SOME STRUCTURAL AND EVOLUTIONARY ASPECTS OF COMPRESSION WOOD TRACHEIDS

Nobuo Yoshizawa and *Toshinaga Idei*

Associate Professor and Associate Professor of Wood Products
Utsunomiya University, Faculty of Agriculture
Department of Forestry, Utsunomiya 321, Japan

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ABSTRACT

Structural changes during the transition between normal wood and compression wood were observed. A comparison was made among gymnospermous species with respect to variations in the common features of compression wood tracheids. The results suggest that compression wood has undergone a certain evolutionary development. In *Taxus, Torreya,* and *Cephalotaxus,* the helical thickenings are retained even in the severe compression wood but not in *Pseudotsuga, Picea,* and *Larix* which instead form helical cavities. Helical thickenings have undergone evolutionary specialization. The rounding of cell shape and the excessive lignification in the S2 layer are considered to be essential elements for the formation of compression wood.

Keywords: Compression wood, gymnosperms, helical thickenings, helical ridges and cavities, lignification, secondary wall.

INTRODUCTION

The association of compression wood formation and its function has been investigated by many authors, along with the physiology of compression wood formation (Onaka 1949; Westing 1965, 1968; Wilson and Archer 1977; Shimaji 1983). Compression wood tracheids are characterized by the rounded outline in cross section, the relatively thick S2 layer with highly lignified zone and helical cavities, and the absence of the S3 layer. However, biochemical factors involved in the differentiation of compression wood tracheids with such features quite different from those of normal wood still remain unexplained. The functional significance of compression wood tracheids also has not been understood sufficiently.

More recently, the origin and evolution of compression wood have been reviewed by Timell (1983). Compression wood occurs in Ginkgoales, Coniferales, and Taxales but not in Cycadales and Gnetales (Westing 1965; Timell 1983), although some variations in the characteristics of compression wood tracheids have been found among extant gymnosperms (Timell 1982, 1983; Yoshizawa et al. 1982). From the fossil records, compression wood in the ancient gymnosperm, *Ginkgo biloba,* seems to have existed since the Permian (Westing 1965), but *Ginkgo* does not form helical cavities (Timell 1978b; Yoshizawa et al. 1982). The members of *Taxus* also do not form helical cavities in their tracheids even in the severe compression wood (Jute and Levy 1973; Timell 1978a; Yoshizawa et al. 1984, 1985a, b). The members of Araucariaceae, which are regarded as more primitive species among conifers, seem to be hard to form helical cavities (Timell 1983). A few primitive angiosperms, on the contrary, seem to form reaction cells resembling compression wood (Onaka 1949; Höster and Liese 1966; Meylan 1981).

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The objective of this paper is to obtain information on the function and evolutionary development of compression wood tracheids. Based on the results, some structural and evolutionary aspects of compression wood tracheids are discussed.

MATERIALS AND METHODS

Materials were obtained from artificially inclined stems or branches of 38 gymnospermous species covering 31 genera (Table 1) and immediately fixed in glutaraldehyde (2%). Transverse and radial sections varying in thickness from 6–20 μm, were made with a sledge microtome. To observe the structure of normal and compression wood tracheids, nonstained sections were examined with a polarizing and a fluorescence microscope. In addition, scanning electron microscopy (SEM) was used to obtain better information about the radial, inner surface of tracheids transitional between normal and compression wood.

RESULTS AND DISCUSSION

Variation among species

A comparison of the characteristics of compression wood in gymnosperms pointed out many variations by species (Table 1). Some features usually associated with compression wood development, such as the roundness of the cross-sectional shape of cells, the lack of the S3 layer, the thickened walls, and the excessive lignification in the S2 layer were confirmed in all of the 38 species examined. Helical ridges and cavities never occurred in the compression wood tracheids of *Ginkgo, Taxus, Torreya,* and *Cephalotaxus.*

