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NOTE

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The generation of longitudinal maturation stress in wood is not dependent on diurnal changes in diameter of trunk

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Abstract A hypothetical mechanism for the generation of maturation stress in wood was tested experimentally. The hypothesis was that the maturation stress could partly originate in a physical mechanism related to daily changes in water pressure and associated diurnal strains. The matrix of lignin and hemicellulose, deposited in the cell wall during the night, would be put in compression by the effect of water tension during the next day. The cellulose framework, crystallizing during the day, would be put in tension by the decrease in tension at night and subsequent cell-wall swelling. This was tested on young saplings of sugi and beech. Half of the saplings were submitted to continuous lighting, which canceled diurnal strains. Saplings were tilted 40 degrees, and their uprighting movement was measured. The uprighting movement is directly due to the production of reaction wood and the concomitant development of large longitudinal maturation stress. It occurred in the continuously lighted plants at least as much as in control plants. We conclude that the generation of longitudinal maturation stress in tension or compression wood is not directly related to variations in water pressure and diurnal strains.

Key words Maturation stress · Growth stress · Cell-wall maturation · Continuous lighting · Diurnal strains

Introduction

Large internal mechanical stresses are developed in new wood layers after their differentiation. These stresses appear after cell lignification, and are named maturation stresses. Together with support stresses, they participate in the accumulation of growth stresses inside tree stems during their development.[1] From a biological point of view, maturation stresses are an adaptative response of the tree to its environment. They allow the control and correction of stem shape and orientation. From a technological point of view, growth stresses are an important source of defects. The origin of maturation stress is still a matter of discussion. Boyd[2] proposed that maturation stress originated in the swelling of lignins. Bamber[3,4] claimed that they originate in the tension of cellulose. Okuyama, Yamamoto, and coworkers,[5,6] using a micromechanical approach, showed that good agreement between observations and model simulations was achieved by assuming that both mechanisms coexisted. These results explained the relation between the magnitude and anisotropy of maturation stress and the angle of the microfibrils inside wood fibers.[6,7] However, the question of the origin of the maturation stress remains open at the level of chemical constituents: what is the cause of the internal stress developed inside cellulose and lignin during maturation?

It seems likely that this stress originates in chemical forces at the molecular level. Such a mechanism should induce a compression inside the matrix of lignin and hemicellulose, and a tension inside the cellulose framework. To date, no evidence of the mechanism involved at the molecular level has been provided. Okuyama et al.[8] suggested that a physical mechanism could eventually be involved, in relation with daily variations of cell turgor pressure. The turgor pressure of a living cell results from the difference between internal osmotic pressure and external hydrostatic pressure. It is known to be the motor of primary cell wall elongation. The periodicity of photosynthetic activity implies daily variations in water pressure. The elastic response of cell walls to this internal pressure is a change in dimension, which generates periodic changes in tree diameter at a macroscopic level, called diurnal strains. Diurnal strains occur both in xylem and inner bark cells, at different magnitudes.[9,10] They can easily be measured using strain gauges pasted tangentially[8,11] at the surface of either of these tissues. Strains inside cambium and differentiating cells cannot be measured directly, but they can be evaluated from those of the xylem and inner bark, and from mechanical considerations. The order of magnitude is some hundreds of

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microstrains in the tangential direction, and some thousands of microstrains in the radial direction. These strains occur periodically on a daily basis during the cell wall formation, i.e., during the deposition and stiffening of lignins and cellulose material. The water status of the tree, directly related to diurnal strains, has been shown to influence tracheid morphogenesis.[12,13] The magnitude of diurnal strains is higher on the side of the stem on which reaction wood is produced.[14,15] Moreover, the deposition of cell wall material is not continuous over time, but is also subject to periodicity. The matrix of lignins and hemicellulose is deposited during the night, when the differentiating cells are swollen, and cellulose crystallization occurs during the day, when the cell is shrunk by high water tension.[16–18] Therefore, a mechanism explaining the induction of stress inside cell wall constituents, in relation with diurnal strain, can be proposed. Lignin and hemicelluloses, deposited during the night, would be compressed by the shrinkage of the cell occurring the day after due to the increasing water tension. Conversely, the cellulose, crystallizing during the day, would be put under tension when the cell wall swells the night after, in relation to decreasing water tension. Integration of this process over time could be responsible for the generation of maturation stress. The strains due to change in water tension are tangential and radial strains, but, because of the possible stress redistribution inside the cell wall material (Poisson's effect), this hypothetical mechanism may also produce longitudinal maturation stress.

This article reports the experimental testing of this assumption. Working on tree saplings in controlled conditions, diurnal strains can be canceled by applying a continuous lighting treatment. The magnitude of maturation strains cannot be measured directly on the saplings because of their small diameter. To detect and quantify maturation strains, the gravitropic reaction of tilted stems is used: occurrence of an uprighting movement is the consequence of high longitudinal stress developed on the reaction wood on one side of the stem.

