Longitudinal shrinkage of compression wood in dependence on water content and cell wall structure

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Abstract

Compression wood from branches of *Pinus silvestris* L. was examined. Wide differences were noted in longitudinal shrinkage of the wood when dried from water saturated state. A relation was found between shrinkage and cell wall thickness, particularly of layer S_2 , and the degree of callose accumulation in the wall. No dependence could be revealed between the shrinkage and the fibril angle in S_2 .

INTRODUCTION

Compression wood occurs in coniferous trees on the lower side of branches or inclined tree trunks. In the case of branches subjected to the action of directional forces, as for instance gravitation or wind, this wood appears on the side opposite to the direction of the acting force. If we change the angle at which the branch was situated, compression wood will form on the side of the branch which will make it return by bending to the correct position. An exhaustive review of problems concerning the occurrence and formation of compression wood is given by Westing (1965, 1968).

Formation of compression wood is the reaction of woody stems to displacement for restoring the appropriate position by active bending resulting from expansion of compression wood. According to the hypothesis of Hejnowicz (1967) the expansion is due to water imbibition into the walls of compression tracheids, causing longitudinal swelling. Compression wood cut out of the stem in fresh state often expands longitudinally. Such wood has been called by Hejnowicz active

compression wood, in distinction from neutral compression wood which shows no expansion when freed from restraining forces in the trunk.

At present some authors believe that lignification generates the active force in compression wood expansion (Boyd 1973a, b; Scurfield 1973). According to Boyd (1972), lignin occupies in the cell wall similar sites as does water. The role of lignin in generation of stress would thus be similar to that of water.

The detection of callose (laricinan) in compression wood (Brodzki 1972) throws new light on the mechanism of expansion of this wood. The fact that air dry callose may after soaking increase its volume sixfold (Eschrich 1965) seems to indicate that this substance is one of the main factors generating longitudinal expansion of compression wood.

In compression tracheids callose occurs inside the helical splits in the S_2 layer. On thin cross sections it is visible in the form of radial branched bands, and on longitudinal sections in the form of long helical bands (Fig. 1 A, B). On thicker cross sections fluorescing callose appears in the form of a homogeneous clear field in the S_2 layer.

Fig. 1. Callose fluorescence in compression wood of *Pinus silvestris* L. in the presence of anilin blue

A — compression wood tracheids in oblique transection. Within the tracheid the section runs on one side parallelly (at the bottom) and on the other perpendicularly to the helical splits containing callose. B — compression wood tracheids in longitudinal section. Callose is visible in the form of helically running bands in the S_2 layer of the secondary cell wall

Compression wood tracheids exhibit not only the presence of callose but also a number of other characters: a greater cell wall thickness, particularly in the S_2 layer, an increased lignin content, a round shape on the cross sections and less steep fibrils in the S_2 layer.

Each of these characters, independently of others may be more or less pronounced, therefore the compression tracheids may differ somewhat in structure from each other. The widest variations are observed in the structure of the S_2 layer of the secondary wall of the cells.

It is known that during drying compression wood shrinks considerably in longitudinal direction. According to Côte (1968) the contraction may amount to 6—7 per cent of the length, whereas in ordinary wood it is as low as 0.1—0.2 per cent. Wooten, Barefoot and Nicholas (1967) report that the contraction of compression wood may exhibit still wider differences within the range of 1.0 to 8.6 per cent. The preliminary studies of the present author confirmed this finding. In view of these observations, the present studies were undertaken in order to establish the relation between the degree of contraction of the compression tracheids and the wall structure. Contraction of the tracheids was investigated in respect to the characters which show the widest variation, thus, the thickness of the S_2 layer and the degree of callose accumulation. The fibril angle was also taken into account.

MATERIAL AND METHODS

As material for investigation served branches aged 3-7 years from about 10-year-old *Pinus silvestris* L. trees.

For examination of compression wood, branch segments cut about 10 cm above their base were used. Wood samples were taken from the entire annual ring on the lower side of these branches.

Fresh wood samples or eventually after soaking were cut on a microtome into tangential sections of 40 and 30- μ m thickness. They were placed on glass in a water drop and their length was measured. After air drying the measurements was repeated in order to determine the extent of shrinkage of the wood. The shrinkage was expressed as the percentual difference in length of wet and air-dried samples. Air-dried wood still contained 13—18 per cent of water (mean ca. 15%). Since the studies were of comparative character, it was not necessary to dry the wood completely.