Some differences also were seen in the severity of compression wood development in the early spring wood among species (Table 1). Early spring wood is often recognized as a thin band of lighter wood in the compression wood zone (Côté et al. 1967), which results in slightly thinner cell walls at the beginning of a growth ring. Lighter early spring wood tracheids are characterized by lacking some common features of compression wood tracheids (Côté et al. 1967; Yoshizawa et al. 1982). In most of the species without light-colored bands, however, the tracheids in the early spring wood were rather thicker walled than in the latewood, and helical cavities often were well developed (Côté et al. 1967; Yoshizawa et al. 1982). According to Harris (1976), compression wood severity of early spring wood tracheids could be classified into three wood types: normal, mild, and severe, the differences of which suggest that a different sensitivity of cambial response to the stimulus of compression wood formation must exist among species.

Transition between normal and compression wood

Usually, the changes of cell-wall structure during the transition from normal to compression wood proceeded as follows (Fig. 1): (1) disappearance of the S3 layer, (2) increase in the intensity of lignification and in the cell wall-thickness, (3) development of helical ridges and cavities, and (4) the rounding of the cross-sectional shape. In the transition from compression to normal wood, the cell-wall structure changed as follows (Fig. 2): (1) disappearance of the helical cavities, (2) reappearance of the S3 layer, (3) decrease in the wall thickness, and (4) decrease

TABLE 1. *Characterization of compression wood based on some anatomical features.*

Family	Species	CW					Wood type of ESW
		S3	S2 (L)	HC	R	HT	
Ginkgoaceae	*Ginkgo biloba*	–	+	–	+		S*
Taxaceae	*Taxus cuspidata*	–	+	–	+	+	S*
	Torreya nucifera	–	+	–	+	+	S*
Podocarpaceae	*Podocarpus macrophyllus*	–	+	+	+		S*
Araucariaceae	*Araucaria brasiliana*	–	+	+	+		M*
Cephalotaxaceae	*Cephalotaxus harringtonia*	–	+	–	+	+	S*
Pinaceae	*Abies firma*	–	+	+	+		M
	Abies sachalinensis	–	+	+	+		M
	Cedrus deodara	–	+	+	+		N
	Larix leptolepis	–	+	+	+	–	M
	Picea abies	–	+	+	+	–	M
	Picea glehnii	–	+	+	+	–	M
	Picea jezoensis	–	+	+	+	–	M
	Pinus pentaphylla	–	+	+	+		S
	Pinus densiflora	–	+	+	+		S
	Pseudotsuga japonica	–	+	+	+	–	M
	Tsuga sieboldii	–	+	+	+		S
	Pseudolarix kaempferi	–	+	+	+		M
	Keteleeria davidiana	–	+	+	+		M*
Sciadopityaceae	*Sciadopitys verticillata*	–	+	+	+		M*
Taxodiaceae	*Cryptomeria japonica*	–	+	+	+		S*
	Cunninghamia lanceolata	–	+	+	+		S*
	Glyptostrobus pensilis	–	+	+	+		N
	Metasequoia glyptostroboides	–	+	+	+		M
	Sequoia sempervirens	–	+	+	+		S*
	Sequoiadendron giganteum	–	+	+	+		S*
	Taiwania cryptomerioides	–	+	+	+		S*
	Taxodium distichum	–	+	+	+		S*
Cupressaceae	*Biota orientalis*	–	+	+	+		M*
	Chamaecyparis obtusa	–	+	+	+		S*
	Chamaecyparis pisifera	–	+	+	+		S*
	Cupressus goveniana	–	+	+	+		S*
	Juniperus rigida	–	+	+	+		S*
	Juniperus chinensis	–	+	+	+		M
	Juniperus virginiana	–	+	+	+		S*
	Thuja occidentalis	–	+	+	+		M
	Thujopsis dolabrata	–	+	+	+		S*
	Libocedrus macrolepis	–	+	+	+		S*

This table is constructed based on the order of species evolution (Lawrence 1951). CW = compression wood, ESW = early spring wood, S2 (L) = lignin-rich layer in S2, HC = helical cavities, R = roundness of cells, HT = helical thickenings, + = present, – = absent. Asterisk denotes species without the lighter band. ESW are classified into 3 wood types by compression wood severity: Normal, mild and severe. Presence/absence of helical thickenings in compression wood is shown only in species with helical thickenings in normal wood.

in the intensity of lignification. These successive changes of cell-wall structure coincided well with previous observations (Fujita et al. 1979; Yumoto et al. 1982b). Structural changes during the transition between normal and compression wood suggest that the responsive presentation appears more quickly in the deposition of cellulose microfibrils in the secondary wall layers and helical thickenings than in the excessive lignification in the S2 layer.

