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Non-linear poro-elastic coupling in real and artificial branches and its possible link to plants mechano-perception.

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Résumé. En conditions naturelles, les plantes sont sans cesse soumises à des sollicitations mécaniques externes, comme le vent ou la pluie, qui affectent et modifient leur croissance [17]. De façon remarquable, cette réponse en croissance n'est pas seulement locale, mais s'observe aussi à grande distance de la zone stimulée et très rapidement après la sollicitation [5]. Cela suggère l'existence chez les plantes d'un transport rapide de l'information sur une longue distance. Cependant, la nature et le mécanisme de transport de ce signal ne sont pas connus.

Récemment, il a été suggéré que ce signal pourrait être une onde de pression générée par la flexion mécanique des branches [12,8]. Afin de tester cette idée et les mécanismes physiques mis en jeu, nous avons développé une branche artificielle en élastomère de silicone (PDMS) consistant en une poutre cylindrique percée de micro-canaux et remplie d'un liquide visqueux [11]. De façon surprenante, la flexion d'une telle poutre génère une surpression dont l'amplitude varie quadratiquement avec la déformation imposée. Pour comprendre l'origine de cette réponse non-linéaire, nous proposons un modèle simple basé sur l'idée qu'une poutre poreuse en flexion tend à comprimer sa section transversale afin de minimiser l'énergie élastique totale du système. Des expériences sur des branches réelles réalisées en collaboration avec l'INRA suggèrent la robustesse de ce mécanisme.

Abstract. The perception of mechanical stimuli in the environment is crucial to the survival of all living organisms, and plants make no exception. At the scale of a tree, the bending of a stem leads to a transient growth response, not only locally but also far away from the stimulated area, suggesting the existence of a long range information signal within the plant network. The nature and mechanism of this long range signal is not well known, but it has been suggested that it could result from a purely hydraulic pressure signal created in response to the mechanical bending of the hydrated wood tissue. Recently, such hydro-mechanical coupling have been directly observed in plants in the PIAF-INRA Laboratory. The objective of this work is to better understand the physical mechanisms responsible for this hydro-mechanical response, by performing experiments on physical poroelastic beams mimicking stems and branches. To this end, we have designed an original three-dimensional micro-fluidic device consisting of a transparent elastomer beam (PDMS) perforated with longitudinal micro-channels and filled with a viscous liquid. The poroelastic response of this biomimetic branch to a sudden bending has then been studied in a closed geometry. The main result of this study is that the bending of the artificial branch generates a global overpressure in the system. This overpressure increases quadratically with the bending deformation, and is controlled by the pore bulk modulus of the media. We propose a simple model to explain our measurements and discuss the results in the context of plants.

1 Introduction.

Since Darwin, scientists know that plants are able to respond to mechanical stimuli, a process called thigmomorphogenesis [7,2,15]. This ability is crucial to the survival of plants, who are continuously exposed to mechanical perturbations such as wind, rain, contact with other plants and so on. For example, at the tree scale, the bending of a branch leads to a rapid change of growth not only locally but also far from the stimulated area suggesting the existence of a long-range signal through the plant [5]. The nature and the mechanism of propagation of this signal is not well known and different hypothesis have been proposed in the literature. One of these is that the signal propagation is purely mechanical [12,8] : an hydraulic pulse could be generated in response to a local mechanical strain, and could propagate rapidly along the water conductive system of the plant.

This hypothesis of a purely hydro-mechanical coupling has been recently investigated in the PIAF-INRA laboratory in Clermont-Ferrand, by Éric Badel, Hervé Cochard and Bruno Moulia [10]. To this end, hydraulic pressure measurements have been made in plant stems or branches subjected to a rapid and controlled bending. Their main result is that the bending of a branch leads to an overpressure that spreads through the vascular system. These experiments are the first to evidence the existence and propagation of an hydraulic pressure wave in plants in response to a localised bending. It is tempting to assume that such hydraulic signals could play an important role in the long range signalling in plants mechano-perception. On the other hand, from a purely physical and mechanical point of view, these results point to interesting and non-trivial questions. What are the physical mechanisms responsible for the hydraulic pulse generation? What set the amplitude of the pressure pulse, its speed of propagation and its damping rate?

