Growing Straight : Evidences of active proprioceptive control in plants

Félix Hartmann, Jérôme Franchel, Stéphane Ploquin, Renaud Bastien, Mélanie Decourteix, Eric Badel, Nathalie Leblanc-Fournier, Bruno Moulia

Physics & Biology of Plant Growth, 2023

Growing Straight

Evidences of active proprioceptive control in plants

Bruno MOULIA,

Caulus A, Franchel J , Brunel-Michac N, Badel E , Decourteix M, Leblanc-Fournier N., Félix HARTMANN

PIAF

INRAE
French National Research Institute for Agriculture, Food and Environment

UCA Université Clermont Auvergne

ERA-CAPS

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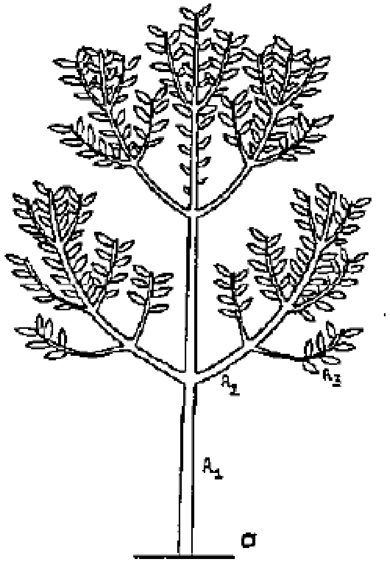
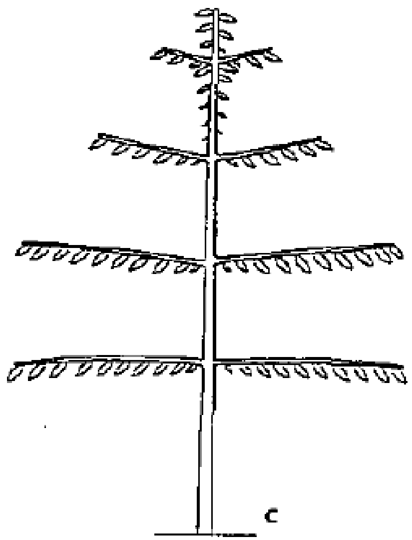
CAP 20-25 I-SITE CLERMONT Clermont Auvergne Project

Growing straight…. toward the vertical or at some angle to it



Ortho-tropic

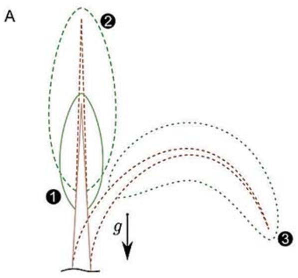


Plagio-tropic

F Hallé

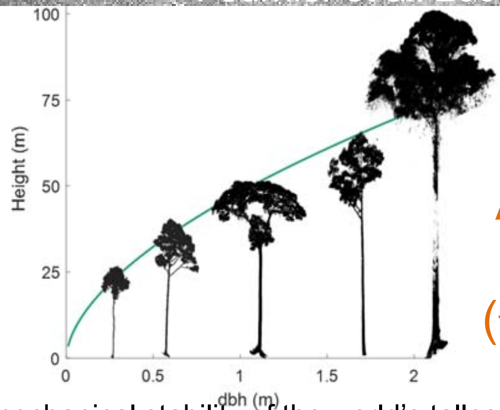
Tropism (orthotropism)

Straight growth in height is unstable if not controlled: Euler self-buckling



Moulia et al. 2019

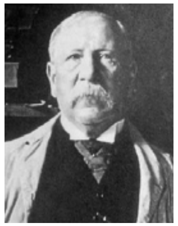

Fournier et al. 2006, 2013



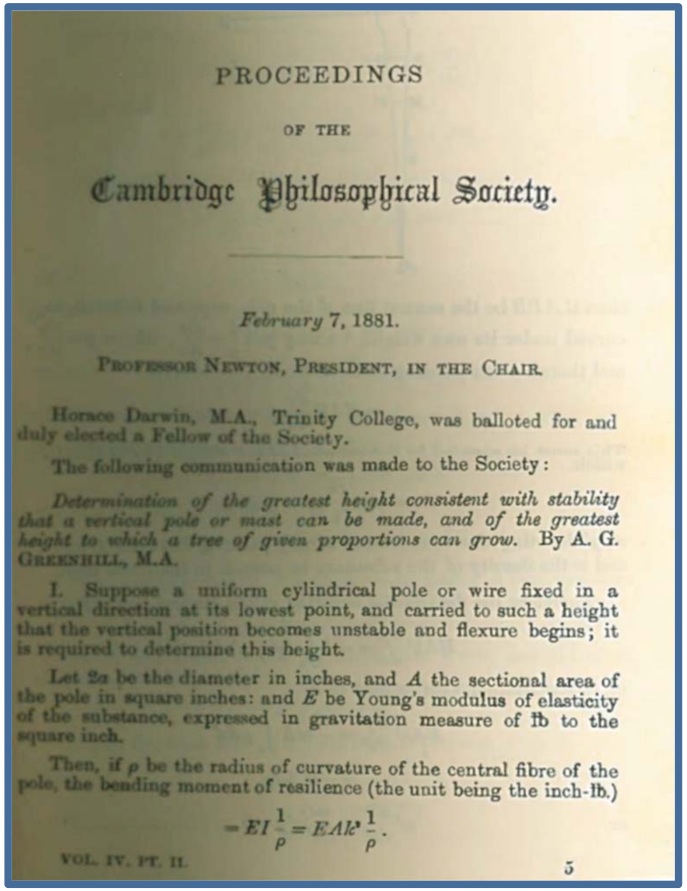
The mechanical stability of the world's tallest broadleaf trees

Jackson et al 2020 Biotropica, 53: 1: 110-120


L Euler


A.G Greenhill


T A Mc Mahon



PROCEEDINGS

OF THE

Cambridge Philosophical Society.

February 7, 1881.

PROFESSOR NEWTON, PRESIDENT, IN THE CHAIR.

Horace Darwin, M.A., Trinity College, was balloted for and duly elected a Fellow of the Society.

The following communication was made to the Society:

Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and of the greatest height to which a tree of given proportions can grow. By A. G. GREENHILL, M.A.

1. Suppose a uniform cylindrical pole or wire fixed in a vertical direction at its lowest point, and carried to such a height that the vertical position becomes unstable and flexure begins; it is required to determine this height.

Let $2a$ be the diameter in inches, and A the sectional area of the pole in square inches: and E be Young's modulus of elasticity of the substance, expressed in gravitation measure of lb to the square inch.

Then, if ρ be the radius of curvature of the central fibre of the pole, the bending moment of resilience (the unit being the inch-lb.)

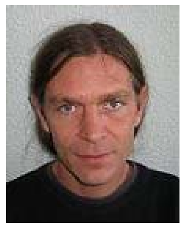
$$= EI\frac{1}{\rho} = EAk^2\frac{1}{\rho}.$$

VOL. IV. PT. II. 5

Allometric growth
Wind response
(thigmomorphogenesis)

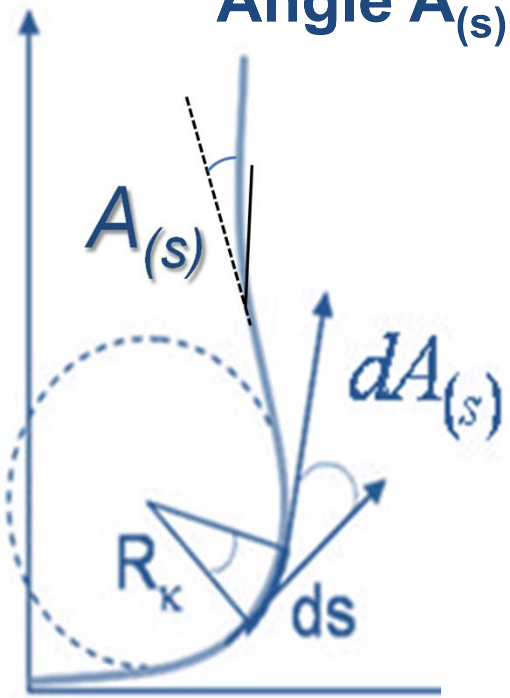

I Elishakoff


M Fournier


T Alméras

Quantifying bending and bending by growth (tropism)

Angle $A_{(s)}$



Curvature $C_{(s)}$

= rate of change in angle A (s) per unit increment of spatial position (ds)

$$dA_{(s)} / ds = C_{(s)}$$

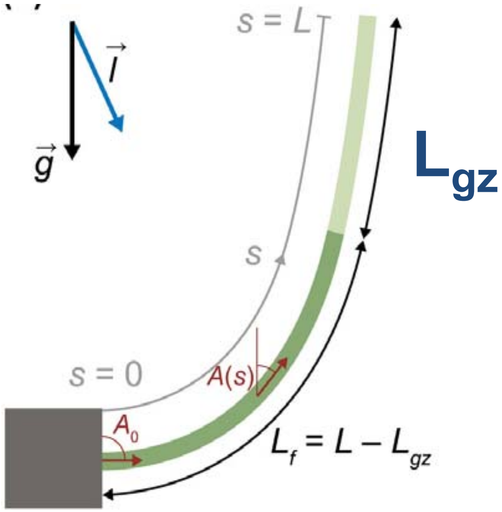
$$\dot{E} = \frac{dl}{ldt}$$

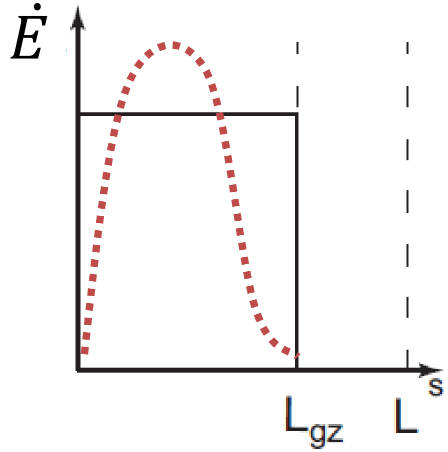
$$\frac{DC}{Dt}(s,t) = ?$$

Growth :