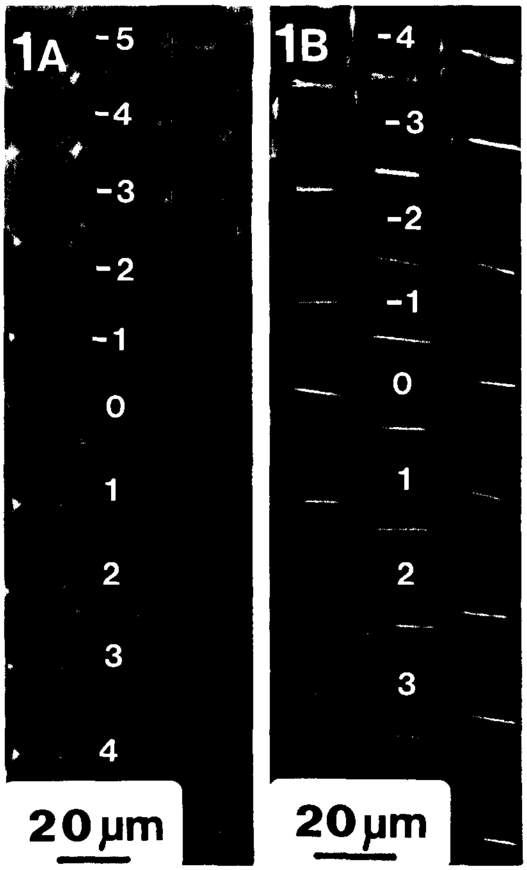

FIG. 1. Cross-sectional transition from normal (lower parts) to compression wood (upper parts) in *Taxus cuspidata.* A: fluorescence micrograph. B: polarizing micrograph. Negative sign indicates the lack of S3 layer. Cell (0) is the last cell possessing S3 layer. A new lignin-rich layer in the S2 layer appeared at cell (−2).

In *Taxus, Torreya,* and *Cephalotaxus,* which have helical thickenings on the inner surface of normal wood tracheids, the transition from normal to compression wood entailed the preservation of helical thickenings (Fig. 3). In these species, the direction of helical thickenings has gradually changed from an S- to a Z-helix, or a Z- to an S-helix during the transition from normal to compression wood, or vice versa, respectively (Fig. 4), corresponding to the changes of the stimulus due to inclination (Yoshizawa et al. 1984, 1985a). The disappearance or restoration of the S3 layer occurred coincidently with or immediately after the beginning of the shift of helices in the course of either transition (Yoshizawa et al. 1985b). On the other hand, helical thickenings of *Pseudotsuga,* and also of *Picea* and *Larix* if present, were replaced by helical cavities, after the disappearance of S3 layer, during the transition from normal to compression wood (Fig. 5).