From the longitudinal sections, cross sections were cut (by means of a freezing microtome holder) in order to determine the thickness of the S_1 and S_2 layers of the secondary wall in the fluorescence and polarization microscopes. Part of the material was macerated in order to examine the structure of the cell wall in a polarizing-interference microscope. The fibril angle in layer S_2 was measured by means of a goniometric ocular on tracheids macerated in acetic acid and hydrogen peroxide (1:1). Since the course of the helical splits is parallel to the arrangement of the fibrils, the fibril angle was determined by measuring the angle of splits.

Callose was detected in sections placed in a drop of anilin blue solution of 1:2500 concentration, pH 8.2 and inspected in a fluorescence microscope (Brodzki 1972). The light source was a maximum pressure mercury-vapour lamp equipped with a BG 3/4 filter or two BG 12/2 filters. A GG9/OG1 filter was used on the ocular.

RESULTS

Water-saturated and then dried compression wood changes in length considerably along the long axis of the tracheids. This kind of change in length of compression wood will be shortly termed shrinkage.

Measurements of shrinkage were performed on series of tangential sections. Each series comprised the complete annual ring of compression wood. Wide differences in shrinkage were found between the successive tangential sections (Fig. 2).

Wood showing lower shrinkage shone but weakly in the fluorescence microscope what indicates a rather low amount of callose. In reflected ordinary light the wood was more whitish. Wood characterized by maximal shrinkage showed in the fluorescence microscope an intensively fluorescing thick callose zone in the S_2 layer of the secondary wall (Fig. 2), where in reflected light it was darker.

In order to check whether the thickness of the section has any influence on shrinkage, serial sections from two neighbouring blocks cut one above the other were compared. In one series the thickness was 30 and in the other 40 μm . The course of shrinkage in both series was similar (Fig. 3), however, shrinkage of the thinner sections was consistently somewhat higher than of the thicker ones. Therefore care was taken to use sections of the same thickness.

Shrinkage was also determined in dried fragments of the annual ring not cut into sections. A fragment of the ring of compression wood from which the series were taken shrunk by 4.9 per cent (Figs. 2, 3). This value, as seen, corresponds to the mean shrinkage value for sections 40 μm thick.

For detailed examination of the S_2 layer two sections showing the lowest shrinkage in the series, further denoted by the symbol CW^- , as well as two of highest shrinkage (CW^+) were taken. It was found in fluorescence microscope analysis of the cross section that the CW^+ tracheids which shrink 7.16 and 7.14 per cent had a thicker callose zone in the S_2 layer and a smaller lumen than the CW^- tracheids (3.92 and 3.61). The tracheids obtained by maceration of CW^+ showed wider and deeper helical splits in the polarizing-interference microscope than did the tracheids from CW^- sections (Fig. 4).

Fig. 2. *Pinus silvestris*, 3rd annual ring on the lower side of a 3-year branch. The wood is of compression type throughout the whole radius of the ring

A — callose fluorescence on transverse section. The bracket indicates the annual ring (with outer part absent on the section). Tracheids from sites indicated by arrows are shown in Fig. 4. B — longitudinal shrinkage of successive 30 μ m thick sections (from comparison of section length in wet and dry state)

It was necessary to verify whether the above described observations are of any general significance. For this purpose tangential sections of CW⁻ and CW⁺ compression wood from different-aged branches (3-7 years) from tress growing on various sites in Lower Silesia were examined. In each the compared CW⁻ and CW⁺ pair was taken from the same annual ring and the same radius. It was found that wide dif-

Fig. 3. *Pinus silvestris* L., 3rd annual ring on the lower side of 3-year branch. The wood is of compression type throughout the whole radius of the ring

Comparison of longitudinal shrinkage of section series from two neighbouring blocks cut one above the other. One series of 30 μm and the other of 40 μm thickness

ferences in shrinkage corresponded always to large differences in the thickness of the S_2 layer and in the degree of callose accumulation (Fig. 5). The tracheids of compression wood of high shrinkage were not only thicker and showed more intense callose fluorescence, but they were more lignified.