Relative elemental Expansion rate Ė

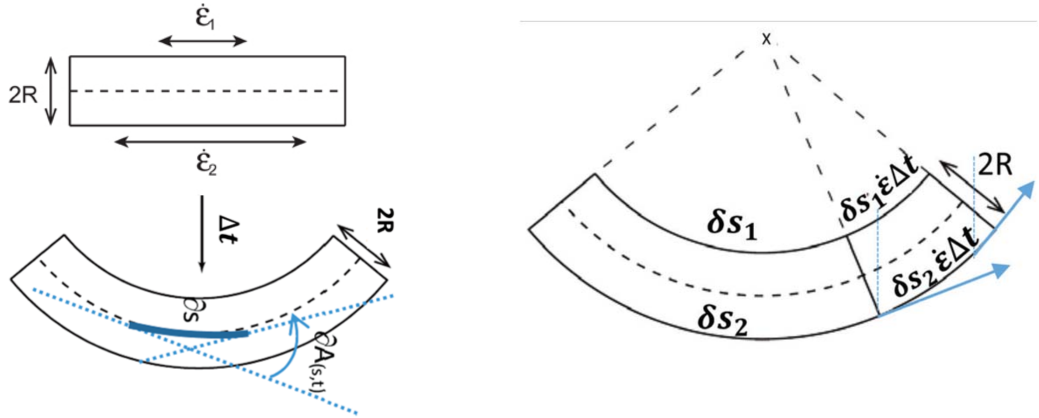
Length of the growth zone L_{gz}

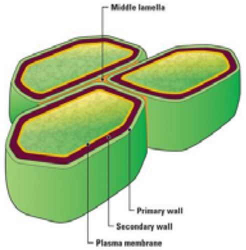




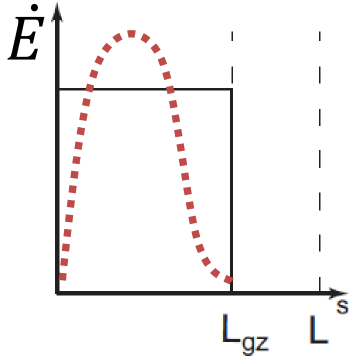
Straight primary growth is ….not straightforward

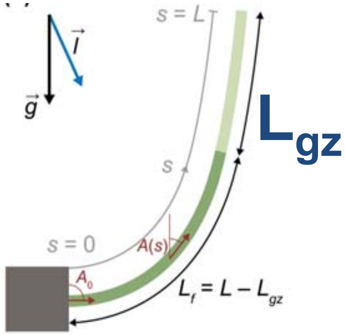
⇨ Kinematics : curvature spreading and angular drift

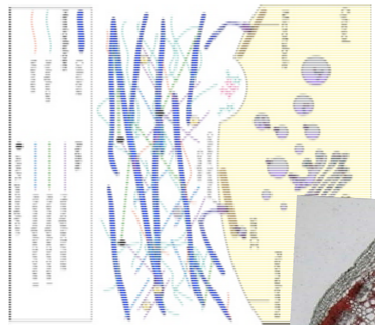


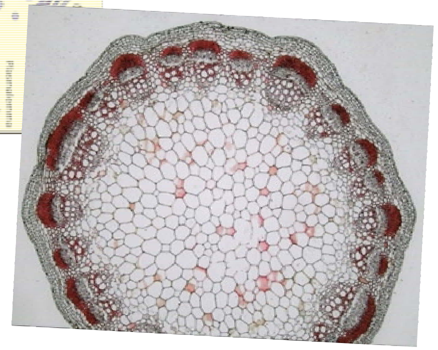


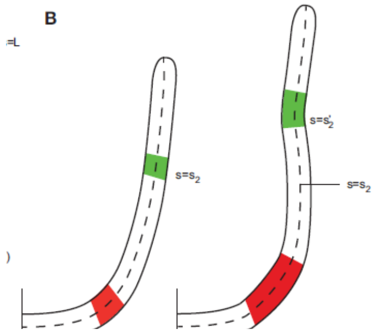
⇨ Cell wall synthesis and lignification : curvature fixing

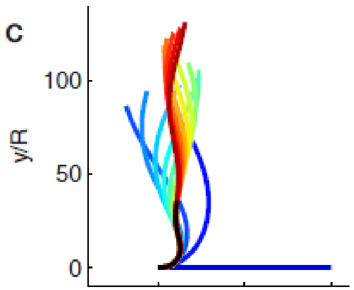






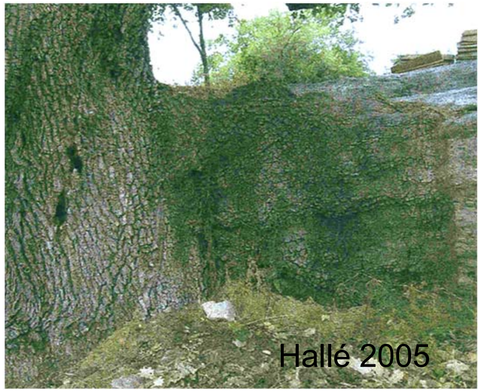






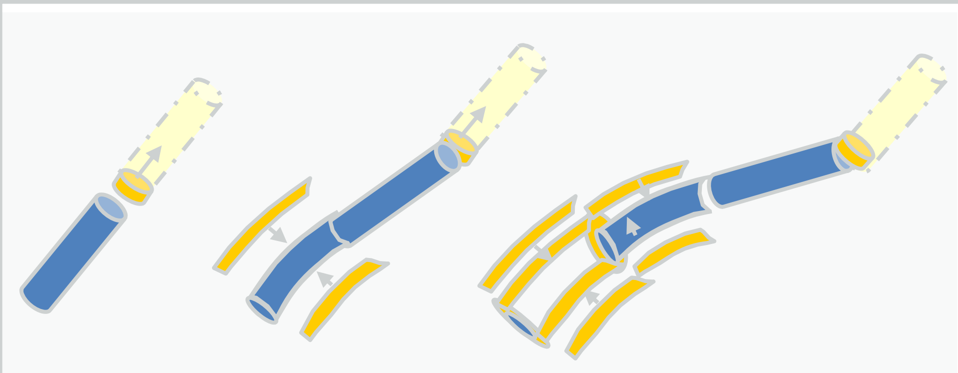
And secondary growth ?

Secondary Growth = viscous coating that locks in
(onto the actual configuration)



Secondary Straight growth is mechanically unstable!

Transverse deposition of cell-wall material
=> <u>**tend to fix-in the current form**</u>
<u>**(slow instability)**</u>



⇨ **any deformation would increase**

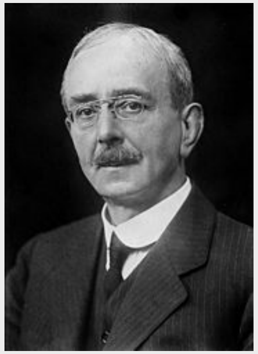
↳All the woody stems would droop down during growth
(slow instability)

Fournier et al. 1994, 2006, 2013

But straight stems are many !

How can it be ?

Our proposal : proprioception drives tropic motors



Sir **Charles Scott Sherrington (Nobel Prize)**

Wayneflet professorship of Physiology
University of Oxford, England, UK

⇨ ***Proprioception in animals***
⇨ ***Sensing of body-shape***

PNAS 2013 From the Cover

Unifying model of shoot gravitropism reveals proprioception as a central feature of posture control in plants

Renaud Bastien[a,b,c], Tomas Bohr[d], Bruno Moulia[a,b,1,2], and Stéphane Douady[c,2]

[a]INRA (Institut National de la Recherche Agronomique), UMR0547 (Unité Mixte de Recherche PIAF Physique et Physiologie Intégratives de l'Arbre Fruitier et Forestier), F-63100 Clermont-Ferrand, France; [b]Clermont Université, Université Blaise Pascal, UMR0547 (Unité Mixte de Recherche PIAF Physique et Physiologie Intégratives de l'Arbre Fruitier et Forestier), BP 10448, F-63000 Clermont-Ferrand, France; [c]Matière et Systèmes Complexes, Université Paris-Diderot, 75025 Paris Cedex 13, France; and [d]Department of Physics and Center for Fluid Dynamics, Technical University of Denmark, DK-2800 Lyngby, Denmark