Based on the structural changes during the transition between normal and

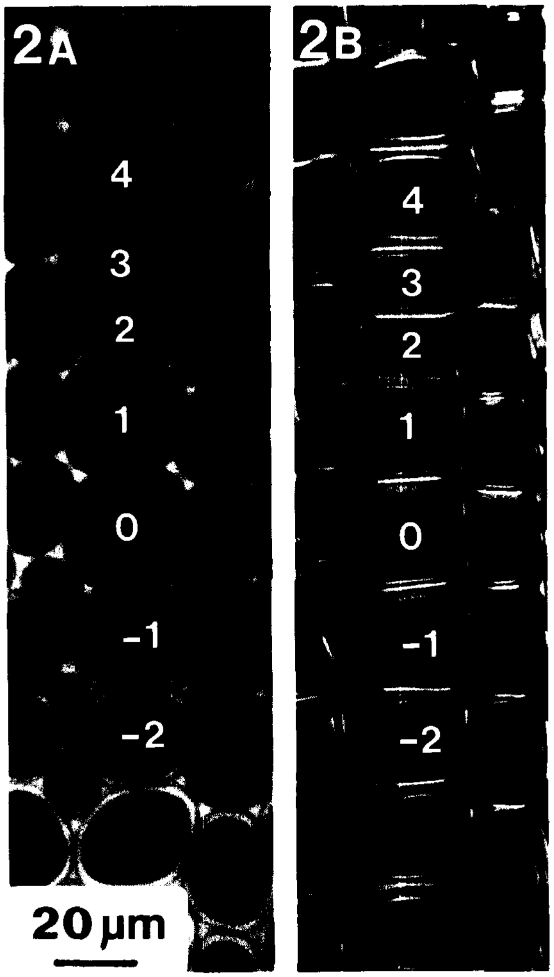

FIG. 2. Cross-sectional transition from compression (lower parts) to normal wood (upper parts) in *Abies firma*. A: fluorescence micrograph. B: polarizing micrograph. Negative sign indicates the lack of S3 layer. The S3 layer reappeared from cell (0) to cell (4). The intensity of lignification in the S2 layer gradually decreased.

compression wood and some variations in characteristics of compression wood tracheids, the rounding of cell shapes and the excessive lignification in the S2 layer are considered to be essential for the formation of compression wood tracheids. Yumoto et al. (1983) pointed out in their extensive investigations concerning the gradation of the severity of compression wood tracheids, that the occurrence of helical cavities and the excessive lignification are thought to have primary importance in the functional significance of compression wood. However, the ability to form helical cavities is not always present in gymnospermous species (Westing 1965; Timell 1978a, b; Yoshizawa et al. 1982). Helical cavities would seem to have developed somewhat later than the other structural characteristics

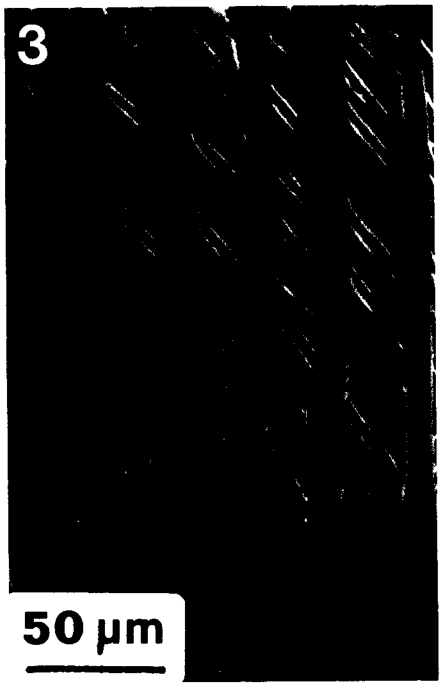

FIG. 3. Tracheids in compression wood of *Torreya nucifera* with Z-helix of helical thickenings. SEM.

of the compression wood tracheids. Further investigation should be made on whether or not helical cavities are involved in the essential elements of compression wood formation.

Structural aspects

It is of interest to note what the structural changes during the transition from normal wood to compression wood mean. The differentiating compression wood tracheids might develop appropriate structural features that differ considerably from those of normal tracheids. Compression wood cells must stabilize the resulting shape of the tissues that exert compressive stress on the tracheids when they have lost high turgor pressure. The rounding is established during the enlargement of cells (Yumoto et al. 1982a, b). The rounding of cells and the excessive lignification in the S2 layer in compression wood, in a morphological sense, are considered to be manifestations of the resulting function of strengthening tissues, so as to overcompensate for the compression stress.

