyploidy in slash pine. *For. Sci.* 4: 283–295.

62) MEYLAN, B. A. and B. G. BUTTERFIELD (1973): A trabecula with a vestured pit. *IAWA. Bull.* 1973/3: 12–14.

63) MOORE, K. E. (1978): Barrier-zone formation in wounded stems of sweetgum. *Can. J. For. Res.* 8: 389–397.

64) MÜLLER, C. (1890): Ueber die Balken in den Holzelementen der Coniferen. *Ber. dtsch. bot. Ges.* 8: 17–46.

65) MÜLLER-STOLL, W. R. and H. BALBACH (1939): Untersuchungen über die Reisigkrankheit der Weinrebe. I. Die Morphologie der Zellstäbe und ihre Verteilung im Holzkörper. *Wein u. Rebe* 21: 277–307.

66) MÜLLER-STOLL. W. R. (1965): Über intrazelluläre Stabbildungen (Trabeculae) im Holz als anatomische Eigenart bei Gehölzen exponierter Gebirgslagen. *Kulturpfl.* 13: 763–799.

67) MÜNCH, E. (1940): Weitere Untersuchungen über Druckholz und Zugholz. *Flora, Jena* 34: 45–57.

68) NEEFF, F. (1922): Über polares Wachstum von Pflanzenzellen. *Jahrb. wiss. Bot.* 61: 205–283.

69) OCHS, G. (1955): Der heutige Stand der Reisigkrankheitsforschung. *Angew. Bot.* 29: 152–159.

70) OCHS, G. (1957): Kritische Gedanken über den diagnostischen Wert der intrazellulären Stäbchen der Rebe. *Wein-Wiss.* 11: 37–38.

71) OHTANI, J. (1977): An observation of the trabeculae in some dicotyledonous woods using scanning electron microscopy. *Res. Bull. College Exp. For., Hokkaido Univ.* 34: 69–78.

72) OWENS, J. N. (1967): Chromosome aberrations in Douglas fir. *Can. J. Bot.* 45: 1910–1913.

73) PANSHIN, A. J. and C. DE ZEEUW (1980): *Textbook of wood technology.* McGraw-Hill, N.Y.

74) PARAMESWARAN, N. (1979): A note on the fine structure of trabeculae in *Agathis alba*. *IAWA. Bull.* 1979/1: 17–18.

75) PENHALLOW, D. P. (1907): *A manual of the north American gymnosperms.* Ginn & Company, Boston.

76) PETERSON, R. S. (1960): Development of western gall rust in lodgepole pine. *Phytopathol.* 50: 876–881.

77) PETRI, L. (1911): Ricerche istologiche sopra le viti affètte da rachitismo. *Atti dell'Accademia Nazionale dei Lincei*; *Classe di Scienze Fisiche, Matematiche e Naturali*; Rendiconti 5, **20**: 155-161.

78) PETRI, L. (1912a): Significato patologico dei cordoni endocellulari nelle viti affètte da arricciamento. *Atti dell'Accademia Nazionale dei Lincei*; *Classe di Scienze Fisiche, Matematiche e Naturali*; Rendiconti 5, **21**: 113-119.

79) PETRI, L. (1912b): Formazione e significato fisiologico dei cordoni endocellulari nelle viti affètte da arricciamento. *Atti dell'Accademia Nazionale dei Lincei*; *Classe di Scienze Fisiche, Matematiche e Naturali*; Rendiconti 5, **21**: 505-511.

80) PETRI, L. (1912c): Ricerche sulle cause dei deperimenti delle viti in Sicilia. I. Contributo allo studio dell'azione degli abbassamenti di temperatura sulle viti in rapporto all'arricciamento. *Mem. Staz. Patol. Veget., Roma* **1912**: 1-212.

81) PETRI, L. (1913): Sul significato patologico dei cordoni endocellulari nei tessuti della vite. *Atti dell'Accademia Nazionale dei Lincei*; *Classe di Scienze Fisiche, Matematiche e Naturali*; Rendiconti 5, **22**: 174-179.

82) PICKETT-HEAPS, J. D. (1974): Plant microtubules. *In*: A. W. ROBARDS, Ed., *Dynamic aspects of plant ultrastructure*. McGraw-Hill, Maidenhead, Berkshire, 219-255.

83) RAATZ, W. (1892): Die Stabbildungen im secundären Holzkörper der Bäume und die Initialentheorie. *Jahrb. wiss. Botan.* **23**: 567-636.

84) RECORD, S. J. (1934): *Identification of the timbers of temperate north America.* John Wiley & Sons, N.Y.

85) RICKEY, R. G., J. K. HAMILTON and H. L. HERGERT (1974): Chemical and physical properties of tumor-affected Sitka spruce. *Wood and Fiber* **6**: 200-210.

86) RUSSOW, E. (1882): Gegenbemerkungen zu den Bemerkungen Dr. C. SANIO's zu meinem Aufsatz "Ueber die Entwicklung des Hoftüpfels, der Membran der Holzzellen und des Jahrringes bei den Abietineen, in erster Linie von *Pinus silvestris*". *Bot. Clb.* **10**: 62-70.