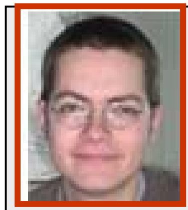
RESEARCH 2021 Science

REVIEW

PLANT SCIENCE

Fluctuations shape plants through proprioception

Bruno Moulia[1]*, Stéphane Douady[2]*, Olivier Hamant[3]*



R Bastien

S Douady

T Bohr

⇨ ***Proprioception in plants***

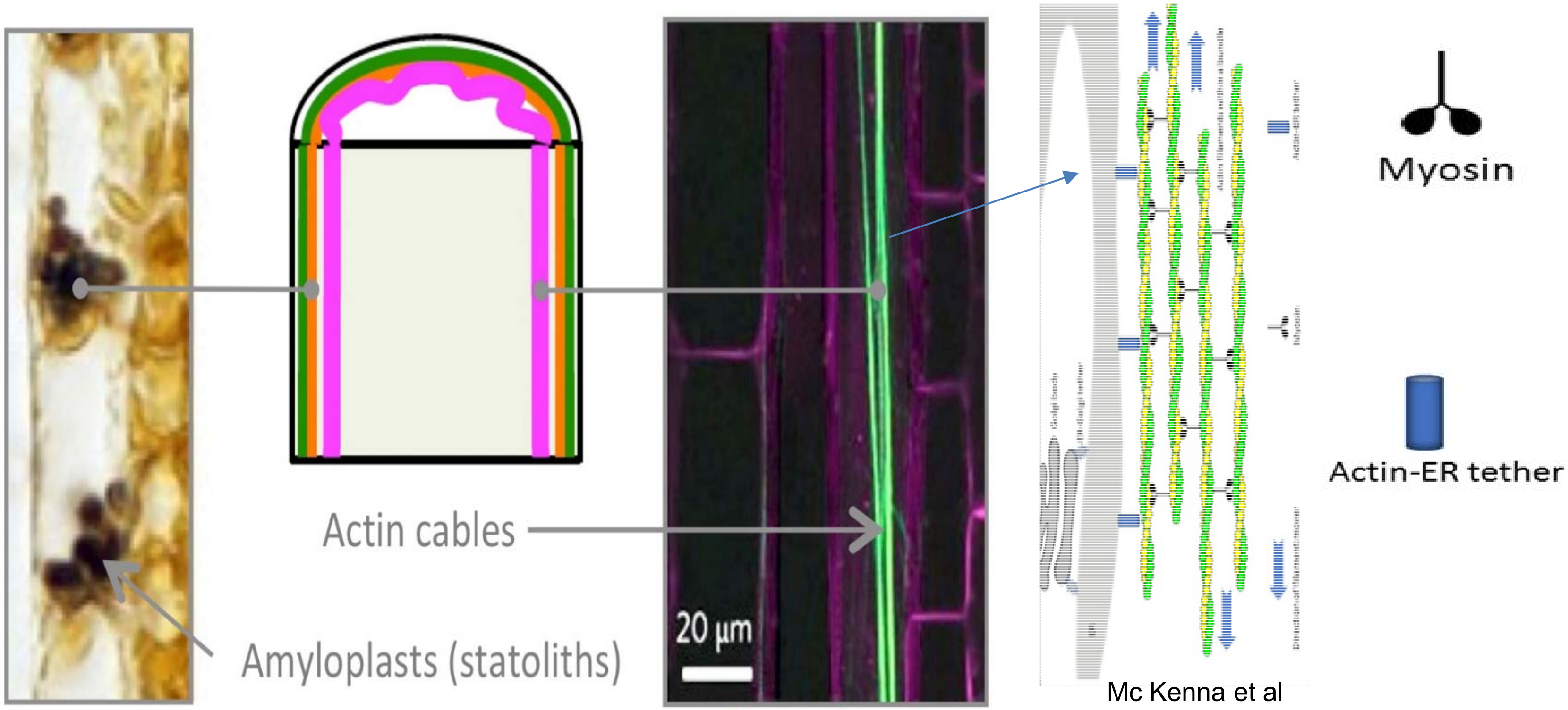
256 cites

O Hamant

⇨ ***Sensing of the curvature C(s) of the organ***

⇨ ***driving of the two tropic motors***
↳ ***active corrective bending (autotropism)***

Sensory apparatus : *Cellular/Molecular aspects proprioception and its cross talk with gravi-cline-sensing*



Mc Kenna et al 2018 BioArchiv

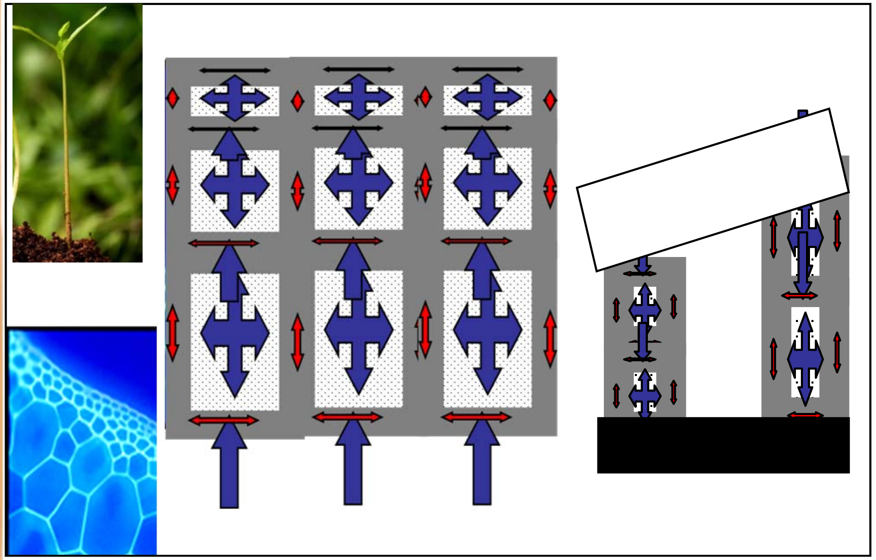
Statocyte

Propriocyte

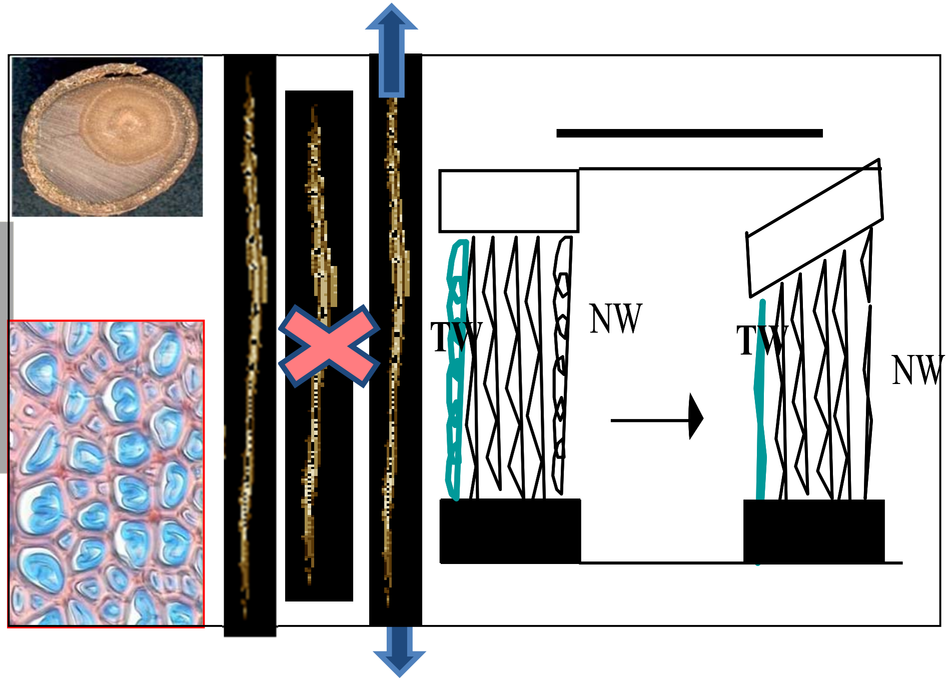
Berut et al 2015 PNAS

Okamoto et al 2015 Nature Plant,
Moulia et al. 2021 Science

2 – the two motors involved in active (tropic) bending



•M1: Osmo-Hydraulic motors
(living tissues) typ σ = 0.5 Mpa
fast



•M2: Polymeric shrinkage motors
=> **Tension woods** (lignified tissues)
typ σ = 5 to 30 Mpa
slow

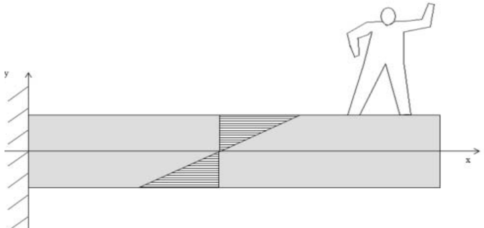
Archer 1987 following Watanabe 1965, Boyd 1972, Bamber 1978, Okuyama et al. 1986, 1994, Wilson & Archer 1979 , Almeras & Fournier 2009

Our proposal : proprioception drives tropic motors so to straighten the organ and avoid instability

Enrico Coen
Biologist

Well ….
On what evidences do you rely on ?