In physics and mechanics, poroelasticity is a natural framework to study the dynamics of a porous deformable solid saturated with a liquid [1,16]. From this point of view, one expects that the bending of a stem or a branch saturated with water induces a water flow. When an elastic beam is bent, some parts are stretched while others are compressed. These local changes of volume must be followed by water expulsion or suction. However, in the linear beam theory, both effect compensate exactly for a symmetrical beam and the *total* change of volume should be zero under pure bending. It is therefore not at all trivial that bending of a branch produces a non-zero mean pressure pulse as observed. While previous theoretical works have studied the linear behaviour of a poroelastic beam *e.g.* [4,14], very few experimental studies have been performed [13]. Moreover, to our knowledge, no study has investigated the poroelastic dynamics of a beam composed of a soft cellular material in the large deformation regime.

2 Experiments on artificial branches.

Minimal ingredients for a biomimetic branch : From a mechanical point of view, a very simple picture of a tree branch is an elastic beam perforated with thin channels drilled in the longitudinal direction and filled with a viscous fluid. This original three-dimensional milli-fluidic device is made of a silicone elastomer (Polydimethylsiloxane) and elaborated using moulding techniques. The elastomer is soft, transparent and isotropic (Young modulus $E \sim 2$ MPa). The size of the channels is $d = 500 \mu\text{m}$. Channels are filled with a viscous fluid (silicon oil or Ucon oil/water mixture) (*see* figure 1 for details).