87) SANIO, C. (1863): Vergleichende Untersuchungen über die Elementarorgane des Holzkörpers. *Bot. Z.* **21**: 85-91, 93-98, 101-111, 113-118, 121-128.

88) SANIO, K. (1873-1874): Anatomie der gemeinen Kiefer (*Pinus silvestris* L.). II. *Jahrb. wiss. Bot.* **9**: 50-126.

89) SATO, K. and S. ISHIDA (1982): Resin canals in the wood of *Larix leptolepis* GORD. II. Morphology of vertical resin canals. *Res. Bull. College Exp. For., Hokkaido Univ.* **39**: 297-316.

90) SCHNEIDERS, E. (1934): *Die Reisigkrankheit der Rebe (Rebenmüdigkeit).* Inaug. Diss. Bonn (not seen, cited in SCHNEIDERS 1938).

91) SCHNEIDERS, E. (1937): Beobachtungen und Untersuchungen über die Reisigkrankheit der Reben (Rebenmüdigkeit). *Gartenbauwiss.* **10**: 110-150.

92) SCHNEIDERS, E. (1938): Über die Zellstäbe und ihre phytopathologische Bedeutung. *Gartenbauwiss.* **11**: 237-250.

93) SCHNEIDERS, E. (1957-1958): Die Zellstab- oder Stauchekrankheit unter besonderer Berücksichtigung der Reisigkrankheit der Rebe. *Weinberg u. Keller* **4**: 249-260, 340-348, 398-409, 425-438, 494-498, 527-534; **5**: 31-36, 76-85, 131-139, 207-215.

94) SCHULZ, P. (1882): *Das Markstrahlengewebe und seine Beziehungen zu den leitenden Elementen des Holzes.* Diss. Berlin (not seen, cited in RAATZ 1892).

95) SIFTON, H. B. (1915): On the occurrence and significance of "bars" or "rims" of Sanio in the cycads. *Bot. Gaz.* **60**: 400-405.

96) SMITH, D. E. (1980): Abnormal wood formation following fall and spring injuries in black walnut. *Wood Sci.* **12**: 243-251.

97) STEARN, W. T. (1973): *Botanical Latin*, 2nd Ed., David & Charles, Newton, Abbot.

98) STELLWAAG, F. (1948): Grundsätzliches zur Beurteilung der Abbaukrankheiten der Rebe, insbesondere der Reisigkrankheit. *D. deutsch. Weinbau, wiss. Beihefte* 2: 115–130, 147–161.

99) STELLWAAG, F. (1953): Stand der Kenntnisse über die Reisigkrankheit der Rebe. *Nachrichtenblatt des deutschen Planzenschutzdienstes* 5: 101–106.

100) STELLWAAG, F. and E. LUSIS (1953): Zur Technik der Untersuchungen über die Reisigkrankheit der Rebe. *D. deutsch. Weinbau, wiss. Beihefte* 7: 90–99.

101) STRASBURGER, E. (1891): *Leitungsbahnen in den Pflanzen.* Gustav Fischer, Jena.

102) STROBEL, G. A. and D. E. MATHRE (1970): *Outlines of plant pathology.* Van Nostrand Reinhold Co., N.Y.

103) TIMELL, T. E. (1981): Recent progress in the chemistry, ultrastructure, and formation of compression wood. *In: The Ekman-Days 1981, Proc. Intern. Sym. Wood Pulp Chem.,* Stockholm, Sweden, June 1981, Vol. 1: 99–147.

104) TSOUMIS, G. (1968): *Wood as raw material.* Pergamon Press, Oxford.

105) WARDROP, A. B. and H. E. DADSWELL (1950): The anture of reaction wood. II. Cell wall organization of compression wood tracheids. *Aust. J. Sci. Res.,* Ser. B, 3: 1–13.

106) WARDROP, A. B. and H. E. DADSWELL (1952): The nature of reaction wood. III. Cell division and cell wall formation in conifer stems. *Aust. J. Sci. Res.,* Ser. B, 5: 385–398.

107) WERKER, E. and P. BAAS (1981): Trabeculae of Sanio in secondary tissues of *Inula viscosa* (L.) DESF. and *Salvia fruticosa* MILL. *IAWA. Bull.,* n. s., 2: 69–76.

108) WESTING, A. H. (1965): Formation and function of compression wood in gymnosperms. *Bot. Rev.* 31: 381–480.

109) WESTING, A. H. (1968): Formation and function of compression wood in gymnosperms. II. *Bot. Rev.* 34: 51–78.

110) WICKER, M. (1970): Structure et densité de bois de tumeurs de chêne et de hêtre. *Rev. gén. Bot.* 77: 499–517.

111) WILHELM, A. F. and H. H. HOPP (1961): Untersuchungen über Rebvirosen. I. Beitrag zur Anfälligkeit von Rebsorten. *Zeitsch. Pflanzenkrank. Pflanzensch.* 68: 129–144.