Amir Porat ,
Physicist



Phenomenology : tilt experiments on a living plant

Bastien et al, 2013 Pnas

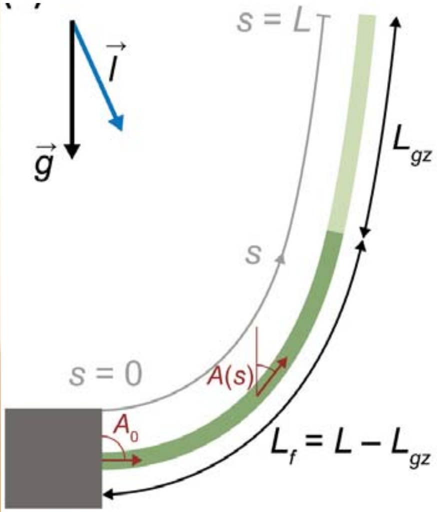
An herb : *Arabidopsis thaliana*

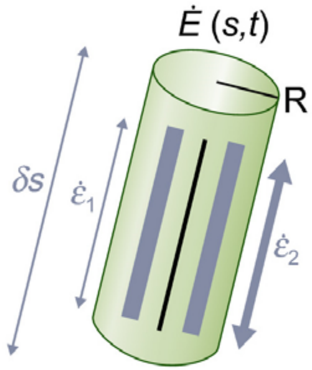
A (young) tree: poplar
(*Populus tremula * alba*)

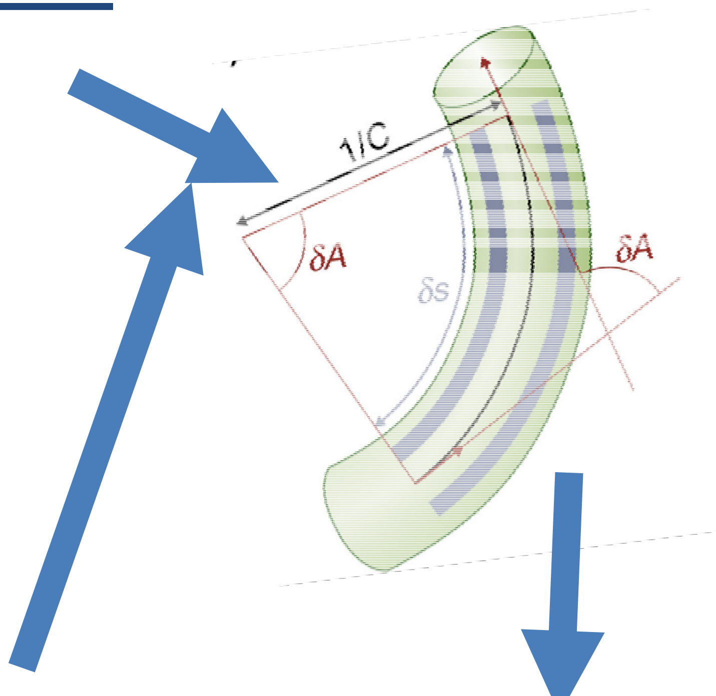
Gertrulla et al, 2015 Plant Cell

Our initial argument : Modelling the gravitropic response

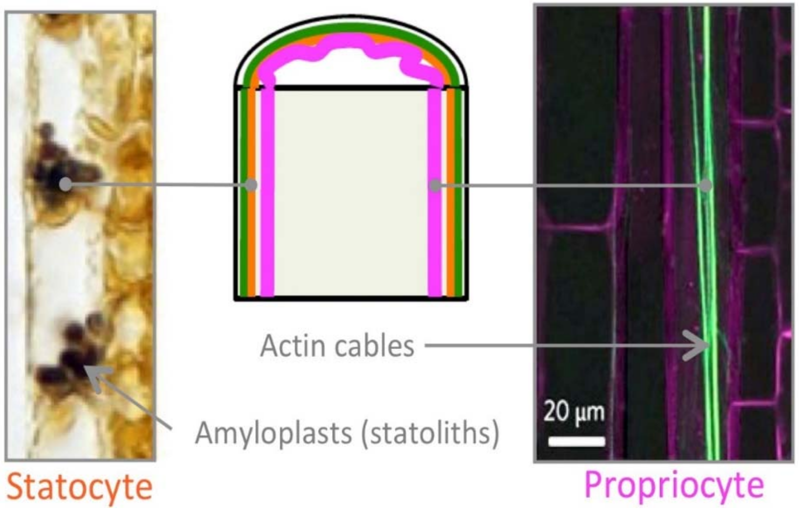
- **Motor : differential elongation growth**



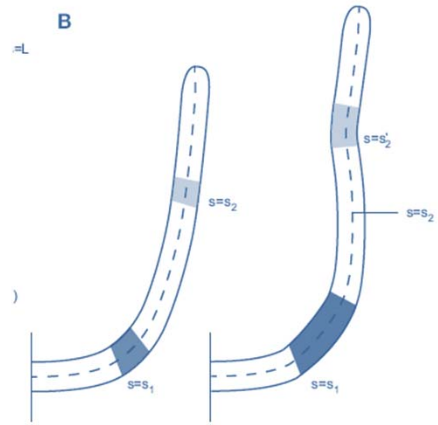




- **Driving : *gravi-proprio-ceptive***



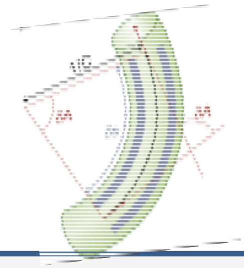
- **Convection by growth**



Bastien et al 2015 Fr Pl Sci, Moulia et al. 2019 J Exp Bot, Moulia et al. 2021 Science,

Our initial argument : Dynamical modelling

⇨The ACĖ model



- Reconfiguration of each element of stem

Motor **Driving**

$$\frac{DC(s,t)R}{Dt} = \dot{E}(s,t)\left(-\tilde{\beta}A(s,t) - \tilde{\gamma}C(s,t)R\right)$$

gravitropic proprioceptive

Rate of change of Curvature
(scaled by the radius of the growth zone)

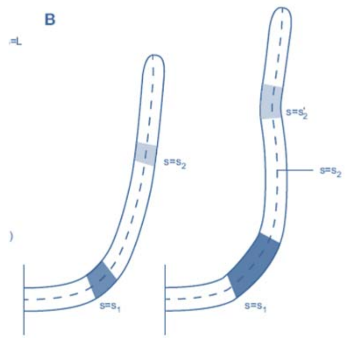
$\tilde{\beta}$: Gravitropic sensitivity

$\tilde{\gamma}$: Proprioceptive sensitivity

Dimensionless

- Convection by growth

$$V(s,t) = \int_{s=L-L_{gz}}^{L} \dot{E}\, ds$$



Bastien et al 2015 Fr Pl Sci, Moulia et al. 2019 J Exp Bot, Moulia et al. 2021 Science,

$\dot{ACE}$ model

Reproduces nicely the motion observed in experiments : posture and straightness control

Model mutants

What if **proprioceptive sensitivity is almost KO ?**

ACĖ model

⇨ **ACĖ Model quantitative prediction**

to avoid the Growth-Posture Instability :

$$\tilde{\gamma} > 1$$

Posture cannot be controlled over growth⇨ unstable

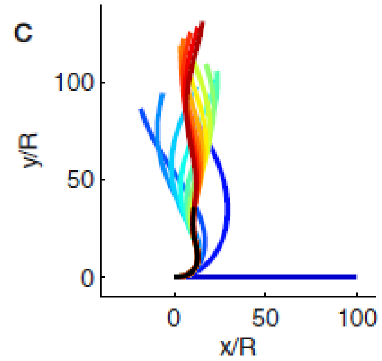
ACĖ
Model
Low $\tilde{\gamma}$

ACĖ model

⇨ **ACĖ Model quantitative prediction**

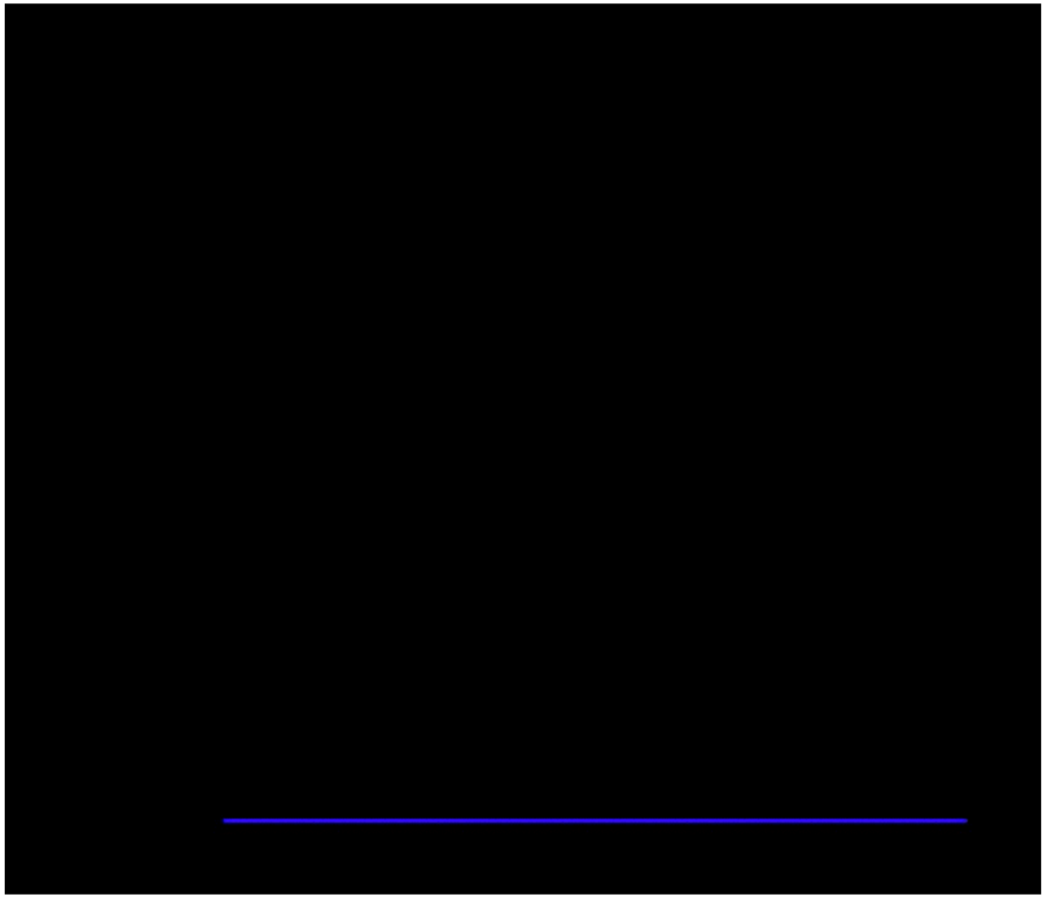
Required proprioceptive sensitivity $\tilde{\gamma}$

