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Biomechanics of Growing Trees: Mathematical Model, Numerical Resolution and Perspectives

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Abstract. The growth of trees is characterized by the elongation and thickening of its axes. New cells are formed at the periphery of the existing body, the properties of the older inner material being unchanged. The calculation of the progressive deflection of a growing stem is not a classical problem in mechanics for three main reasons: 1- the hypothesis of mass conservation is not valid; 2- the new material added at the periphery of the existing and deformed structure does not participate retroactively to the total equilibrium and tends to “fix” the actual shape; 3- an initial reference configuration corresponding to the unloaded structure cannot be classically defined to formulate the equilibrium equations. This paper proposes a theoretical framework that allows bypassing these difficulties. Equations adapted from the beam theory and considering the strong dependencies between space and time are given. A numerical scheme based on the finite element method is proposed to solve these equations. The model opens new research perspectives both in mathematics and plant biology.

Keywords: gravitropism, growth stresses, wood formation, lignified stems, surface growth, modeling, finite element method.

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INTRODUCTION

Modeling the biomechanics of growing structures is an exciting challenge in developmental biology. However coupling between space and time, which is specific to growth problems, is difficult to formalize. It must be first distinguished between organisms or organs that develop new cells within an existing volume or surface, e.g. volume growth of bones or soft tissues [1], and organisms or organs with an expanding frontier, e.g. radial growth of tree stems [2]&[3] or horns [4]. In the first case, the change in volume originates from the mechanical deformation of the domain due to the insertion of new cells within the continuum [5]. In the second case, it is assumed that new material points are formed at the surface of an existing domain, but that this growth process does not in itself induce strains in the inner core of this domain. This paper is concerned with the last hypothesis which is illustrated and applied to tree growth.

Trees are complex structures that result both from genetic factors (genotype) and growth strategies (phenotype). The evolution in time of tree form defines tree “architecture” [6], which includes both tree topology and geometry. Tree architectural development allows such a “fixed” organism to prospect its near environment in order to optimize resources necessary to its survival, e.g. light and soil water and nutrients. Growth strategies are thus linked with the ability to control the branching process and the geometry of existing branches. This control operates through the investment of photoassimilates, i.e. the main biological compounds used to build plants, to specific organs associated to specific functions, e.g. water and nutrients uptake, photosynthesis, water transport, mechanical support. The growth of tree branches can be split into two modes corresponding to branch elongation, which results from the activity of the apical meristem (primary growth), and branch thickening, which is due to cambial activity (secondary growth). This growth can be defined as “surface growth” as these primary and secondary meristems are located at the periphery of the axis, i.e. at the tip and just under the bark respectively, which results in a centrifugally extension

of the branch. Consequently, it is assumed that: 1- the inner part of the branch is not directly deformed by the appearance of new material at its periphery; 2- the new material appears on a deformed structure and does not support any mechanical stress at the date of its formation. Consequently, when considering quasi-static forces, e.g. gravity, applied on the growing structure, the progressive increase and accumulation of mechanical stresses leads to a non-classical stress profile and also results in a deformed shape different from the usual beam theories (see [7] for more details).

Modeling the biomechanical response of growing branches thus necessitates reconsidering the classical formalism of the continuum mechanics, accounting for the addition of new material points at the surface of the domain. The main difficulty here is to define a reference configuration on which the equilibrium equations can be integrated, as the studied domain changes in time.

MATHEMATICAL FORMALISM FOR THE MECHANICS OF GROWING BEAMS

The development of a new mathematical formalism for the biomechanics of growing beams, e.g. plant stem or branches, necessitates defining a “virtual” reference configuration that accounts for the strong dependencies between space and time (Figure 1). This configuration corresponds to the elongation path due to the activity of the primary meristem. It is time dependant and does not include or result from mechanical deformations. The actual configuration (Figure 1C) defines the real deformation of the beam resulting from a progressive addition of new material, i.e. an increase in the total biomass of the plant stem. When the total weight of the beam is removed from the actual configuration, the unloaded configuration (Figure 1B) does not correspond to the virtual reference configuration. This “shaping” effect is due to the fact that the new wood cells are created on a deformed structure and that they are not themselves mechanically deformed at the date of their apparition. Writing the equilibrium equations of the beam with respect to the virtual reference configuration then necessitates considering both the actual strains and stresses and the virtual strains and stresses that would be necessary to transform the unloaded configuration to the virtual reference configuration.

FIGURE 1. (A) Virtual reference configuration; (B) unloaded actual configuration; (C) actual configuration under the total force f . ε (resp. ω) is the reduced translational (resp. bending) strain that must be considered to describe the “shaping” component of growth with respect to the virtual reference configuration. e (resp. w) is the reduced total translational (resp. bending) strain in the actual deformed beam with respect to the virtual reference configuration.

