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Generation process of growth stresses in cell walls:
Relation between longitudinal released strain and chemical composition

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Summary. To advance the discussion on the evolution mechanism of tree growth stresses, the relation between released strain and the chemical components was investigated experimentally. The expansive released strain in the longitudinal direction assumed large values as the lignin content increased in the compression wood, but there was no relation between released strain and lignin content in the normal wood region. The contractive released strain assumed large values as the cellulose content and its crystallinity increased. Their correlation was very high and clear. From these facts, it is considered that the lignin deposition plays an important role in the generation of the growth stresses in compression wood but is not important in normal or tension wood regions. Cellulose microfibrils contract along their longitudinal axis during cell maturation, and the stress included by the contraction creates a longitudinal growth stress in normal and tension woods.

Introduction

It has been reported that longitudinal compressive stresses in compression wood became large as microfibril angle (MFA) and lignin content increased (Yamamoto et al. 1991). This suggests that the generation of compressive growth stresses in compression wood can be explained by the lignin-swelling hypothesis proposed by Watanabe (1965) and Boyd (1972).

On the other hand, it was reported that extremely large tensile stresses in the L-direction for broad-leaved species (hardwoods) were caused by the gelatinous layer in the case of the species that processed such layers and to a small MFA in species lacking G-layers in the tension wood (Okuyama et al. 1990). These facts suggest that the cellulose-tension hypothesis proposed by Bamber (1978) is applicable to the generation of tensile growth stresses in tension wood. Accordingly, two hypotheses cannot explain the behavior of growth stresses that are observed in normal and reaction woods independently and uniformly.

According to experimental and theoretical evidence, it was considered that growth stresses were generated by an interaction of the swelling of a matrix substance induced

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by a deposition of lignin between the microfibrils and the longitudinal contraction of the cellulose microfibrils during cell wall maturation (Archer 1987; Yamamoto and Okuyama 1988; Okuyama et al. 1990; Yamamoto et al. 1991). The behavior of growth stresses was studied with a model which simplified the cell wall and a qualitative explanation could be given as to the relation between growth stresses and MFA. Nevertheless, the possibility of the generation of tensile stress in cellulose microfibril is a matter of argument.

In this report, we correlate growth stress in the L-direction and cell wall constituents and discuss the role of lignin and cellulose in the generation of growth stresses and especially the contribution of microfibrils in the generation of tensile growth stress, verifying the possibility of longitudinal contraction of cellulose microfibrils, based on quantitative relations.

Experiment

Materials

The following materials were used.

(1) Japanese cedar, Sugi (*Cryptomeria japonica* D. Don)

Tree age:	34 years
Breast height diameter:	21 cm
Tree height:	14.5 m

(2) Japanese cypress, Hinoki (*Chamaecyparis obutusa* Endl.)

Tree age:	21 years
Breast height diameter:	21 cm
Tree height:	8.5 m

(3) Yellow-poplar (tuliptree) Yurinoki (*Liriodendron tulipifera* L.)

Tree age:	15 years
Breast height diameter:	21 cm
Tree height:	8.0 m

The Japanese cedar had straight trunks. Japanese cypress had been planted on a slope and had compression wood on the lower side of the stem. Eccentricity of the crosscut section occurred in Japanese cypress and yellow-poplar.

Yellow-poplar is one of the species that has no gelatinous fibers on the upper side of an inclined trunk. This tree had been planted in a garden and had an inclined stem.

Measurement of released strains

As described in a previous report (Yamamoto et al. 1989), the released strains in the L-direction were measured on the standing trees by a strain gage method. In the case of the Japanese cedar, eleven measuring stations that consisted of several measuring points on the periphery were selected at various heights of the stem. Therefore the sum of all measuring points was 48. At various heights 30 points containing compression wood were measured in the Japanese cypress.

In the case of yellow-poplar, fifteen points were selected at the peripheral positions at which eccentricity was recognized.

Measurement of chemical components

After the measurement of released strains in the L-direction, wood powder of 42–60 mesh was prepared from 5 × 2 × 2 cm sections matched with the measuring points of the released strains.

Determination of lignin content

The lignin content in the wood powder was determined by the Klason method. The lignin content of the yellow-poplar was corrected by means of a determination of acid-soluble lignin as measured by the ultraviolet absorption at 205 nm, because yellow-poplar contains several percentages of acid-soluble lignin (Irwin and Busche 1960).

Determination of alpha-cellulose content

Holocellulose content in the wood powder was determined by the chlorite method. The alpha-cellulose content was determined by extraction with 17.5% $NaOH_{aq}$ of the holocellulose powder.

Determination of crystallinity

The crystallinity of the yellow-poplar wood powder was determined by X-ray diffraction.

Results and discussion

Distribution of released strain in the L-direction

Released strains in the L-direction of the Japanese cedar ranged from a minimum value of −0.007% to a large contraction of −0.07%. These are unusually large contractive strains for normal soft wood. The Japanese cypress had expansive released strains in the L-direction along the lower side of the crooked stem because of the presence of compression wood. At increased height, the released strain changed to contraction. The level of the contractive strains were smaller than that of the

Japanese cedar. The values of longitudinal released strains of the yellow-poplar ranged from −0.01% to −0.1%. Expecting the normal value of about −0.03%, there were positions that had large contractive strains at a level that never appeared in the normal wood region, but the tendency of strain distribution did not correspond to the eccentricity that could be observed in the tension wood.