$$\tilde{\gamma} \gg \sqrt{\tilde{\beta}\,\frac{L_{gz}}{R}}$$

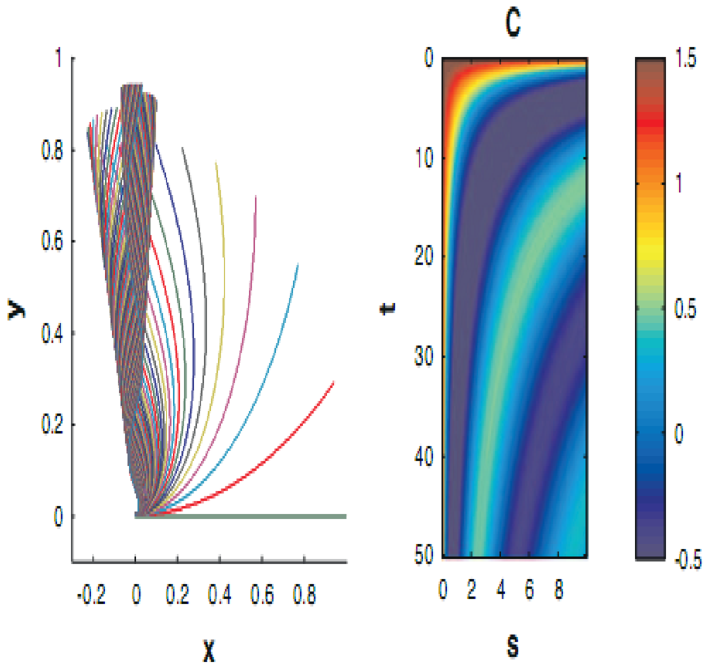


Angle gravisensing : model A

$$\frac{\partial C(s,t)}{\partial t} = -\beta A(s,t)$$



$$A(s,t) = A_0 J_0(2\sqrt{\beta s\, t})$$

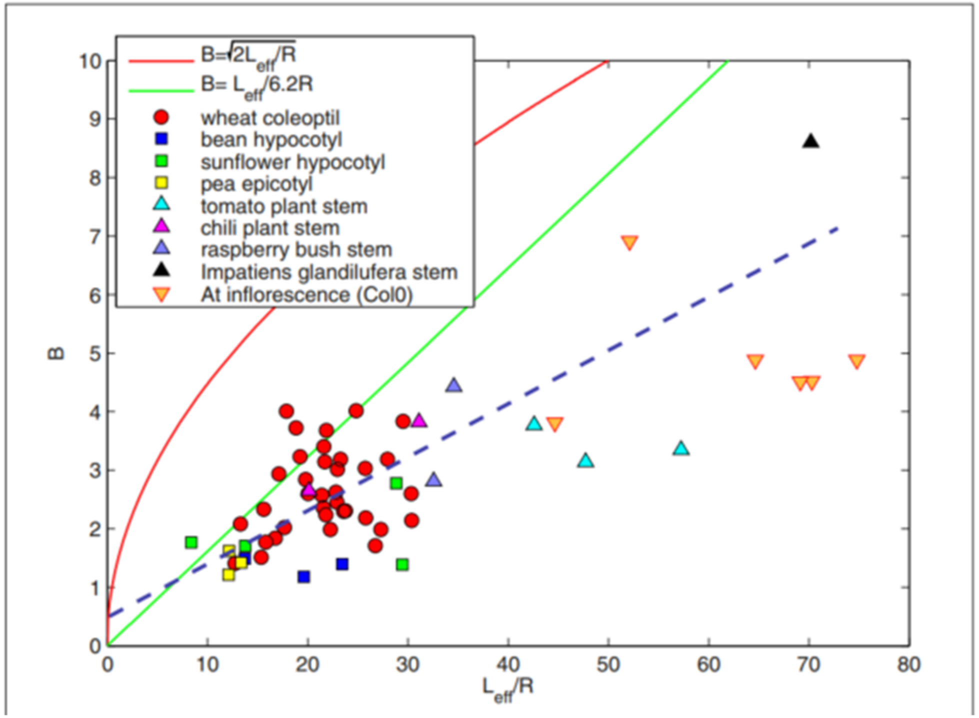


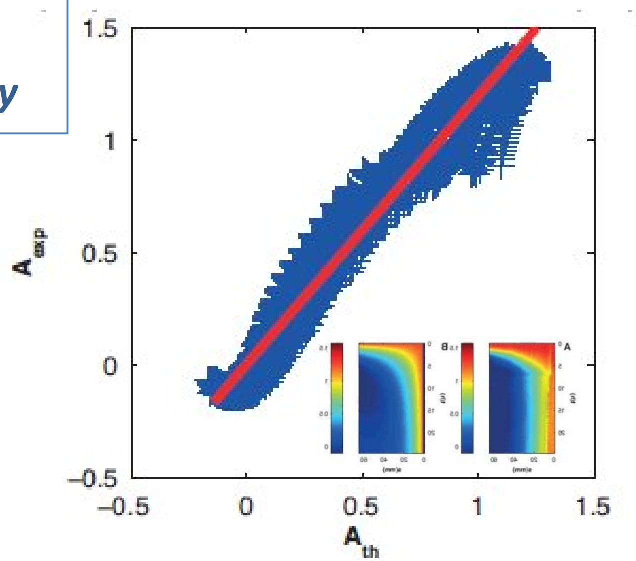
↳ The gravitropic feedback alone brings infinite oscillations (because of non-linearity and distributed growth) !

Experimental assessment

on 13 species sampling lang angiosperms phyllogeny

Fits the whole straigthening kinematics
with no bias (and only 2 parameters !)





$$\tilde{\gamma} > 1$$

$$\tilde{\gamma} > \sqrt{\tilde{\beta}\,\frac{L_{gz}}{R}}$$

Seleective pressure ?

***The* gravi-proprioceptive model:**
universal core of gravitropism and posture control:
orientation and straightness

Our proposal : proprioception drives tropic motors so to straighten the organ and avoid instability

Enrico Coen
Biologist

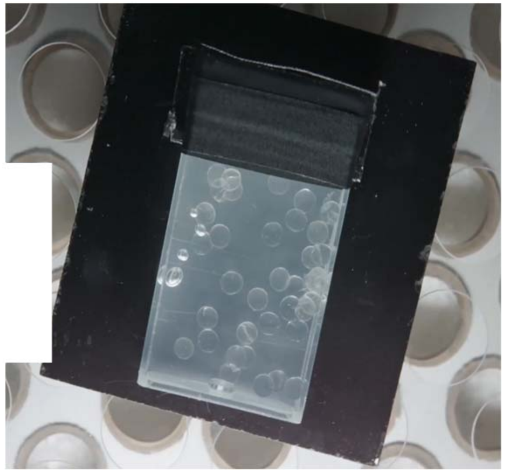
Amir Porat ,
Physicist

Any more direct evidence ?

Direct Experimental assessment

response to tilt-bend-then-clinostat- experiments (TBTC)

Okamoto et al 2015 Nature Plant



suspension of the amyloplats = suspension of gravitropic perception
↳proprioception only (if any)