Callose is localized in the helical splits (Brodzki 1972). Since the splits are not as deep as the S_2 layer, the thickness of the callose layer is smaller than that of S_2 . The difference may be seen best in the polarization microscope, owing to the sharply delineated border between S_1 and S_2 (Fig. 6). The differences in the thickness of the callose layers of CW^- and CW^+ are somewhat wider than those in the thickness of the S_2 layers.

Fig. 4. Compression tracheids differing widely in longitudinal shrinkage. Photographs of sites denoted by arrows in Fig. 2A. The shrinkage is marked in the lower right corner of the picture

A and C — Callose fluorescence in compression tracheids on cross section; B and D — Tracheids after maceration of sections seen in interference microscope

Callose deposition occurs during the formation of the S_2 layers. When analysing compression wood in the zone of wood differentiation, intensive fluorescence of callose in the S_2 layer is noticeable (Fig. 7). Callose appears in this layer earlier than does lignin. Tangential sections taken from the zone with profuse callose where the S_2 layer is not yet lignified, show a higher shrinkage than those from the same wood in mature state where the process of lignification in the S_2 layer is finished.

It was also checked whether the fibril angle in the S_2 layer has any influence on the shrinkage of compression wood. For this purpose 10 compression wood samples were randomly chosen from the material within the shrinkage range 2.74-6.41 per cent.

The results are shown in Table 1. As seen there is no definite relation between shrinkage and the fibril angle in the S_2 .

Fig. 5. Comparison of callose fluorescence in compression wood differing in longitudinal shrinkage, from 6 different *Pinus silvestris* L. individuals.

Two pictures placed one above the other correspond to wood from the same annual ring. Upper row — high shrinkage. Lower row — low shrinkage. The shrinkage is given in the lower right corner

Fig. 6. Compression wood tracheids from *Pinus silvestris* L. in cross section seen in polarizing microscope

A and B — 5th annual ring of 5-year branch, C and D — 5th annual ring of 6-year branch. Shrinkage is indicated in left lower corner

Table

Fibril angle (with respect to tracheid axis) and longitudinal shrinkage of tangential section 30 μ m thick in wood sample from different branches of *Pinus silvestris* L. The samples were located 10—13 mm from the pith (3rd to 6th annual ring)

No.	Shrinkage, %	Fibril angle in S ₂ layer
1	2.74	43.92
2	2.82	38.00
3	2.85	47.92
4	3.03	45.05
5	3.42	44.70
6	5.10	44.70
7	5.28	43.65
8	5.49	39.80
9	6.16	46.77
10	6.41	41.80

Fig. 7. Zone of differentiation of compression wood cells from *Pinus silvestris* L. in the presence of anilin blue seen in fluorescence microscope

A — Callose fluorescence and own unmasked fluorescence of lignin (arrow); B — The same as in A but the own fluorescence of lignin masked by crystal violet

DISCUSSION

Jaccard and Frey (1928) investigating the fibril angle (measured in relation to cell axis) in the wood of coniferous trees established that in normal wood this angle is always smaller than in compression wood. They advanced, on the basis of these findings, the hypothesis that the fibril angle in the cell wall affects the mechanical properties of compression wood. Attention should, however, be called to the fact that differences in fibril angle may result from reasons other than the differentiation into normal and compression wood. For instance young wood lying nearer to the pith has a fibril angle larger than mature wood (Preston, 1952).

Wooten, Barefoot and Nicholas (1967) studied the influence of the fibril angle in the S_2 layer on the shrinkage of compression wood. In order to produce differences in the properties of this wood they tilted 2-year *Pinus taeda* seedlings to various angles and after one year collected blocks of compression wood formed on the lower side during the period of tilting. They determined the shrinkage of whole blocks and then selected for further study those displaying a whole range of shrinkage. From them they prepared radial sections on which they measured shrinkage and the fibril angle in the S_2 layer. They found that this angle in compression wood was smaller (a steeper helix) than in the corresponding opposite wood. Probably the opposite wood situated on the upper part of the branch, on account of excentric annual growth, was closer to the pith than the compression wood. It is known that in young wood its properties including the fibril angle, change with the distance from the pith (Preston, 1952). Thus, the authors were dealing in their experiments with wood variability resulting from the increasing distance from the pith, superposed on variability, due to the formation of compression wood. The results must of necessity be complicated and their interpretation is difficult. It should be borne in mind that these results concern young wood and cannot always be extended to mature wood. For instance, one might believe on their basis that in mature compression wood the helix of fibrils is steeper than in mature normal wood and this certainly is not true.

