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The origin of maturation stress in tension wood: using a micro-mechanical model to discriminate between hypothetical mechanism.

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Abstract

Tension wood generates axial tensile stress and tangential compressive stress during its formation, but the mechanism causing this stress is not yet fully understood. A micro-mechanical model is used to test different hypothetical mechanism, based on the assumption that one of the constituents of tension wood undergoes a dimensional change during the formation of the wall. The consistency between the outputs of the model and known facts about tension wood behaviour is used to assess and discuss various hypothetical mechanisms.

Introduction

During its formation, tension wood develops large mechanical stress called maturation stress [3]. It provides woody angiosperms with an essential adaptation to the terrestrial environment: a motor system, that allows achieving adaptive reorientations of the stems, and is necessary just to maintain them at a constant angle during growth [1]. At the microscopic level, the mechanism that generates this axial tensile stress is not yet fully understood. Rapid progress has been recently achieved in the description of the ultra-structure of tension wood, its chemical composition, biochemical activity, mechanical behaviour and state of stress. Different models have been proposed to explain why and how an axial tensile stress appears in tension wood fibres during their formation [5, 6]. Here we propose a micro-mechanical model designed to simulate some hypothetical mechanisms of stress generation, and assess their consistency with known facts.

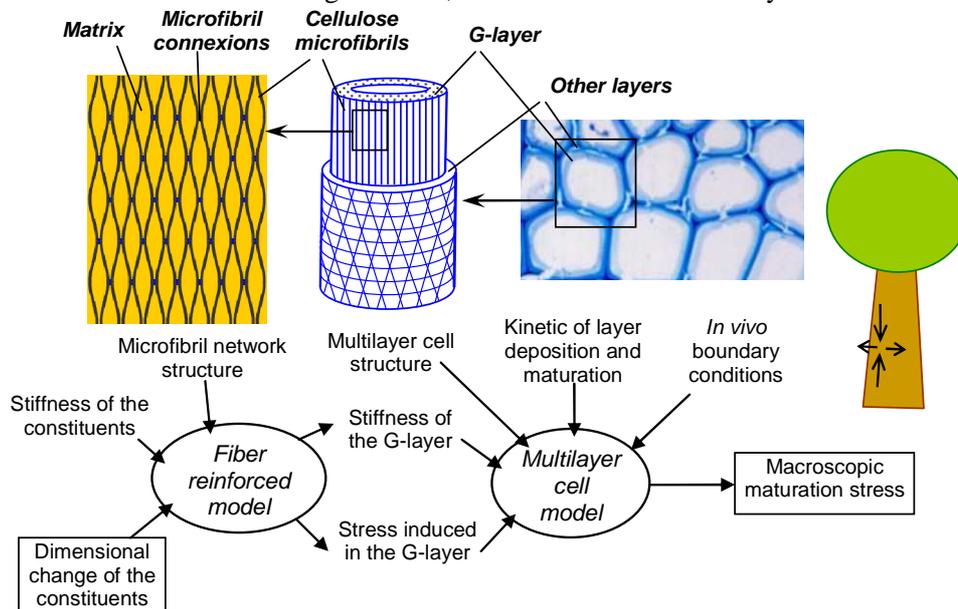


Figure 1. Micro-mechanical model of maturation stress induction in tension wood. The model predicts the macroscopic maturation stress based on two sub-models. The first computes the stiffness of the cell wall material and its state of stress in response to a dimensional variation of one of its elementary constituents. It assumes a fiber-reinforced structure and accounts for lateral connections between microfibrils. The second model figures the multi-layered structure of the fiber, and computes the macroscopic state of maturation stress. It account for the *in vivo* boundary conditions and the progressive deposition of the layer.

Material and Methods

The tension wood fibre is represented by a multilayer cylinder (Fig. 1) using a previously developed formulation [2] that accounts for the *in vivo* boundary conditions and the progressive thickening of the cell wall during its formation. This model is coupled with a specifically developed finite element model that computes the behaviour of the cell wall material as a fibre-reinforced composite, given the behaviour of elementary constituent (microfibril and matrix), and the structure of the microfibril network (possibly accounting for lateral connections between microfibrils). The model assumes that maturation stress originates in the dimensional change of one of the constituents of the fibre during the maturation process (caused *e.g.* by the polymerization of a substance, the action of an enzyme or a change in moisture content). It computes the resulting macroscopic stress, for given parameters of the wall structure. Four hypotheses were tested: (i) a shrinkage of the matrix, (ii) a swelling of the matrix, (iii) an axial shrinkage of microfibrils (iv) a lateral shrinkage of the connection between microfibrils.

Results

The observed state of stress of tension wood at the end of its formation is tensile in the fibre direction, and compressive the tangential direction [7]. Only hypotheses (ii) and (iii) were found to possibly comply with this fact, because (i) and (iv), assuming a shrinkage at the level of the matrix or the lateral connections, both generate a tensile tangential stress. Because the axial contraction of microfibrils seems contradictory with their crystallinity, our analysis concentrated on the hypothesis (ii) of a matrix swelling. Macroscopically, it always generates compressive tangential stress, but the sign of the axial stress was found sensitively dependant on 3 features: the ratio of matrix stiffness to microfibril stiffness, the lateral connectivity of the microfibrils network, and the relative timing of stress induction and cell wall deposition. In a virtually isolated piece of wall material, the swelling of the matrix generates a tensile force in the microfibril direction if they are laterally bound by stiff connections, and if the matrix is much less stiff than the microfibrils. However, at the cell level, the matrix swelling also creates some inward radial swelling of the G-layer, generating some tangential contraction. If the connections between fibrils are tangential, this geometrical coupling results in a compressive axial stress, not a tensile stress. This is actually consistent with the known behaviour of tension wood in response to variations in water content [4]. But the situation is different if one accounts for the progressive deposition of the cell wall layers. If the swelling of each elementary wall layer occurs just after its deposition, then its radial swelling cannot push inner layers, because there is no inner layer at that time. The simulations show that this mechanism results in an axial tensile stress at the end of the formation of the cell wall. It seems compatible with known behaviour of tension wood in response to changes in water content [4] or to the suppression of the G-layer [5].

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