tilting

Clinostat on

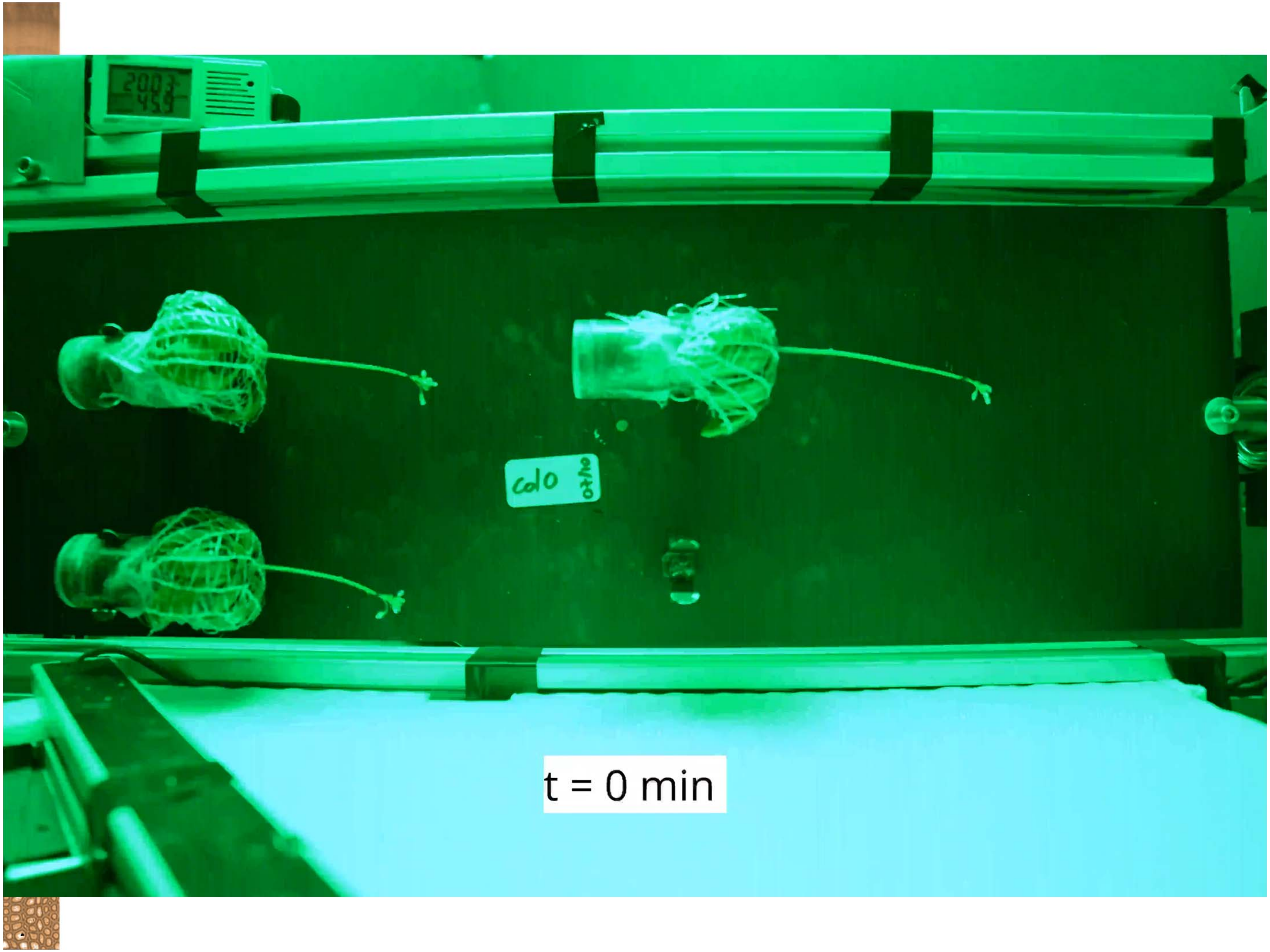
t=0

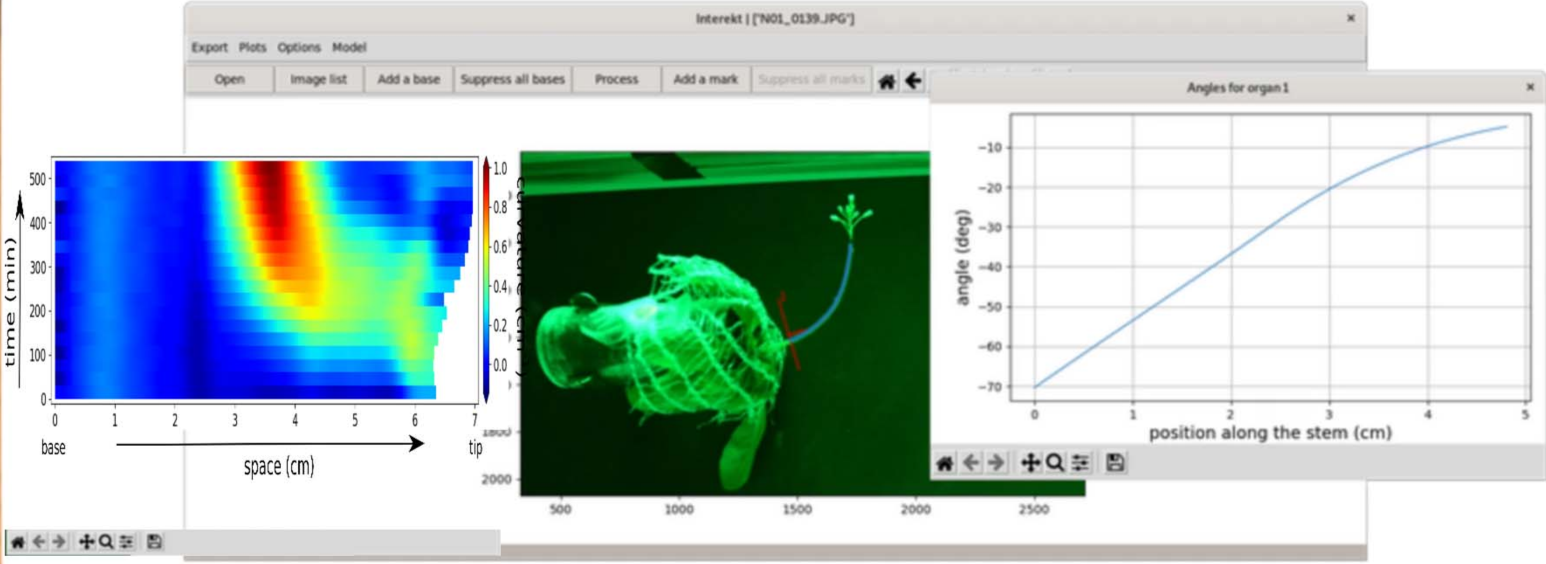
t=1h

$$\frac{DC(s,t)}{Dt} = -\dot{E}\tilde{\gamma}C(s,t)$$

Gravitropic drive

Proprioceptive drive

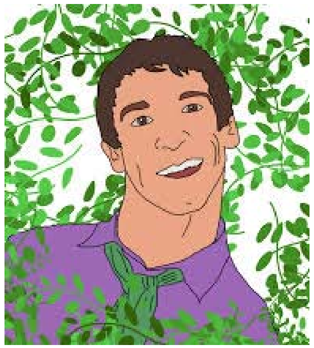

t = 0 min



Interekt is freely available at:
https://forgemia.inra.fr/felix.hartmann/interekt

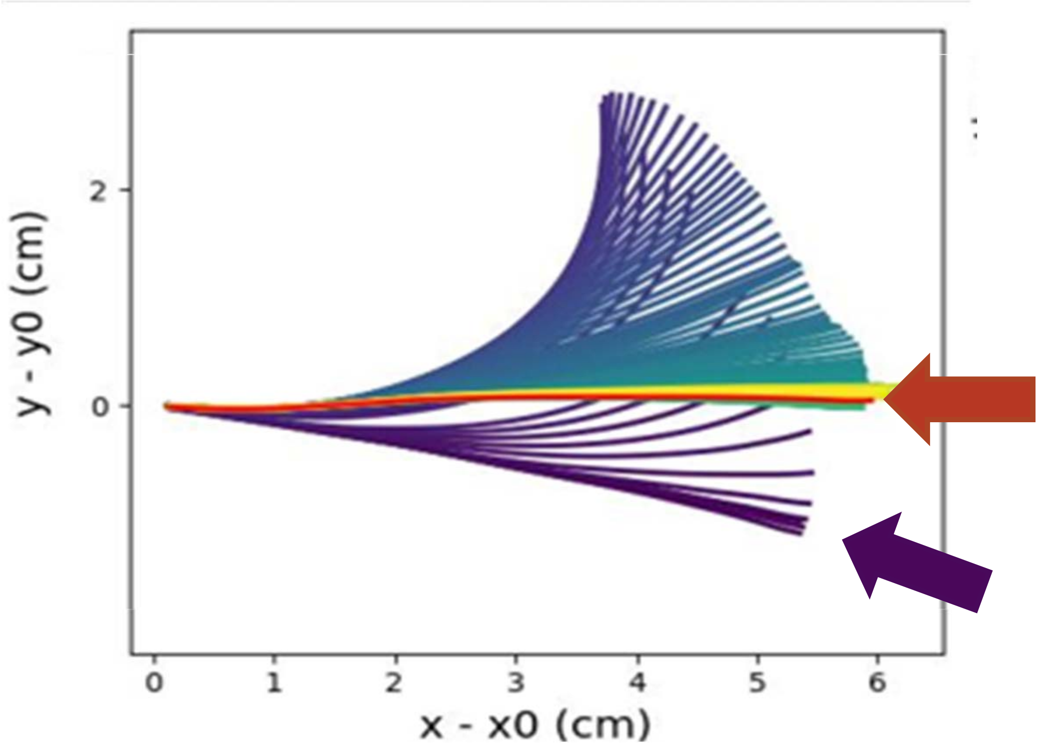
For a detailed description: Hartmann, Chauvet-Thiry *et al.* (2022) Chapter 9 in *Plant Gravitropism — Methods and Protocols*, E.B. Blancaflor (editor)

Félix HARTMANN



Hugo CHAUVET-THIRY

Crucial point : control also the curvature due to passive mechanical sagging !