112) WILSON, B. F. and R. R. ARCHER (1977): Reaction wood: Induction and mechical action. *Ann. Rev. Plant Physiol.* 28: 23–43.

113) WINKLER, C. (1872): Zur Anatomie von *Araucaria brasiliensis. Bot. Z.* 30: 581–585, 597–608.

114) WIPF, L. and D. C. COOPER (1940): Somatic doubling of chromosomes and nodular infection in certain Leguminosae. *Amer. J. Bot.* 27: 821–824.

115) WŁOCH, W. (1976): Cell events in cambium, connected with the formation and existence of a whirled cell arrangement. *Acta Soc. Bot. Polon.* 45: 313–326.

116) WŁOCH, W. (1981): Nonparallelism of cambium cells in neighboring rows. *Acta Soc. Bot. Polon.* 50: 625–636.

117) WOOD, J. R. and D. A. I. GORING (1971): The distribution of lignin in stem wood and branch wood of Douglas fir. *Pulp Paper Mag. Can.* 72: T95–T102.

118) YUMOTO, M. and J. OHTANI (1981): Trabeculae in compression wood tracheids. *Proc. Hokkaido Branch, Japan Wood Res. Soc.* 13: 9–12 (in Japanese with English summary).

119) YUMOTO, M (1982): A preliminary observation on the structure of compression wood tracheids near the growth ring boundary. *Proc. Hokkaido Branch, Jap. Wood Res. Soc.* 14: 44–47 (in Japanese with English summary).

120) YUMOTO, M., S. ISHIDA and K. FUKAZAWA (1982 a): Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea glauca.* I. Time course of the compression wood formation following incli-

nation. *Res. Bull. College Exp. For., Hokkaido Univ.* **39** : 137–162.

121) YUMOTO, M., S. ISHIDA and K. FUKAZAWA (1982 b): Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea glauca.* II. Transition from normal to compression wood revealed by a SEM-UVM combination method. *J. Fac. Agr., Hokkaido Univ.* **60** : 312–335.

122) YUMOTO, M., S. ISHIDA and K. FUKAZAWA (1983): 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. *Res. Bull, College Exp. For., Hokkaido Univ.* **40** : 409–454.

123) ZALASKY, H. (1973): Brachiate tracheids in deformed wood of *Abies. Bi-Month. Res. Note., Environ. Can., For. Serv.* **29** : 23.

124) ZALASKY, H. (1975 a): Cell deformities in bark and sapwood caused by *Rhytidiella moriformis* and *Keissleriella emergens* infections in poplar. *Can. J. Bot.* **53** : 780–783.

125) ZALASKY, H. (1975 b): Chimeras, hyperplasia, and hypoplasia in frost burls induced by low temperature. *Can. J. Bot.* **53** : 1888–1898.

126) ZALASKY, H. (1975 c): Low-temperature-induced cankers and burls in test conifers and hardwoods. *Can. J. Bot.* **53** : 2526–2535.

127) ZALASKY, H. (1976): Xylem in galls of lodgepole pine caused by western gall rust, *Endocronartium harknessii. Can. J. Bot.* **54** : 1586–1590.

128) ZIEGLER, H. and W. MERZ (1961): Der "Hasel" wucks : Über beziehungen zwischen unregelmässigem Dickenwachstum und Markstrahlverteilung. *Holz als Roh- u. Werkstoff* **19**: 1–8.

129) ZOBEL, B., C. WEBB and F. HENSON (1959): Core or juvenile wood of loblolly and slash pine trees. *Tappi* **42** : 345–356.

* The substance of Italian papers was cited from the German literature especially BODE (1938), MÜLLER-STOLL and BALBACH (1939), SCHNEIDERS (1957–1958) and MÜLLER-STOLL (1965). In the vinicultural literature a certain degree of confusion was observed in citation (*e. g.*, SCHNEIDERS 1938 cited as 1937 by BÄRNER 1937 b, MAMELI 1916 b as 1914 by BRÜCKBAUER 1957). Unfortunately, I could not ascertain the correct year numbers, because most of the journals on which the confusion was found are not available in our university, though copies of the papers could be obtained. Therefore, some of the references might be incorrectly cited here.

要　　約

　トラベキュレーとその関連構造の外部，内部構造，およびそれらの出現のパターンについて研究を行った。関連構造とは IAWA のトラベキュレーの定義から逸脱するが，それと類似あるいはある種の関係を持つと考えられる構造を指す。トラベキュレーと大部分の関連構造との個体発生的相同関係を確認し，それらの構造の形成原因についての詳細な考察を行った。またトラベキュレーとその関連構造に関する研究小史を付け加えた。

　1）　供試木にはグラウカトウヒ (*Picea glauca*) の若齢木を用い，SEM (走査電子顕微鏡)，UVM (紫外線顕微鏡)，PLM (偏光顕微鏡)，通常の光学顕微鏡，および SEM と UVM, PLM を組み合わせた手法等で観察を行った。試料は本来あて材細胞の形成，構造を調べる目的で採取されたもので，正常材とあて材の双方が含まれている。