Material and methods

Plant material

Experiments were performed both on a gymnosperm species (sugi; *Cryptomeria japonica*) and on an angiosperm species (beech, *Fagus sylvatica*). Experiments on sugi took place between February and April 2004, and experiments on beech between June and July 2005. For each species, eight 3-year-old saplings were selected. At the beginning of the experiments, sapling diameter ranged between 1.0 and 1.2 cm for sugi and between 1.2 and 1.4 cm for beech. Their height ranged between 75 and 100 cm for sugi and between 120 and 130 cm for beech.

Growth conditions

The saplings were grown in pots in a field at Nagoya University, and were brought into growth chambers before the experiments. During the entire experiment, temperature was kept at 26°C, air humidity at 70%, and abundant water was supplied. Saplings were divided into two sets of four paired plants, and grown in separate growth chambers. They were first left for 1 month under alternate lighting (12 h light, 12 h darkness) for acclimation. The saplings were then repotted in larger pots and tilted 40° from the vertical. Immediately after tilting, one set of saplings was submitted to continuous lighting (24 h/day) while the other set was kept as a control with alternate lighting. Light intensity during light periods was the same in the continuous and alternate lighting treatments.

Measurements

The diurnal strains at the surface of the inner bark were recorded continuously on all saplings during the experiment using the usual method.[14] This was performed in order to check that the continuous lighting canceled diurnal strains. The saplings were observed every week after they were tilted. The diameter at the base was recorded at a fixed position with a caliper. The angle of the top part of last year's shoot was recorded using a commercial clinometer. Measurements were repeated three times at each date and averaged. The precision of this rough measurement method is within 1 degree, which was thought sufficient for the purpose of this study. The diameter at the base and angle at the top were then averaged on each set of four saplings, to compare continuous lighted plants with control plants.

Results and discussion

Cancellation of diurnal strains

Records of tangential strains showed that diurnal fluctuations in diameter are almost completely canceled by the continuous lighting treatment (Fig. 1). The remaining variations were thought to be due to the periodicity of water supply and to some imperfect control of the climatic condi-

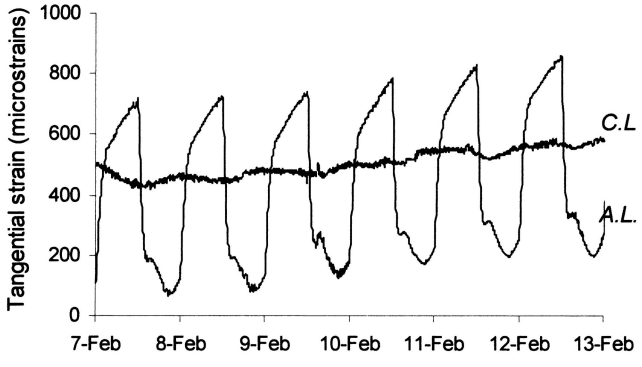

Fig. 1. Typical fluctuations of tangential strains at the surface of the inner bark of *sugi* saplings submitted to alternate lighting (*A.L.*) or continuous lighting (*C.L.*)

tion inside the chamber. The amplitude of diurnal strains ranged between 600 and 1200 microstrains for the alternate lighting treatment, and between 50 and 150 microstrains for the continuous lighting treatment.

Growth of continuously lighted plants

In both treatments and for both species, the saplings had normal extension and radial growth. A slight leaf chlorosis was noticed on the continuously lighted plants of both species at the end of the experiment. Over the experimental period, the diameter at the base increased by 2 or 3 mm for the sugi saplings, and between 2 and 4 mm for the beech sapling (Figs. 2, 3). This increase was slightly larger for saplings submitted to the continuous lighting treatment for both species.

Gravitropic reaction

The uprighting movement of stems started some days after the beginning of the experiment. The stems bent upward, mainly in their distal parts. This was quantified by the angle of the top segment of the previous year's main shoot (Figs. 4, 5). The uprighting movement was quicker on beech saplings than on sugi saplings. It occurred both on continuously lighted and in control plants. The rate of uprighting was similar for the treatment and control during the first 2 weeks. Afterward, the magnitude of the uprighting was larger in continuously lighted plants than in controls (Figs. 4, 5).