R Chelakkot, Bombay

L. Mahadevan, Harvard

Sensing the actual curvature C(s)

But changing the intrinsic rest-state curvature $C_r(s)$

$$\frac{DC(s,t)R}{Dt} = \frac{DC_r(s,t)R}{Dt} - \frac{DM_B(s,t)R}{E_Y I(s,t)\,Dt}$$

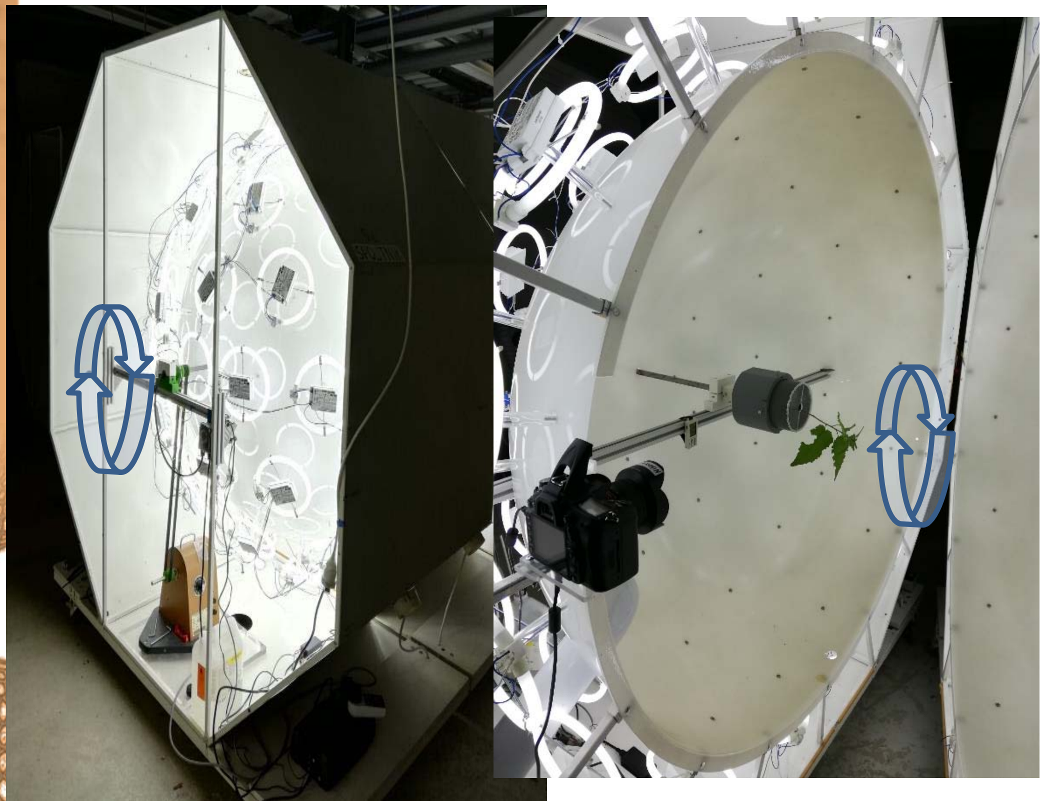
$$\frac{DC_r(s,t)R}{Dt} = \dot{E}(s,t)\left(-\tilde{\beta}A(s,t) - \tilde{\gamma}C(s,t)\right)$$

N= 35 replicates

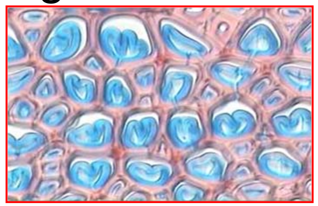
⇨ **fine-tuned proprioceptive drive (more than spring-back)**

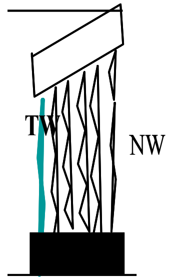
Direct Experimental assessment in trees

Tilt-Bend-Then-Clino- in isotropic Light experiments (TBtC_iL)