　　2)　トラベキュレーとその関連構造を便宜上5つの基本型（トラベキュレー, plate, confluence, adhesion, tangential confluence), および2つの変形型 (pit-including from, 異常型) に分けた。

　　i)　トラベキュレーはその長軸が半径方向の桿状, 糸巻状の構造である (IAWA による定義)。そのセントラルコアは半径壁の中間層から分離している。トラベキュレーは基本型の中で最も多く見られるものであり, また変異に富んでいる。

　　トラベキュレーの S_3 層におけるミクロフィブリルの配向はその長軸におおむね平行である。S_2 層においては, 細いトラベキュレーの中央部ではほぼ長軸と平行するが, 比較的太いものでは軸に対しらせん状となる。S_2 層のミクロフィブリルは, トラベキュレーの基部において, それを含む細胞の S_2 層のミクロフィブリル配向と一致する互に反対方向の2つの束に分かれ, これは基部に根様の突出部を形成する。トラベキュレーのセントラルコアは一般に中間層よりやや弱い UV 吸収を示すが, 形ばかりでなく, 吸収の強さ, その分布パターンもコアによりかなりの変化を示す。

　　良く発達したあて材仮道管中におけるトラベキュレーには一般に仮道管壁と同様らせんみぞが認められるが, その発達の程度はかならずしもそれを含む仮道管のものとは一致しない。時おり細胞間隙がトラベキュレーの基部に形成されることがあり, 極端な場合には両方の基部にある間隙が融合して一つの共通の空隙となることもある。

　　正常なトラベキュレーの径は, それを含む細胞の壁厚ばかりでなく, セントラルコアの径とも関係している。

　　ii)　Plate は半径方向の平板状構造を指す。トラベキュレーと異なる点は, その断面が丸くなく, かなりあるいは極度に楕円形を呈することである。Plate の幅は様々であり, トラベキュレーと Plate の間にはすべての中間的構造が存在する。しばしば Plate は長いトラベキュレーの列の先頭に位置する。

　　Plate の S_2 層, S_3 層におけるミクロフィブリルの配向はそれを含む細胞の壁におけるものと, その辺縁部を除いて, ほぼ同一である。Plate はその切断面における質感, UV 吸収の強さおよび分布パターンにおいて, それを含む細胞の壁と同様の性質を示す。

　　iii)　Confluence はそれを含む細胞の半径壁と連続している桿状, 平板状の構造である。そのセントラルコアもまた半径壁の中間層と連続している。

　　Confluence の特徴は, 半径壁との連続性を除いて, Plate と同一である。Confluence はしばしば壁孔様構造を含む。

　　iv)　Adhesion は一つの細胞の両方の接線壁の間に形成される狭窄様の構造を指す。それを含む細胞の外側および内側に接する細胞の間の中間層がその adhesion のセントラルコアであるといえる。

　　トラベキュレー, plate, confluence, adhesion の間には連続的な中間段階の存在が認めら

れる。

v) Tangential confluence は接線方向に位置する confluence である。細胞の先端あるいはその近傍に見られ，しばしば壁孔様構造を含む。

vi) Pit-including form はトラベキュレー，plate, confluence, tangentil confluence の内，壁孔様構造を持つものを指す。大多数の pit-including from は confluence である。この壁孔様構造は壁孔膜，トールスと類似した構造を持ち，UV 顕下で有縁壁孔と同様の性質を示す。またこの壁孔様構造と有縁壁孔との間には連続した中間的構造の存在が認められ，実際に有縁壁孔と相同であると考えられる。

vii) 異常型は上記のものの内，その正常な形状から逸脱するものである。ある構造を異常型とみなすか否かはその逸脱の程度による。いくつかの異常の種類，すなわち全体の形の異常，セントラルコアの形の異常，細胞壁沈着における異常等が区別される。

3) トラベキュレーとその関連構造 (tangential confluence を除く) は様々な長さの列あるいは単独で見出される。列の長さは形成層帯における原基形成の位置により左右されると考えられる。列の方向はかならずしも仮道管の長軸と直角ではなく，常に放射組織の方向と一致する。

トラベキュレーと，tangential confluence を除く関連構造は晩霜の影響を受けた初期早材部および人為的に形成されたあて材から正常材への移行部に特に多く見出された（正常材からあて材への移行部においても出現の頻度はかなり高かった）。前者の場合，adhesion と長い列をなすトラベキュレーが多く，後者では confluence の出現頻度が高く，長い列はまれであった。

これらの構造はしばしばゆるいグループをなして在存する。時おり 2〜3 本のトラベキュレーの列がごく接近して互に平行に走ることがあり，またいくつかの異なる基本型から成る異性列も見られた。一つの細胞内のごく限られた個所にいくつかの異なる基本型のものがごく接近して出現することもある。またいくつかの構造が単独あるいは短かい列を成して半径方向にかなりの間隔を持って配列することがある。