Considering the remarks above and according to the Navier-Bernoulli’s hypothesis, the equilibrium of an inextensible growing cantilever beam submitted to the gravity can be written with respect to the virtual reference configuration as

$$\left\{ \begin{array}{l} \frac{d\alpha}{ds}(s) = \kappa(s) \\ \frac{\partial}{\partial s} \left(EI \frac{\partial \beta}{\partial s} \right) + n \cos(\alpha + \beta) = \frac{\partial}{\partial s} (\mu + EI\omega_0) \\ \frac{\partial \mu}{\partial t} = \frac{\partial EI}{\partial t} \left(\frac{\partial \beta}{\partial s} - \omega_0 \right) \end{array} \right. \quad (1)$$

With the boundary conditions

$$\begin{cases} \alpha(0) = \alpha_0 \\ \beta(0, t) = 0 \\ \frac{\partial \beta}{\partial s}(L(t), t) = 0 \\ \mu(s, \gamma(s)) = 0 \end{cases}$$

where α_0 is the beam insertion angle with respect to the horizontal, n is the stress resultant due to the lineic weight, ω_0 corresponds to strains that do not originate from mechanical processes (e.g. maturation strains), $\gamma(s)$ is the date of apparition of the first material point at arc length s , $L(t)$ is the beam length at time t , E is the modulus of elasticity of the constitutive material, I is the second moment of inertia of the beam cross section ($I = \pi r^4/4$ for a circular beam of radius r), $\mu = EI\omega$ is the equivalent moment associated with the reduced bending strain ω (see Figure 1), $\kappa(s)$ is the curvature that defines the shape of the reference curves at arc length s , $\alpha(s)$ is the angle of the tangent to the reference curve at arc length s with respect to the horizontal and $\beta(s)$ is the rotation angle of the actual beam cross-section at arc length s and time t with respect to the reference configuration.

NUMERICAL RESOLUTION

A weak formulation of (1) is given by:

giving $V_t = \{v \in H^2([0, L(t)]) / v(0) = 0\}$, find $\beta(\cdot, t) \in V_t / \forall v \in V_t$

$$\int_0^{L(t)} EI \frac{\partial \beta}{\partial s} \frac{dv}{ds} ds + \int_0^{L(t)} n \cos(\alpha + \beta) v ds = \int_0^{L(t)} (\mu + EI\omega_0) \frac{dv}{ds} ds \quad (2)$$

and

$$\begin{cases} \frac{d\alpha}{ds}(s) = \kappa(s) \\ \frac{\partial \mu}{\partial t} = \frac{\partial EI}{\partial t} \left(\frac{\partial \beta}{\partial s} - \omega_0 \right) \\ \alpha(0) = \alpha_0 \\ \mu(s, \gamma(s)) = 0 \end{cases}$$

The problem can be solved using a finite element method. Hermite's finite elements allow insuring the C1-continuity of rotation β , but necessitate to introduce one supplementary equation and initial condition:

$$\begin{cases} \frac{\partial^2 \mu}{\partial s \partial t} = \left(\frac{\partial^2 EI}{\partial s \partial t} - \frac{1}{EI} \frac{\partial EI}{\partial s} \frac{\partial EI}{\partial t} \right) \left(\frac{\partial \beta}{\partial s} - \omega_0 \right) + \frac{1}{EI} \frac{\partial EI}{\partial t} \left(\frac{\partial \mu}{\partial s} - n \cos(\alpha + \beta) \right) \\ \frac{\partial \mu}{\partial s}(s, \gamma(s)) = 0 \end{cases} \quad (3)$$

First numerical simulations of growing beams with circular cross sections were performed considering $r_0 = 1cm$, $\alpha_0 = \pi/4$, $\omega_0 = 0$, $\rho = 1000kg.m^{-3}$, $E = 10000MPa$, $\frac{dL}{dt} = 50cm.y^{-1}$ and $\frac{dr}{dt} = 0.1cm.y^{-1}$. The results were compared with a classical calculation where growth was not considered (Figure 2).

THEORETICAL PERSPECTIVES AND APPLICATIONS

The new mechanical framework proposed for the calculation of the biomechanical response of growing trees leads to new partial differential equations where space and time are strongly connected. The theoretical properties of

this set of equations still remains unknown and specific mathematical analyses should be carry out to verify the existence and uniqueness of a solution. Such a mathematical formulation of growth applied at the whole tree level, i.e. considering a branching structure, also opens new perspectives in biology. It is indeed well known that a tree can control the shape of its stem and branches by modifying its growth in diameter, e.g. allocating more biomass to wood rings and developing anisotropic cross sections, by changing its growth direction, i.e. modifying the growth path that defines the virtual reference configuration, as well as by developing internal auto-equilibrated stresses, called maturation stresses (see [7]), that can change the shape of the whole structure..Maturation strains are already considered in the equations through the variable ω_0 . A modification of the growth path, e.g. with respect to light direction in the case of phototropism, can be introduced in the definition of the curvature $\kappa(s)$ that can also depend on environmental variables and/or the actual mechanical state of the beam. This modification would make the problem much more complex introducing nonlinearities. Considering these new biological variables would be allow different growth strategies to be defined. Optimization procedures could also help defining ideotypes, i.e. plant shapes with optimized physiological functions.

FIGURE 2. (A) Reference configuration; (B) classical beam without growth; (C) growing beam : analytical solution with the hypothesis of small deflection; (D) numerical solution; (E) analytical solution with no growth in diameter.

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