At the beginning of the deposition of the S2 layer, on the other hand, a tangential contraction in the cell-wall lamellae seems to occur in compression wood (Wardrop and Davies 1964; Boyd 1973). Additional wall materials are subsequently added to the top of the newly created ribs (Côté et al. 1968; Timell 1979), and more lignification occurs in the outer layer of the S2 layer. Helical ridges, which gradually extend toward the lumen through the S2 layer (Casperson and Zinsser 1965; Fujita et al. 1973), seem to have a springlike structure, suggesting that

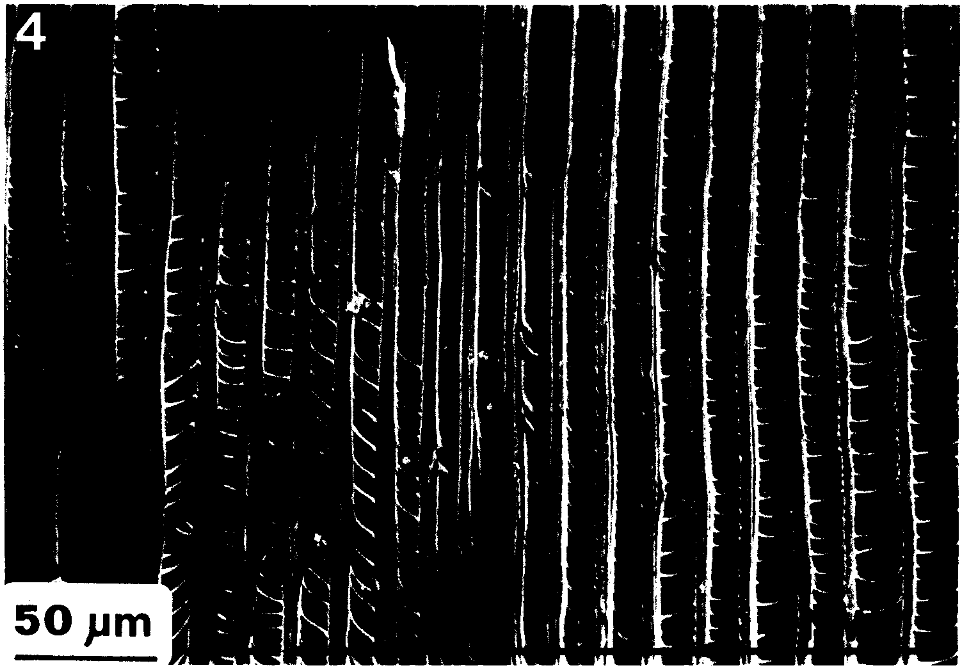

FIG. 4. Transition between normal and compression wood in *Taxus cuspidata* subjected to the alternate treatments of vertical and inclined position. SEM. (Yoshizawa et al. 1985a.)

helical cavities and ridges may play an important role in relaxing compressive strains at the cellular level. It would appear that an excessive lignification in the S2 layer prevents the contraction of the wall lamellae from extending outward. However, such an excessive lignification of the S2 layer can be found in *Ginkgo, Taxus, Torreya,* and *Cephalotaxus.* In these species no helical cavities are formed (Table 1). Interestingly, among the structural characteristics in the tracheids of compression wood, the excessive lignification in the S2 layer remained to the last, even after the appearance of the S3 layer, during the transition from compression wood to normal wood (Fig. 2). Compression wood cells might be reinforced with an extra lignin, when they were subjected to a compressive strain, to stabilize the resulting shape. A relationship between lignification and the contraction of the wall lamellae, as suggested by Boyd (1973), should be further investigated.

Evolutionary aspects

As described above, helical cavities are not always present in extant gymnospermous species. Probably helical cavities have appeared relatively late. When the formation of compression wood gradually ceases, the fact that helical cavities are the first to disappear (Fujita et al. 1979; Yumoto et al. 1982a) makes it probable that they have occurred secondarily in the course of the phylogenic evolution of compression wood (Yoshizawa et al. 1982). This viewpoint can be supported by the less evolved *Pseudotsuga* whose helical thickenings were completely replaced with helical cavities in the severe compression wood, after shifting the direction