Wooten, Barefoot and Nicholas claim that in compression wood there is a correlation between the fibril angle in S_2 and the extent of longitudinal shrinkage. That means that the steeper the fibril helix in S_2 the greater is the shrinkage of the tracheids. In the present observations a noticeable relation could not be found between the fibril angle and the shrinkage of compression wood. Our observations were performed on tracheids from sections randomly chosen at more or less the same distance from the pith from various branches aged 3 to 7 years.

The above named authors used various inclinations of the seedlings in order to obtain wide differences in the compression wood. The same diversity is, however, found in compression wood forming in natural conditions on the lower part of branches along the segment beginning more or less 10 cm from the branch base and reaching to its top. These differences occur between wood layers of the same ring and appear probably owing to frequent and wide changes in the situation of the branch during tree growth, which is influenced by the increase in its weight due to growth, the falling of dew and periodical winds from the same direction, etc. It is known that the time of induction of compression wood, is only 24h (Kennedy and Farrar, 1965). If we examine tangential sections from such a branch, the differences in the

properties of compression wood are no smaller than those the above mentioned authors found in radial section from shoots tilted at various angles. Investigations on tangential sections are also noteworthy because they give the possibility of describing in detail the properties of compression wood formed within a short period. Owing to the application of this method, results have been obtained which indicate unequivocally that there are wide variations in the shrinkage of compression wood, reaching 1—8 per cent. The shrinkage of this wood is the greater the thickness of the cell walls, particularly of the S_2 layer and the higher the callose accumulation in this layer.

Boyd (1973a, b) and Scurfield (1973) reached the conclusion that compression wood tends to expand longitudinally owing to the swelling of cell walls as a result of deposition in them of lignin. Lignification is more intensive in compression than in normal wood. The walls of the compression tracheids are poor in cellulose and more porous, therefore lignin can easily penetrate into their walls and be deposited in large quantities. The increased lignin content could, thus, play a role in generation of the expanding force.

The views of Boyd and Scurfield on the role of lignin in eliciting stress in compression wood were advanced at a time when the presence of callose in this wood was not yet known. The occurrence of callose which changes its volume owing to water imbibition should be taken into account in the elucidation of force generation and of the mechanism of compression wood contraction during drying. Callose probably interacts with lignin in the generation of longitudinal stress in compression wood. It would result from the present observations that there exists a close correlation between the degree of callose accumulation in layer S_2 and the extent of longitudinal shrinkage of the tracheids. At any rate, callose occurring in helical slits has a strong influence on the extent of longitudinal shrinkage, owing to its high water content.

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*Zmiany długości drewna kompresyjnego w zależności od zawartości
wody, oraz struktury ścian komórkowych*

Streszczenie

Przebadano drewno kompresyjne *Pinus silvestris* L. w gałęziach w wieku od 3 do 7 lat w mikroskopie fluorescencyjnym z zastosowaniem błękitu anilinowego, w mikroskopie polaryzacyjnym i polaryzacyjno-interferencyjnym.

Drewno kompresyjne cięto na kolejne skrawki styczne i wyznaczano procentową różnicę długości skrawków namoczonych i powietrznie suchych, czyli ich kurczliwość. Stwierdzono duże różnice w kurczliwości różnych warstw drewna kompresyjnego. Skrawki styczne z tego samego słoja rocznego różniące się kurczliwością użyto do sporządzenia skrawków poprzecznych w celu określenia grubości poszczególnych warstw ściany komórkowej i zawartości kalozy. Stwierdzono, że kurczliwość jest tym większa, im grubsza warstwa S2 i większa zawartość kalozy.

Zmierzono także kąt ułożenia fibryl w warstwie S2 na wybranych i zmacerowanych skrawkach pokrywających szeroki zakres kurczliwości. Nie zaobserwowano zależności między kątem ułożenia fibryl w S2, a kurczliwością wybranych skrawków.