トラベキュレーとその関連構造 (tangential confluence を除く) は，異常な細胞分裂によって生じたと考えられる細胞の半径方向の枝分かれ，あるいは細胞の吻合様の構造等に接近して出現することがある。またトラベキュレーと，tangential confluence を除く関連構造の近傍には，しばしば異常な接線面壁孔が見出される。

4) トラベキュレー，plate, confluence, adhesion は互に接近して出現することが多く，またしばしば一つの共通の列を成す。さらにこれらの型の間にはすべての中間的構造が存在することから，これらの構造は一つの共通の原因によって形成されると推定される。一方 tangential confluence は上記の型のものとともには出現せず，またそれらの構造との中間型も見出されていない。したがって tangential confluence は他の異なる種類の構造である可能性が大きいといえる。

　5)　以上の事実，その他の事実，および文献からトラベキュレーとその関連構造の形成原因
について詳細な考察を行った。tangential confluence を除いて，これらの構造の形成には核の
ある種の活動が関係していると考えられる。異常な細胞分裂がその主要因であるとする一つの
仮説を提出した。これはこれまでに出されたほとんどすべての仮説をも説明するものである。

Explanation of photographs

Note：　　　　The scale of magnification is given in the unit of micrometer.

Plates I to IV.　Trabeculae

Photo　1.　　A rod-like trabecula in a normal wood tracheid. A neck is seen at the right base (arrow). The inner most layer is the S3.

Photo　2.　　A rod-like trabecula in a well-developed compression wood tracheid. Distinct spiral grooves are present running nearly in parallel to the long axis of the trabecula. Minute compression failures are seen on each rib. The inner most layer is the S2.

Photo　3.　　A trabecula in a well-developed compression wood tracheid. The grooves on the trabecula are not distinct. A compression failure occurring on the whole trabecula is seen at left.

Photo　4.　　Thick trabeculae in mild compression wood tracheids. They may be elliptic in cross section. The orientation of the microfibrils of the inner most layer (S2) is helical along the long axes of the trabeculae.

Photo　5.　　Longitudinal cut surface of a relatively thick trabecula in a mild compression wood tracheid. A thick layer which would correspond to the middle lamella (thick arrow) and that to the S2 layer (double arrow) are distinguishable.

Photo　6.　　Longitudinal cut surface of a thick trabecula in a well-developed compression wood tracheid. Layers which would be identical to the middle lamella (thick arrow), the S 1 (fine arrow) and the S2 layer (double arrow) are seen.

Photo　7.　　A trabecula in a well-developed compression wood tracheid. The course of the microfibrils of the S2 layer running through the trabecula is well illustrated.

Photo　8.　　Longitudinal cut surface of a trabecula in a well-developed compression wood tracheid. Intercellular spaces at the bases of the trabecula are seen.

Photo　9.　　Longitudinal cut surface of a thick trabecula in a well-developed compression wood tracheid. Since the opposite view gave a similar image, this structure is believed not to be a part of the host cell wall but a trabecula. Intercellular spaces are fused into a common room.

Photo 10.　　A trabecula in a moderate compression wood tracheid. The microfibrils of the wall of the trabecula are divided into two bundles running nearly in parallel to the orientation of microfibrils in the S 2 layer of the host cell. Because of such a pattern of microfibrilar deposition, depressions are formed at the bases of the trabecula (arrow).

Photo 11. A trabecula in a mild compression wood tracheid. Grooves are seen only at the base of the trabecula. The grooves might be different from those found in well-developed compression wood tracheids in nature.

Photos 12 a–c. Transverse views of a trabecula in a normal wood tracheid represented by SEM–UVM combination method (a : SEM, b : UVM, c : PLM). UV-absorption of the central core is not so strong as that of the middle lamella. The trabecula shows no birefringence between crossed nicols.

Photos 13 a–c. Transverse views of a trabecula in a mild compression wood tracheid (SEM–UVM combination method). UV-absorption of the trabecula shows a quite similar distribution pattern to that of the host cell wall.

Photos 14 to 21. UV-photographs of cross sections of trabeculae showing the variety of the central core in the strength and distribution pattern of UV-absorption, and in form. Since these photographs were taken from the samples containing the transitional zone from compression to normal wood, some of them show features of slight compression wood tracheids.

    A core with a similar strength of the absorption to the middle lamella (Photo 14) ; almost no absorption in the mid portion of the core (Photo 15) ; a core with a similar strength of UV-absorption to the wall (Photo 16) and that shifted from the central position (Photo 17) ; elongated central cores with a part of weak absorption (Photo 19) and with strong absorption (Photo 18) ; an elongated core orienting at right angles to the long axis of the host cell (Photo 20) ; a core in a more or less irregular form (Photo 21).

Photos 22 a, b. A short row of trabeculae in typical compression wood (not cut exactly along their long axis) (a : UVM, b : PLM). At the base of a trabecula lower UV-absorption and strong birefringence of the S 1 layer are seen (arrows).