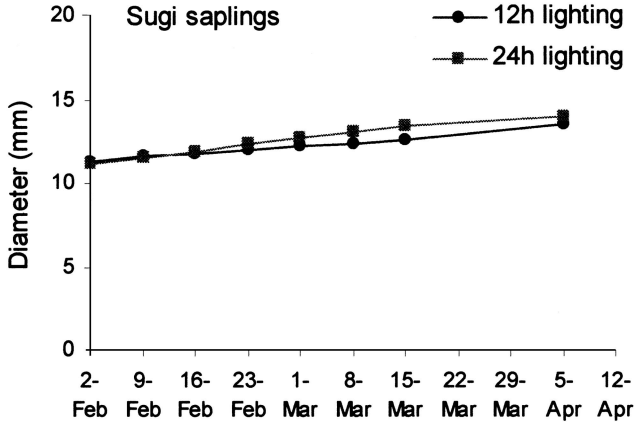

Fig. 2. Change in mean base diameter of sugi saplings for the continuous lighting (24 h) and alternate lighting (12 h) treatments

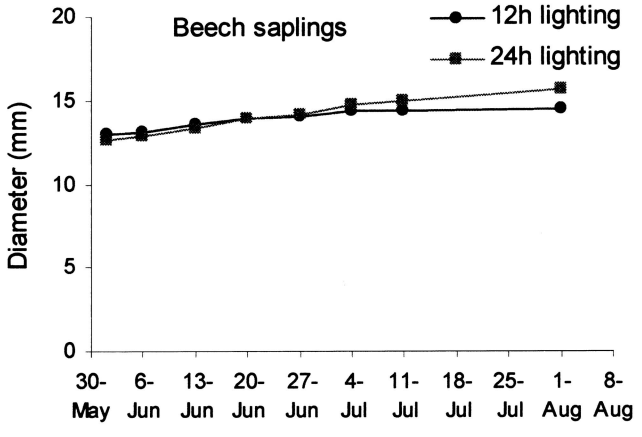

Fig. 3. Change in mean base diameter of beech saplings for the continuous lighting (24 h) and alternate lighting (12 h) treatments

Conclusions

In both species, continuously lighted plants showed the ability to react to a gravitational stimulus and bend upward. The rate of uprighting was even larger for the continuously lighted plants than for the controls, probably because of a larger diameter growth, associated with higher light availability. It is well established that such an uprighting

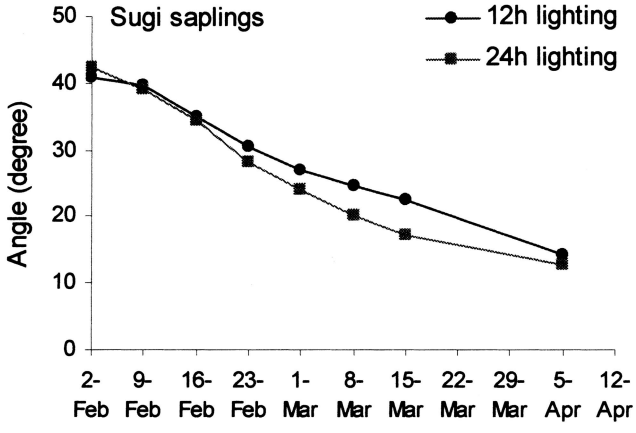

Fig. 4. Change in mean angle relative to vertical of the top part of the sugi saplings for the continuous lighting (24 h) and alternate lighting (12 h) treatments

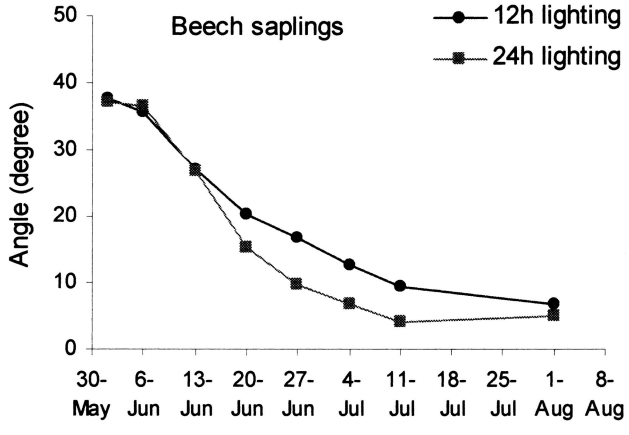

Fig. 5. Change in mean angle relative to vertical of the top part of the beech saplings for the continuous lighting (24 h) and alternate lighting (12 h) treatments

movement is made possible by the production of prestressed reaction wood. In angiosperm plants such as beech, tension wood is produced on the upper side of the stem. In gymnosperm plants such as sugi, compression wood is produced on the lower side. The mechanical function of these tissues in terms of uprighting is achieved by the development of a large longitudinal stress, which is a compression stress for gymnosperms and a tension stress for angiosperms. It is therefore clear that a large longitudinal stress was developed in the stem of the continuously lighted plants, despite the absence of significant diurnal strains. We conclude that diurnal strains are not directly involved in the generation of longitudinal maturation stress in tension wood or in compression wood. The mechanism by which stresses are induced in the material during wood maturation is still an open question. The involvement of chemical forces acting on wood constituents during the lignification process remains the most likely hypothesis.

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