Major chemical components and released strain

The relation between lignin content and released strain

Figure 1 shows the relationships between lignin content and the released strains in the L-direction of Japanese cedar, Japanese cypress and yellow-poplar. In the Japanese cypress, the expansive released strains tended to increase as the lignin content increased in the compression wood region. This result supports the hypothesis that the increase in lignin content takes part in the generation of compressive growth stresses in compression wood as described in a previous report (Yamamoto et al. 1991). On the other hand, in the normal wood region where contractive released strains were measured, no relationship was observed between contractive released strains and lignin content. This result was similar to that observed for the normal wood region of Japanese cedar. In the yellow-poplar, the lignin content tended to decrease slightly as contractive released strains increased, but a clear correlation was lacking. These facts suggest that large compressive growth stresses in the compression wood region are generated by an increase of lignin but the volume of lignin does not control the magnitude of the tensile growth stresses in the normal wood region.

Alpha-cellulose content and released strain

Figure 2 shows the relationships between alpha-cellulose content and the released strains in the L-direction. In the Japanese cedar, the alpha-cellulose content increased as contractive released strain increased. A similar correlation was observed in the

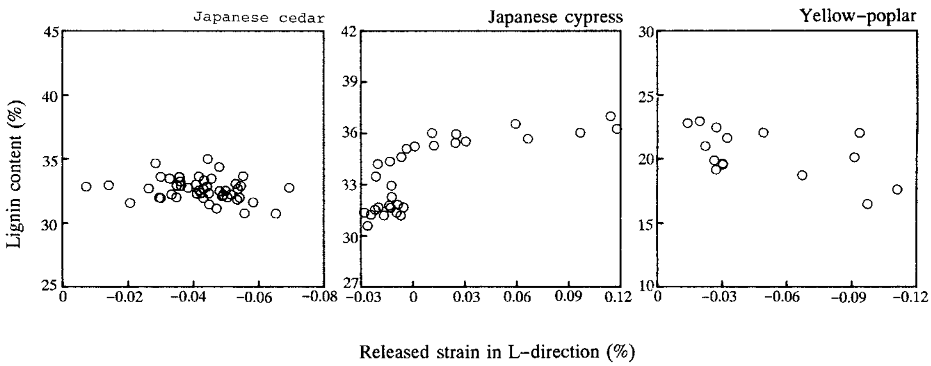

Fig. 1. Relationship between released strain in the L-direction and the lignin content

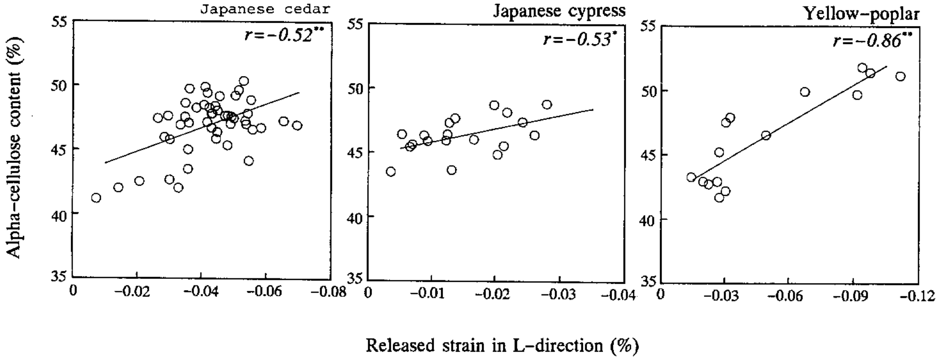

Fig. 2. Relationship between released strain in the L-direction and the alpha-cellulose content

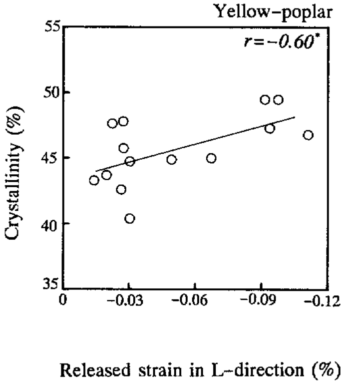

Fig. 3. Relationship between released strain in the L-direction and the crystallinity

normal wood region of the Japanese cypress, but the correlation was less clear in this case, because the measured range of released strains was relatively small. In the yellow-poplar, the contractive released strain became large as the alpha-cellulose content increased. Tension wood in yellow-poplar generated a large contractive strain in spite of the absence of gelatinuous fibers. It is considered that the increase of cellulose microfibrils generated large tensile growth stresses in the L-direction.

These results suggest that alpha-cellulose content (the amount of microfibrils) greatly contributes to generation of tensile growth stresses not only in tension wood but also in normal wood.

Crystallinity and released strain

Figure 3 shows the relationship between released strain and crystallinity of cellulose of the wood powder in the case of yellow-poplar. The contractive released strain tended to increase as the crystallinity increased. This fact coincides with the experience that large contractive released strains are detected at measuring positions that have high values of Young's modulus in the L-direction. Larger amounts of cellulose with its high crystallinity would make the Young's modulus large in the cell wall. It is clear that crystallization greatly contributes to the generation of tensile growth stresses, and the contraction of the cellulose microfibrils during cell maturation controls the generation of tensile growth stresses in both normal and tension wood regions. High tensile growth stresses in the L-direction are generated by increases of cellulose microfibril content and its crystallinity.

Conclusions

In this report, we discussed the relationships between released strain in the L-direction and the amounts of lignin and alpha-cellulose, and the crystallinity of the cellulose. In the compression wood region, a positive correlation was observed between released strains in the L-direction and the lignin content. In the normal wood region, no correlation was observed between the strain and the lignin content, but a clear correlation existed between released strains in the L-direction and the alpha-cellulose content. In normal and tension wood regions, the lignin has little influence on the magnitude of the tensile growth stresses, which are instead controlled by the cellulose microfibrils. The generation of the tensile growth stresses in the L-direction is caused by the contraction of the microfibrils, accompanied by an increase in the crystallinity of the cellulose.

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