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Trees feel mechanical strain: from genes expression to cambium activity modulation

Eric Badel, Ludovic Martin, Nathalie Leblanc-Fournier, Jean-Louis J.-L. Julien, Catherine Coutand, Mélanie M. Decourteix, Catherine Lenne, Bruno Moulia

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Trees acclimation to strains induced by wind: from genes expression to stem structure

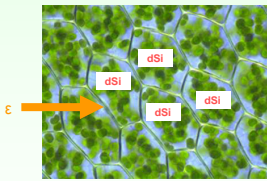
¹L. Martin, ²E. Badel, ¹N. Leblanc-Fournier, ¹M. Decourteix, ¹C. Lenne, ²C. Coutand, ²B. Moulia and ¹J.L. Julien

1 Université BLAISE PASCAL, UMR547 PIAF, F-63177 AUBIERE
2 INRA, UMR547 PIAF, F-63100 CLERMONT-FERRAND

An integrative model of mechanosensing: S³m

Mechanical signals are important factors that control plants growth and development. External mechanical loadings, such as wind, lead to a decrease of primary growth, an increase of secondary growth, modifications of stems mechanical properties and biomass reallocation to roots.

Biomechanical studies on tomato and poplar demonstrated that tissue strains are sensed by plants (1), (2). A biomechanical model was proposed, assuming that each cell produces a signal (dSi) whose intensity depends on strain level (ε), volume and sensitivity of the cell. At organ or tissue level, the integrative thigmomorphogenetical signal Si can be predicted by integrating the longitudinal strains (Sstrains), applied to the tissue (3).

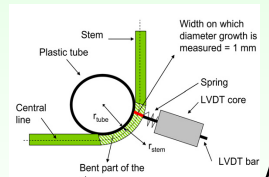


$$Si = k \cdot \iiint \epsilon_{(x,y,z)} dx dy dz = k \cdot S_{strains}$$

Competent tissues

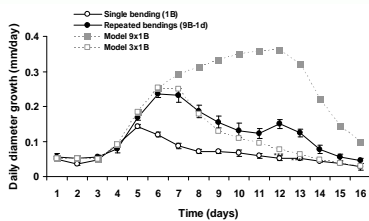
k = tissue sensitivity

Controlled stem bending



Experimental bending device which allowed to quantify the level of longitudinal strains during the stem bending.

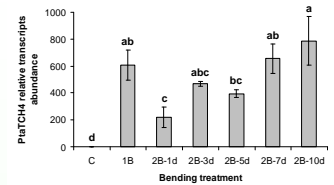
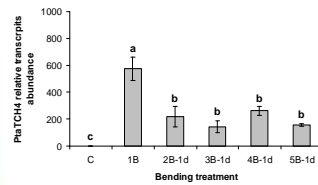
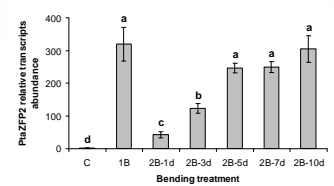
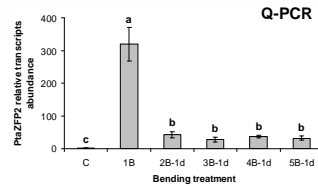
Plants accommodation to repeated mechanical stimuli



Response of secondary growth to repeated daily bending. Open circles represent growth response to one single bending (1B). Closed circles represent growth response to 9 successive bendings at 1-day intervals (9B-1d). Dash squares, model of additive effects (linear time integration, 9x1B). Open squares, model with a sensitivity shift after 3 daily bendings (3x1B; accommodation).

In nature, mechanical stimuli do not occur as a single bending. In this experiment, successive bendings were separated at day scale, mimicking the alternance between windy or quiet weather.

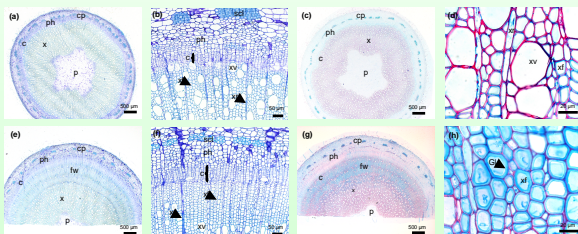
As soon as a second bending was applied, a diminution of growth and molecular responses to subsequent bending were observed. Our results show that plants acclimate rapidly to mechanical loadings and a desensitization period of a few days occurs after a single transitory bending. This acclimation process provides a basis for a mechanistic analysis of response sensitivity to mechanical loadings such as wind (4).



Mechanoresponsive genes expression after repeated daily bending.

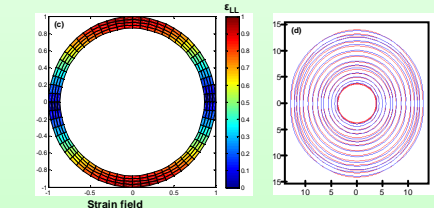
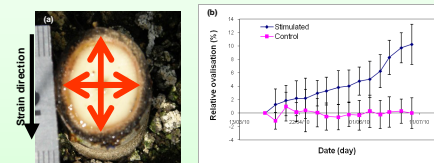
C : control (no load). 1B : one single bending. xB-yd : x bendings each separated by y days. *PtaZFP2* : Populus tremula alba Zinc Finger Protein2 gene. *PtaTCH4* : Populus tremula alba Touch4 xyloglucan endotransglucosylase/hydrolyase gene. Significant differences ($P < 0.05$) of responses are indicated by different letters.

Multiple mechanical stimuli affect anatomical pattern and secondary growth rate



Stem anatomical modifications induced by multiple bendings.

(a) to (d) Control plants. (e) to (h) Plants subjected to 6 bendings, 2 successive bendings separated by 1 day, 3 days without solicitations between each set of bendings. (a, b, e, f) Toluidine blue staining. (c, d, g, h) Blue astra-safrafratine staining. c: cambium, cp: cortical parenchyma, fw: flexure wood, gl: G layer, ph: phloem, pi: pith, scl: sclerenchyma, x: xyelm, xf: xylem fiber, xr: xylem ray, xv: xylem vessel.



Cambial activity induced by local strains applied to the stem: experimentations and modelling.

Plants were subjected to 3 successive daily bendings per week during 4 months. (a) Transversal section of a stimulated plant. (b) Relative ovalisation induced by bending. (c) Strain field for living tissues. (d) Weekly growth rate measurements (blue lines) and growth rate modeling (red lines).

$$\Delta R(i, t) = \Delta C(i, t)(1 + \alpha \epsilon_{LL}(t))$$

In response to bendings, cambium activity is impacted by the strain. Growth rate is identically stimulated according to the strain level both in the stretched part and in the compressed part of the stem. Wood differentiation is modulated according to the type of mechanical loading (tension and compression).

References :

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- (3) Moulia B., Der Loughian C., Bastien R., Martin L., Rodriguez M., Gourcilleau D., Barbacci A., Badel E., Franchel J., Lenne C., Roedel-Drevet P., Allain J.M., Frachisse J.M., de Langre E., Coutand C., Leblanc-Fournier N., and Julien J.L. (2011). Integrative mechanobiology of growth and architectural development in changing mechanical environments. In P. Wojtaszek [ed.], *Mechanical Integration of Plant Cells and Plants*, Signaling and Communication in Plants 9, 269-302. Springer-Verlag Berlin Heidelberg.