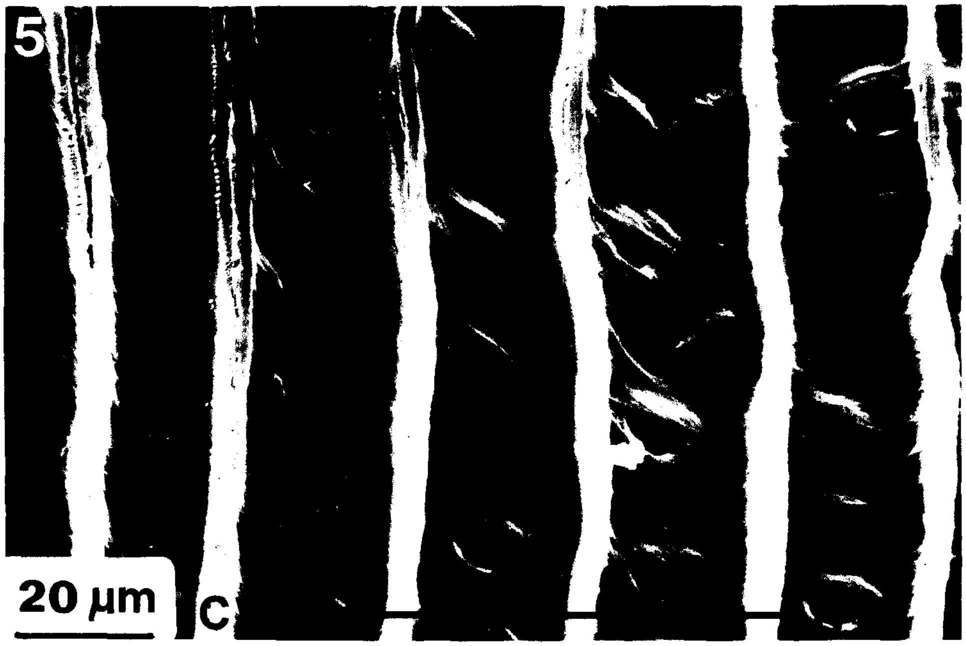

FIG. 5. Transition from normal to compression wood in *Pseudotsuga japonica*. SEM.

of the thickenings from an S- to a Z-helix (Fig. 5). Helical cavities and thickenings often coexist in one and the same tracheid (Yoshizawa et al. 1985b). However, such a phenomenon was never observed in *Picea* and *Larix,* which often have helical thickenings in the latewood tracheids, as well as in *Taxus, Torreya,* and *Cephalotaxus.*

Appearance of helical thickenings in gymnosperms is supposed to be very old, and they are considered to be vanishing as a phylogenic trend (Jute and Levy 1973; Timell 1978b), as exemplified by their absence in most of the gymnospermous taxa. The members of Taxaceae and Cephalotaxaceae still distinctly retain this old feature in compression wood as well as in normal wood. *Pseudotsuga, Picea,* and *Larix* may at present be at the stage of evolutionary development where the thickenings are just disappearing from compression wood tracheids, suggesting that helical thickenings have undergone evolutionary specialization by their loss.

It is considered that compression wood has undergone evolutionary development, as pointed out by Timell (1983). With respect to the extant gymnosperm orders, compression wood appears to be present in all members except for Cycadales and Gnetales, the most primitive and the most advanced ones among gymnosperms respectively (Westing 1965), although differences in the severity of compression wood development are seen, especially in the early spring wood (Table 1). Interestingly, as also seen in the structural changes during the transition from compression wood to normal wood, the helical cavities are the first to disappear (Fujita et al. 1979; Yumoto et al. 1982a). Certainly *Ginkgo* can form compression wood, but no helical cavities in compression wood tracheids. The same is true for *Taxus, Torreya,* and *Cephalotaxus,* but not for *Pseudotsuga.* It also is of interest to note that the members of the Winteraceae, which is generally considered as one of the most primitive among the angiosperms, seem to form reaction wood similar to compression wood (Meylan 1981), and that in Magnoliaceae no reaction wood is formed (Onaka 1949).

More information regarding the evolutionary development of compression wood is still required to describe the origin and evolution of compression wood among extant gymnosperms.

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