Photo 23. Matched SEM-photograph of the trabecula shown in Photo 16. The central core can be recognized as a slight depression.

Photo 24. Matched SEM-photograph of the trabecula shown in Photo 18. The elongated central core is seen in a different texture from the secondary wall.

Photos 25 a, b. Transverse cut surface at the base of a thick trabecula in a well-developed compression wood tracheid (SEM–UVM combination method). The spiral grooves reach the "outer" most layer of the S2. The S1 layer is seen as a brighter ring. The central core is flatened.

Photos 26 a, b. Transverse cut surface of a thick trabecula in a well-developed compression wood tracheid (SEM–UVM combination method). An intercellular space is seen in the middle of the trabecula. The space is encircled with a zone of strong UV-absorption (middle lamella).

Photos 27 a, b. Transverse cut surface of a trabecula in a mild compression wood tracheid (SEM–UVM combination method). The wall of the trabecula is fused with the S2 layer of the host cell but the central core is not connected with the middle lamella.

Plates V and VI. Plates

Photo 28. A plate in a normal wood tracheid. The inner most layer is the S3. The orientation of the microfibrils of this layer on the plate is nearly perpendicular to the long axis of the tracheid as on the host cell wall.

Photo 29.   Twin plates found in the transitional zone from normal to compression wood. The inner most layer is the S2. Spiral grooves on the plates run in parallel to those of the host cell wall except at their margins. Depressions are seen at the bases of the plates (arrows) as is the case of trabeculae (Photo 10).

Photos 30 a–c.   Transverse views of a plate in a mild compression wood tracheid represented by SEM–UVM combination method (a: SEM, b: UVM, c: PLM). No connection to the radial wall of the host cell is seen. The central core has a similar strength of UV-absorption to the middle lamella. The texture of the cut surface and other natures of the plate under an UVM and PLM are the same with those of the host cell wall.

Photos 31 a–c.   Longitudinal views of a plate found in the transitional zone from normal to compression wood (SEM–UVM combination method). The plate shows the same natures with the host cell wall in a SEM and under an UVM and PLM.

Photo 32.   A relatively narrow plate in a well-developed compression wood tracheid. The angle of spiral grooves to the long axis of the tracheid is slightly greater than that of the host cell wall. Minute compression failures are seen.

Photo 33.   Twin wide plates in typical compression wood. They are the widest of those found in the present study by SEM.

Photo 34.   A transverse view of a plate in a typical compression wood tracheid. The texture of the cut surface is quite similar to that of the host cell. The central core shows a slight sigmoid curve.

Photo 35.   Twin plates in the transitional zone from compression to normal wood. They have the characteristics of both normal and compression wood, i. e., the presence of the S3 layer and intercellular spaces.

Photos 36 a, b.   Longitudinal views of similar plates (cross section of tracheids) found in the transitional zone (a: UVM, b: PLM). They are apparently a part of the host cell wall.

Plate VII. Confluences

Photo 37.   A confluence in the transitional zone from normal to compression wood. The occurrence of pebble-like deposits is one of the characteristic features of this zone. The inner most layer is the S2.

Photo 38.   A confluence in a mild compression wood tracheid. The inner most layer is the S2. The orientation of microfibrils in the S2 layer is similar to that of the host cell wall except at the tip of the confluence.

Photos 39 a–c.   Transverse views of a confluence represented by SEM–UVM combination method. The confluence is not simply attached to a radial wall but an extension of the host cell wall. The central core is also confluent to the middle lamella. The texture of cut surface and behavior of the walls of the confluence under an UVM and PLM are quite similar to those of the host cell wall.

Photos 40 a–c.   A transverse view of a confluence being bent back.

Plate VIII. Adhesions

Photo 41. An adhesion found in a normal wood tracheid. The tangential walls of two immediately adjacent tracheids situated on the pith and cambial side of the host cell are in contact with one another, and the middle lamella between these two tracheids can be said to be the central core of the adhesion.

Photo 42. An adhesion in a normal wood tracheid. If this adhesion were planed more deeply, this would give a similar appearance to that shown in Photo 41.

Photo 43. An intermediate structure between the adhesion and confluence. The arrow indicates a cavity.

Photo 44. A row of adhesions in well-developed compression wood. The middle lamella between the right and left tracheid gives a different texture from the secondary walls.

Photo 45. Three adhesions in normal wood. Adhesions often occur in several adjacent tracheids slightly shifted to the longitudinal direction of the host cells.

Photo 46. Tangential cut surface of an adhesion. A trabecula is seen on this side of the adhesion.

Photo 47. An adhesion in contact with a ray.

Photos 48 a, b. An intermediate structure between the adhesion and confluence in a normal wood tracheid showing an invagination (arrow) (a: SEM, b: UVM).

Plate IX. Tangential confluences (All photos were taken on the radial surface of the samples.)

Photo 49. A tangential confluence near the tip of a mild compression wood tracheid. Front views of the bordered pits prove this surface is the radial. The appearance of this tangential confluence is quite similar to that of radial confluences,

Photo 50. A tangential confluence with a pit-like structure. This pit-like structure quite resembles those found in radial confluences (Plates X and XI).