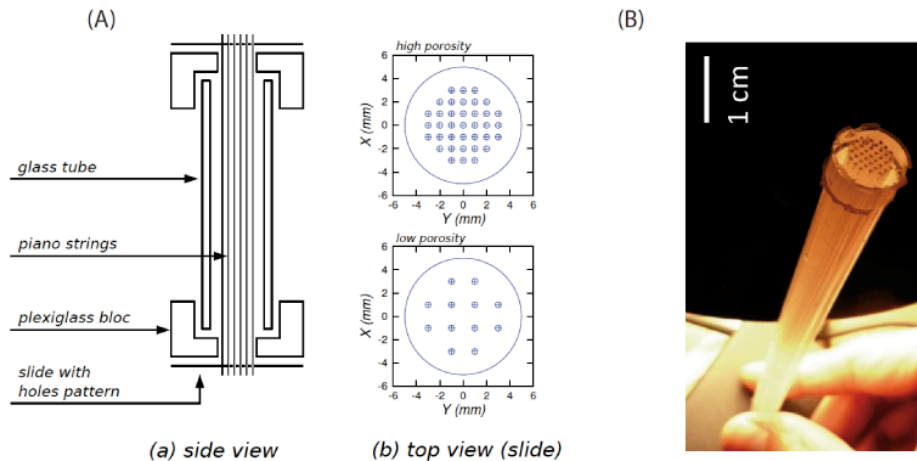


Figure 1. (A) Moulding set-up. (B) Picture of a poroelastic beam

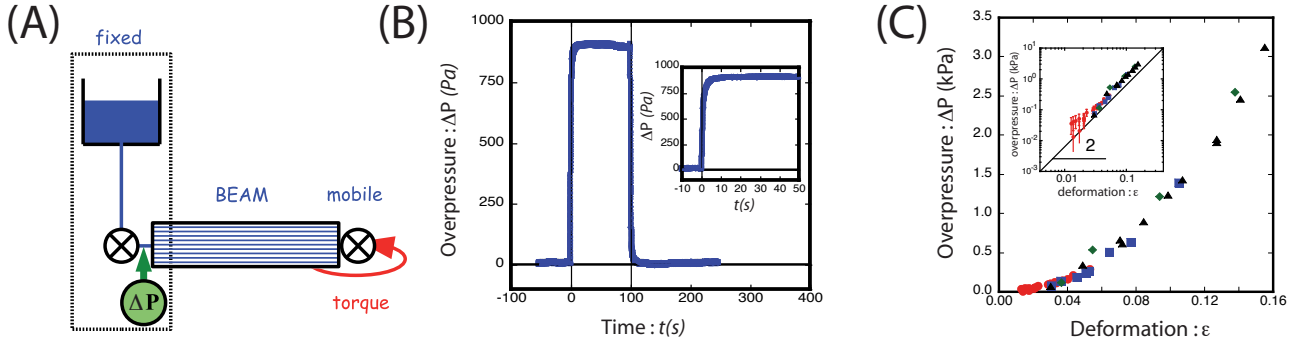


Figure 2. (A) Experimental set-up. (B) A typical pressure signal. Bending (at $t = 0$ s) leads to a stationary overpressure after a transient poro-elastic time and goes back to initial value after unbending (at $t = 100$ s). (C) Non-linear dependance of the amplitude of the stationary pressure pulse as a function of the bending deformation. Each point corresponds to one experiment.

Experimental set-up : All the experiments presented here are performed in the situation of a closed system *i.e.* there is no exchange of fluid between the inside and the outside of the beam. For practical reasons, we work in the geometry of a cantilever beam : the pressure signal is recorded from one fixed end of the beam while deformation is imposed rapidly by the displacement of the other end of the beam (*see* figure 2.A). To ensure reproducibility, the displacement of the mobile part of the beam is performed with help of a linear actuator. A picture of the beam is taken afterward from which is extracted the mean curvature : $\langle \mathcal{C} \rangle = \Delta\theta/L$ where L is the length of the beam and $\Delta\theta$ is the angle difference between both extremities of the beam. The bending deformation ϵ is defined as the maximal longitudinal deformation induced by bending and is given by $\epsilon = (D/2)\langle \mathcal{C} \rangle$ where D is the diameter of the beam.

Main characteristics of the pressure signal when bending : A typical hydraulic pressure signal is presented on figure 2.B . We see on this figure that pressure reaches a non-zero value which is maintained stationary as long as bending is imposed. Second the transient regime over which the pressure sets up is well accounted for by the relaxation poro-elastic time of the beam. This is in qualitative agreement with the hypothesis of an hydraulic pulse generated by bending and is coherent with experiments performed on plants. Interestingly, we also find that the amplitude of the overpressure ΔP varies quadratically with the bending deformation ϵ (*see* figure 2.C). These features come up two questions we will now address : (1) Why bending creates an overpressure ? (2) Why the pressure response is non-linear whereas the material is still in its linear response regime ?

3 A simple elastic model for the pressure response to bending.

In contrast with the prediction of the linear elastic beam theory, the observed over-pressure shows that bending leads to a global change of volume in the system. A possible explanation is the following. When an elastic beam is bent, the longitudinal elastic deformations (extension and compression) increase with the distance to the neutral surface. Now, if the beam is composed of a porous media, the system can reduce the bending elastic energy by deforming its cross-section and gather the material closer to the neutral surface. This ‘squeezing’ of the cross-section is, in turn, associated with a global decrease of the pore area and gives rise to a decrease of the volume of the beam in response to bending (*see* figure 3).

(1) **Minimisation of the total elastic energy.** The total elastic energy is given by the sum of the elastic energy associated with bending in the longitudinal direction and squeezing in the transverse direction. The bending elastic energy of a beam of circular cross-section of diameter D , length L , effective Young modulus E , and bent at a constant curvature \mathcal{C} , is given by [9] :

$$U_{\text{bend}} = \frac{EV}{32} D^2 \mathcal{C}^2 \quad (1)$$

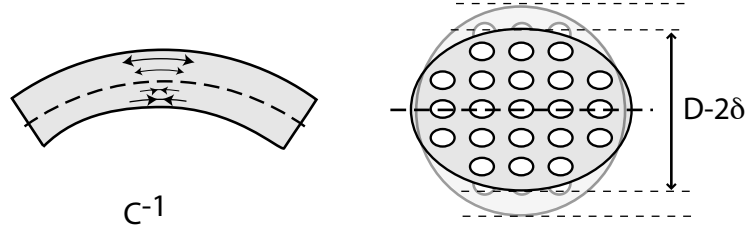


Figure 3. Ovalisation process : the elastic energy associated with the curvature of the beam (left) is decreased by the squeezing of the section of the beam (right)