Photo 51. An enlargement of Photo 50.

Photo 52. A tangential confluence near the tip of a compression wood tracheid. It gives an impression that it was formed by a mechanical force.

Photo 53. A tangential confluence with a pit-like structure. The appearance of this pit-like structure may be slightly different from those found in radial confluences.

Photo 54. A tangential confluence formed at the tip of a compression wood tracheid.

Photo 55. A tangential confluence with a pit-like structure in a ray tracheid. The pit-like structure is quite similar to those found in radial confluences.

Photo 56. An enlargement of Photo 55.

Plates X and XI. Pit-including form

Photo 57. A confluence with a pit-like gap in a mild compression wood tracheid.

Photo 58.   A confluence with a slit-like opening. Pit-like structures are variable in size from a small slit-like opening to a big ones as shown in the former and this photograph and are usually found in confluences. A half of a thick trabecula is seen on this side of the pit-including confluence.

Photos 59 a–c.   A long confluence with a pit-like structure in a normal wood tracheid represented by SEM–UVM combination method (a: SEM, b: UVM, c: PLM). A pit-membrane-like structure with no appreciable UV-absorption is also seen between the "borders".

Photos 60 a–c.   A short confluence with a pit-like structure in a mild compression wood tracheid (SEM–UVM combination method). A torus-like thickening is also seen (arrow) which has no appreciable absorption in accordance with the fact that lignification of tori had not occurred in the material examined. The form and lignin distribution pattern of the pit-including form are quite similar to those of the bordered pit.

Photo 61.   A plate with a pit-like structure. This is an isolated instance of pit-including plate during the present study.

Photo 62.   A pit-like structure found at the tip of a tracheid.

Photo 63.   Twin confluences with pit-like structures in normal wood. Pit-including forms can constitute a row.

Photo 64.   A similar case to Photo 63 but in well-developed compression wood. The opposite view of the right one is shown in Photo 70, and that of the left was rather a deformed bordered pit similar to that seen in Photo 65.

Photos 65 to 70.   The occurrence of intermediate forms between malformed bordered pits to the typical pit-including form. Torus-like structures are found in Photos 66 and 69. These photographs demonstrate that the pit-like structures are really transformed bordered pits.

Plates XII to XV. Abnormal forms

Photo 71.   A curved trabecula in a mild compression wood tracheid. Curvature occurs in the horizontal plane.

Photo 72.   A disconnected and curved trabecula. Curvature occurs in the vertical plane. Disconnected trabeculae were often found in long rows.

Photo 73.   A disconnected and broken trabecula. This trabecula constitutes a common row with that shown in the above photo. The right half would have been broken by a mechanical force during preparation.

Photo 74.   A disconnected trabecula in a mild compression wood tracheid.

Photo 75.   A disconnected trabecula with protuberances found in a well-developed compression wood tracheid. The trabecula makes a common row with that shown in Photo 2. On the opposite tangential wall a minute cavity is seen.

Photo 76.   A trabecula with uneven wall deposition. This trabecula is deviated from the exact horizontal orientation.

Photo 77.   A disconnected trabecula with abnormal wall deposition. Deformed protuberances on the trabecula and a central-core-like filament on the opposite side are seen.

Photo 78.   A similar abnormal form with a minute holes. A cavity is seen on the opposite tangential wall.

Photo 79.   An abnormal form running in parallel to a normal one. A broken central-core-like filament emerging from and disappearing into cavities on the tangential walls is seen.

Photo 80.   Two broken abnormal forms. These constitute a common row with those shown in the above photo. Cell wall materials are deposited only on the middle of the central core. The breaking of the filaments indicates their fragile nature.

Photo 81.   An abnormal trabecula with spiny protuberances.

Photo 82.   An abnormal trabecula with little wall deposition.

Photos 83 to 85.   An abortive trabecula andj plate. The host cell seems to have been dead in the early stage of the differentiation, since nearly no wall materials are deposited as inferred from the shape of the bordered pits (Photo 83) and as shown in Photo 84. The central cores of trabeculae and plates are thought to generally have the illustrated shapes respectively.

Photo 86.   A structure which is thought to be a malformed confluence.

Photos 87 a, b.   Transverse views of an abnormal trabecula in a mild compression wood tracheid represented by SEM–UVM combination method (a: SEM, b: UVM). The dimension of the central core shown in Photo 87 b corresponds with that of the thin thread in Photo 87 a. The core appears to be composed of several units.

Photos 88 a–c.   An abnormally thick trabecula with an irregular-shaped core (a: SEM, b: UVM, c: PLM).

Photos 89a–c.   An abnormal confluence with a thick central core represented by SEM–UVM combination method. The region of strong UV-absorption in Photo 89 b is seen in different texture in Photo 89 a.