where $\epsilon = (D/2)\mathcal{C}$ is the bending deformation defined in the experiment and $V = \pi D^2 L/4$ is the volume of the beam. When the section of the beam is squeezed by a factor δ , the moment of inertia of the beam is reduced ($D \rightarrow D - 2\delta$) and the bending energy can be approximated as :

$$U_{\text{bend}}(\delta) \approx \frac{EV}{32} (D - 2\delta)^2 \mathcal{C}^2 \quad (2)$$

We can see in this expression that a transverse compression $\delta > 0$ decreases the bending energy. However, this transverse deformation has a cost in term of elastic energy that we need to estimate. By analogy with the elastic energy stored in a compressed bar $[(1/2)EV(d\ell/\ell)^2]$, we write the squeezing energy U_{squeeze} associated to the deformation of the transverse deformation of the cross-section as :

$$U_{\text{squeeze}}(\delta) \approx \frac{EV}{2} \left(\frac{2\delta}{D} \right)^2 \quad (3)$$

where $\epsilon_{\perp} = 2\delta/D$ are the typical transverse deformation (Figure 3). The equilibrium value of δ is found by minimising the sum of the bending energy U_{bend} and the squeezing energy U_{squeeze} , that is : $\frac{d}{d\delta} (U_{\text{bend}} + U_{\text{squeeze}}) = 0$. At the lowest order ($2\delta \ll D$), this gives :

$$\frac{2\delta}{D} \approx \frac{D^2 \mathcal{C}^2}{16} \quad \text{or} \quad \epsilon_{\perp} \approx \frac{\epsilon^2}{4} \quad (4)$$

This analysis therefore shows that the transverse deformation of the beam cross-section ϵ_{\perp} varies with the power 2 of the bending deformation ϵ . Now, in the 2D cross-section plane, we can write that the relative change of the pore area associated with this transverse compression writes : $\Delta A_c/A_c = -(1 - \nu_c)\epsilon_{\perp} \approx -(1 - \nu_c)\epsilon^2/4$ where A_c is the pore area and ν_c is a 2D surface area Poisson ratio characterising the change of pore area for a given 2D deformation. In the case of a 2D sheet containing holes, the prefactor $(1 - \nu_c)$ is of the order of unity [6]. In our parallel channel geometry, this pore area change is equal to the pore volume change : $\Delta A_c/A_c = \Delta V_c/V_c$, where V_c is the pore volume. Therefore :

$$\frac{\Delta V_c}{V_c} \sim -\frac{\epsilon^2}{4} \quad (5)$$

This simple model then predicts that bending a porous beam leads to a global volume change of the channel that is proportional to the square of the bending deformation. This non-ovalisationlinear effect comes from the flattening of the cross-section when the porous beam is bent, due to a competition between the longitudinal bending deformation and the transverse cross-section deformation. This effect is reminiscent of the ovalisation phenomenon observed in bent elastic tubes and first described by Brazier [3]. When a tube of circular section is bent, its section flattens before collapsing at large deformation. We shall now take into account the presence of an incompressible fluid in the porosity of the beam to express the relation between the relative change of the total volume of the channels expected in an open system and the overpressure observed in a closed system.

(2) **Relation between volume change with pressure change.** In the situation where liquid can not be exchanged with the outside (what we have called a closed system), bending a porous beam at constant volume can be divided in two steps : in the first step, the beam is bent slowly up to \mathcal{C} , and the fluid is let free to be drained out from the beam. In this case, a volume $-\Delta V_c < 0$ is removed from the beam according to equation (5) while the pore pressure remains zero. In the second step, we maintain the bending curvature \mathcal{C} constant and inject the volume of liquid ΔV_c in order to recover the initial volume of the system ($\Delta V_c = 0$). This injection of fluid is then associated to an increase of the pore pressure ΔP , which is the quantity we are looking for. The relation between ΔP and ΔV_c is given by the ‘‘pore bulk modulus’’ B defined by : $\Delta P = -B\Delta V_c/V_c$. which combined with equation (5) gives the relation between the bending deformation ϵ and the pressure response ΔP :

$$\Delta P \sim B \frac{\epsilon^2}{4} \quad (6)$$

Our model therefore recovers the quadratic relation between the pressure and the bending deformation observed experimentally. In this model, the overpressure ΔP is essentially controlled by the pore bulk modulus B of the porous beam. The measured bulk modulus of the PDMS branch is $B = 2.5 \cdot 10^5$ Pa. Equation (6) then predicts that a 10% curvature deformation will generate an overpressure of order $\Delta P \sim 10^3$ Pa, in good agreement with the experiments (*see* figure 2.B).

4 Comparison between real and artificial branches.

In order to test the naive picture we used to design artificial branches, the same experiment has been performed on real branches. Even though experiments on real branches is much more difficult than on artificial branches because of the intrinsic variability of living systems, we observed the same quadratic pressure response to bending as for artificial branches (*see* figure 4). This suggests that we have captured with our naive model the basic features involved in the generation of the hydraulic pulse that was already

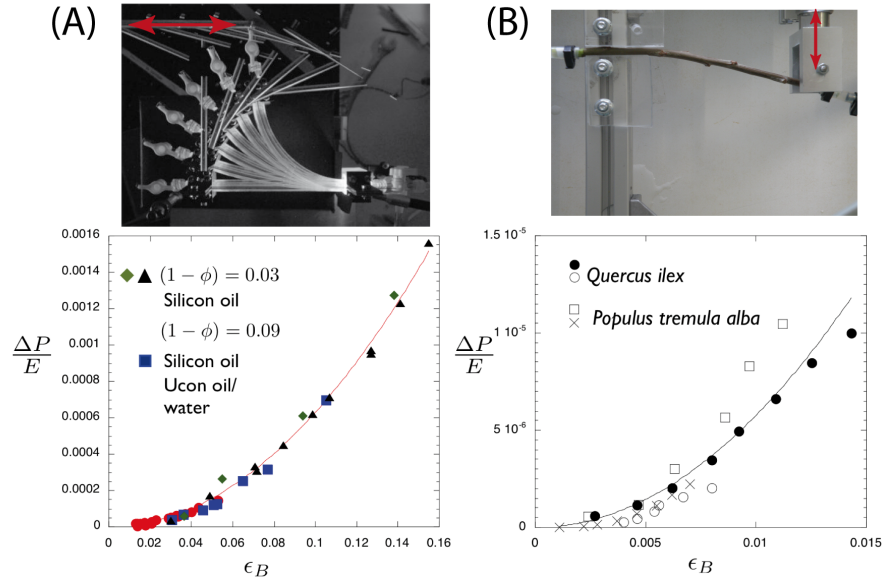


Figure 4. Stationary overpressure normalised by the young modulus for artificial and real branches (hybrid poplar and green oak). Rescaling gives $\frac{\Delta P}{E} = 0.06 \times \epsilon^2$ for artificial branches and $\frac{\Delta P}{E} = 0.02 \times \epsilon^2$ for real branches.

observed in plants and that the mechanisms involved in the process are robust. Moreover, for a given geometry, the bulk modulus of a material B depends on the Young module E : $B = E \times f(\phi)$ where $f(\phi)$ is a function of the geometry of the beam. Wood being much harder than the elastomer we used for the elaboration of the artificial branches ($E_{\text{wood}} \sim \text{GPa}$ whereas $E_{\text{elastomer}} \sim \text{MPa}$) we expect that the amplitude of the steady overpressure measured in both systems scales like the young modulus of the material which is indeed the case.

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