Photos 90 to 93.   Occurrence of abnormal forms in an anastomosed tracheid. The anastomosis would be formed by an abortive periclinal cell division. Deformed trabeculae (Photo 90 arrows and Photo 93) and plate-like structures (Photo 91) are seen. The complicated part [where amorphous structures are seen is enlarged in Photo 92. Similar cases observed by light microscopy are shown in Photos 123 to 127.

Plates XVI to XXI. Pattern of the occurrence and miscellaneous photographs

Photo 94.   Twin form with a trabecula and a pit-including confluence in normal wood.

Photo 95.   A disconncted trabecula making a short row with a plate in mild compression wood.

Photo 96.   Twin form with a short confluence and an adhesion in mild compression wood.

Photo 97.   Occurrence of an abnormal tangential pit near a trabecula in normal wood. Similar examples are also seen in Photos 100, 111 to 113 and 127.

Photos 98 a, b.   Occurrence of a trabecula, plate and abnormal trabecula in the close vicinity in a normal wood tracheid (SEM–UVM combination method). The thickness of the central-core-like filament of the abnormal trabecula seen in the SEM-Photograph corresponds well with that of the dark spot found in the UVM-Photograph.

Photo 99.   Three rows of trabeculae in typical compression wood running in parallel to each other. One emerges from the radial wall, one is almost embedded (thick arrow) and the other is almost planed off (fine arrows); cambial side left. A similar case in normal wood is shown in Photo 108.

Photo 100.   Massed occurrence of trabeculae and confluences in mild compression wood. An abnormal tangential pit is seen.

Photo 101.   Occurrence of two trabeculae, a plate and an adhesion in a limited area of normal wood. The plate and adhesion are also shown in Photos 28 and 41 respectively.

Photo 102.   Three rows of trabeculae (mostly abnormal) and two adhesions. Enlargements of some of these abnormal trabeculae are shown in Photos 78 to 82.

Photo 103.   Occurrence of five trabeculae, two plates, two adhesions and a confluence aligned in a radial direction leaving considerable intervals. This type of occurrence is not rare and implies a genetical tendency of a particular initial liable to form these structures.

Photo 104.   Two long rows of plates. These rows are more than twice the length as those shown in this photograph. The occurrence of such long rows of plates is very rare.

Photo 105.   A row of trabeculae beginning with a wide plate. Such a case of the occurrence is not rare; cambial side right.

Photo 106.   A row of trabeculae beginning with a narrow plate; combial side right.

Photo 107.   A row of trabeculae with a plate in the middle of the row.

Photo 108.   Two rows of trabeculae running in parallel to one another. Some of the units of the row are deviated in alignment. A similar case in compression wood is shown in Photo 99.

Photo 109.   The occurrence of four pairs of plates in two tracheids leaving almost the same intervals. An adhesion is also seen at the top of the photograph.

Photo 110.   A long row of trabeculae running in parallel to the direction of a ray but not at right angles to the long axes of the tracheids.

Photo 111.   Massed occurrence of adhesions found in early-earlywood affected by late frost (arrow). Confluences and abnormal tangential pits are also seen. Such features are common in frost affected tissues; cambial side right.

Photo 112.   Massed occurrence of adhesions found in a not-frost-affected region. Here also confluences and abnormal tangential pits are seen.

Photo 113.   Massed occurrence of plates. Very wide plates are seen. Such a type of occurrence of plates was rare. A row of trabeculae is seen at right bottom.

Photo 114.   A heterogeneous row composed of an adhesion and plates differing in width; cambial side right.

Photo 115.   A row comprising two trabeculae and two plates; cambial side right.

Photo 116.   A pit-including confluence making a common row with plates; cambial side right.

Photo 117.   A short row composed of a trabecula and two pit-including confluences; cambial side right.

Photo 118.   A twin form with a trabecula and a pit-including confluence.

Photo 119.   A long row of trabeculae penetrating parenchyma cells of a resin canal tissue. Trabeculae are thick in late-latewood.

Photo 120.   . An disconnected trabecula with spiny projections.

Photo 121.   Abnormal trabeculae found in the first- and second-formed tracheid in early-earlywood. These trabeculae belong to the same row with that shown in Photo 119.

Photo 122.   A disconnected and a thick abnormal trabecula.

Photos 123 to 127.   Occurrence of anastomoses of tracheids. Plates stretching over seemingly two tracheids are seen in Photos 124 and 126, and amorphous structures are clearly seen in Photo 125. In Photo 127 trabeculae, a plate and an adhesion occur in the neighborhood. SEM-observation of a similar case is shown in Photos 90 to 93.

Photos 128 to 130.   Radially branched tracheids. They were found in early-earlywood affected by late frost. An adhesion (Photo 128 arrow), a trabecula (Photo 129 arrow) and a confluence (Photo 130 arrow) are seen in the close vicinity of the branching.

Plate II

Plate III

Plate IV

Plate VI

Plate VIII

Plate X

Plate XII

Plate XIV

M. Yumoto

Plate XVI

M. Yumoto

Plate XVIII

110

50

111

50

112

50

113

50

Plate XX