Tension wood : traces back the active bending events





tilting

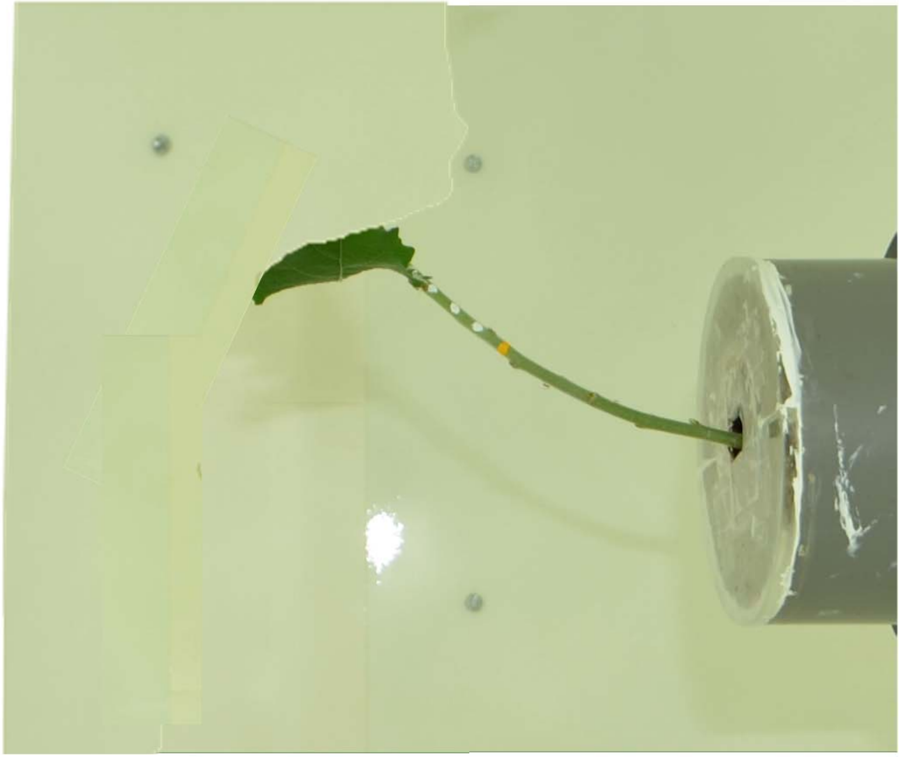
t=0

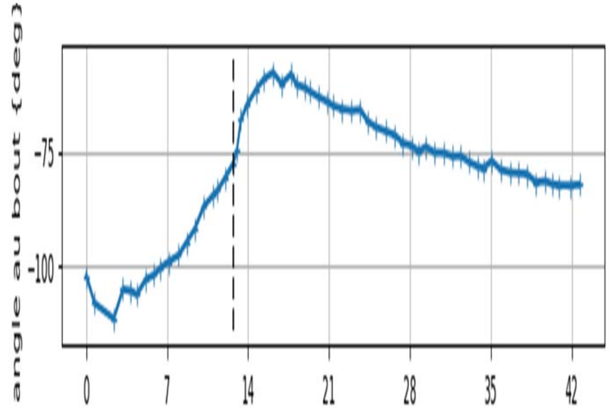
Clinostat on

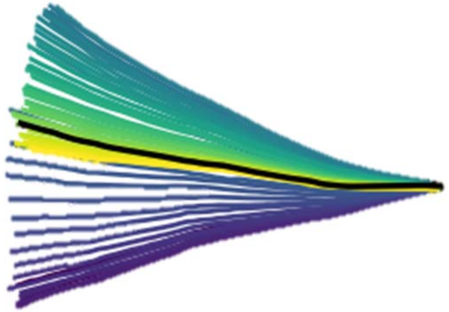
t=15 days

Proprioceptive drive

Proprioceptive cue: woody stem





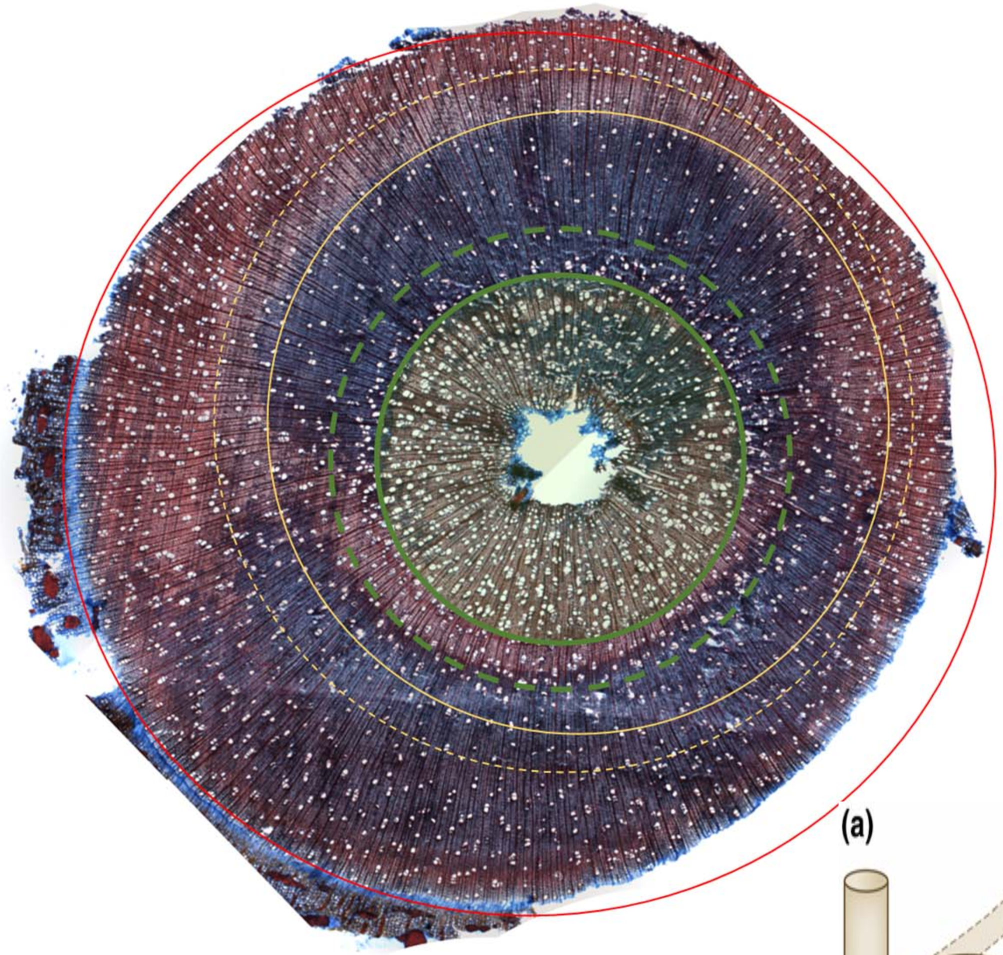


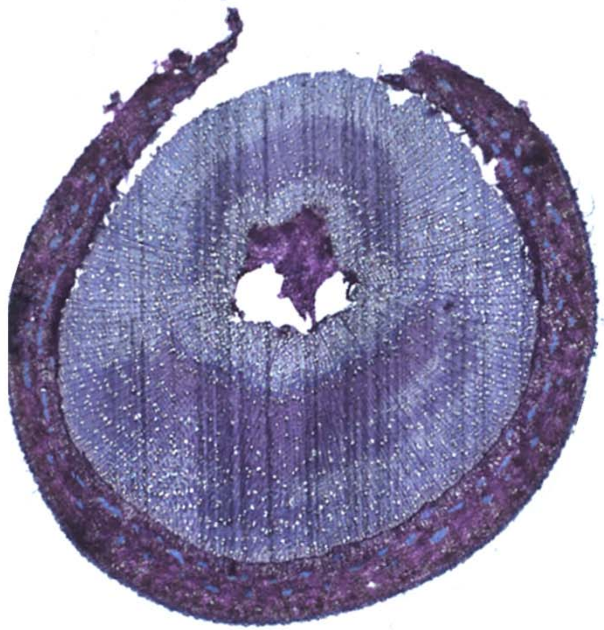
10 replicates

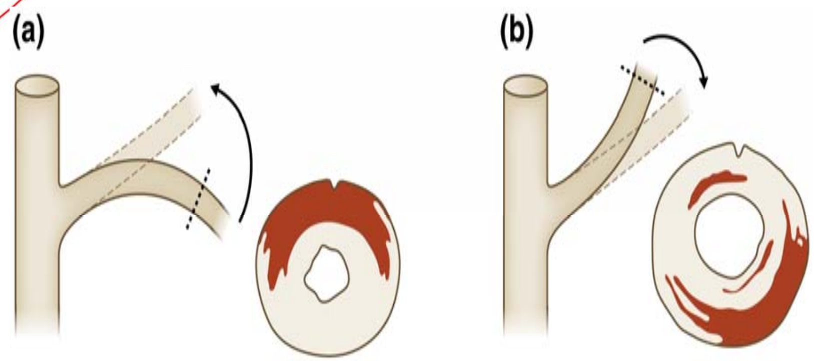
Caulus et al 2022

⇨ fine-tuned proprioceptive drive (more than spring-back)

Proprioceptive cue: woody stem : tension wood





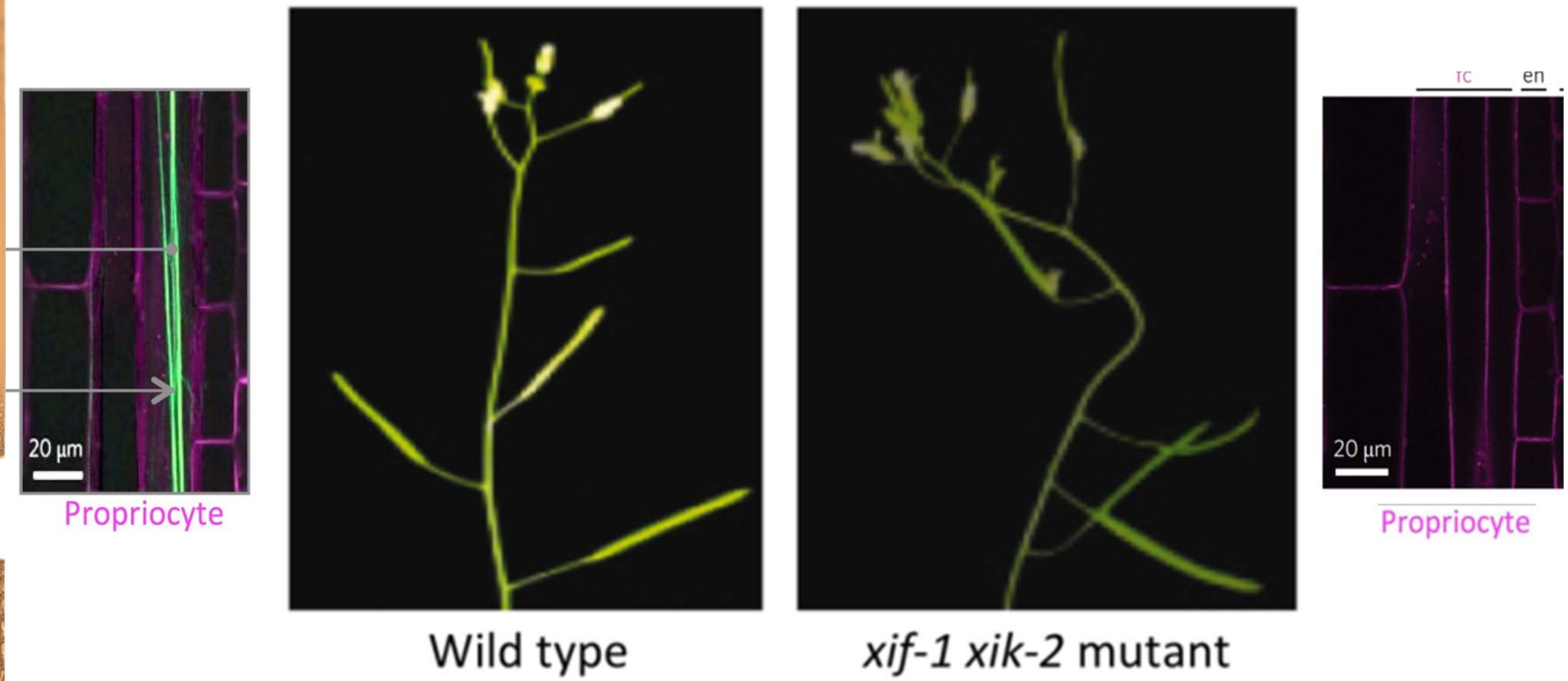


⇨ **Active proprioceptive drive**

More evidence in the molecular biology style

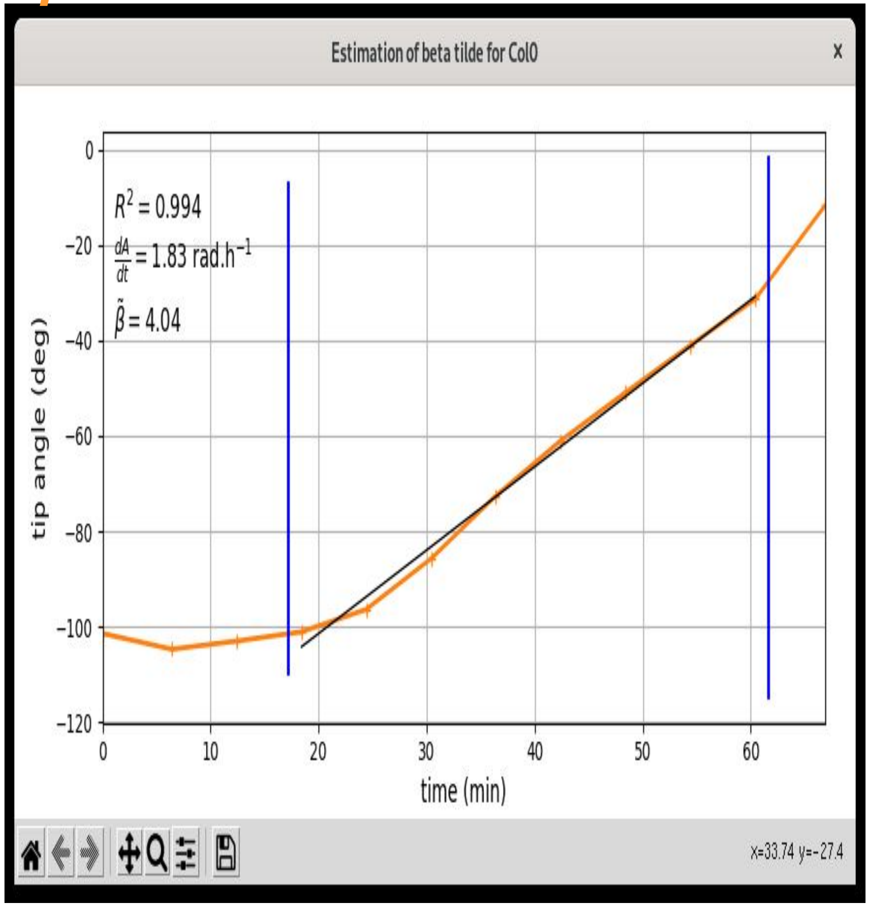
↳ Genic control ? ⇨ Evidence by KO mutant

Example of Arabidopsis wildtype and myosin XI mutants

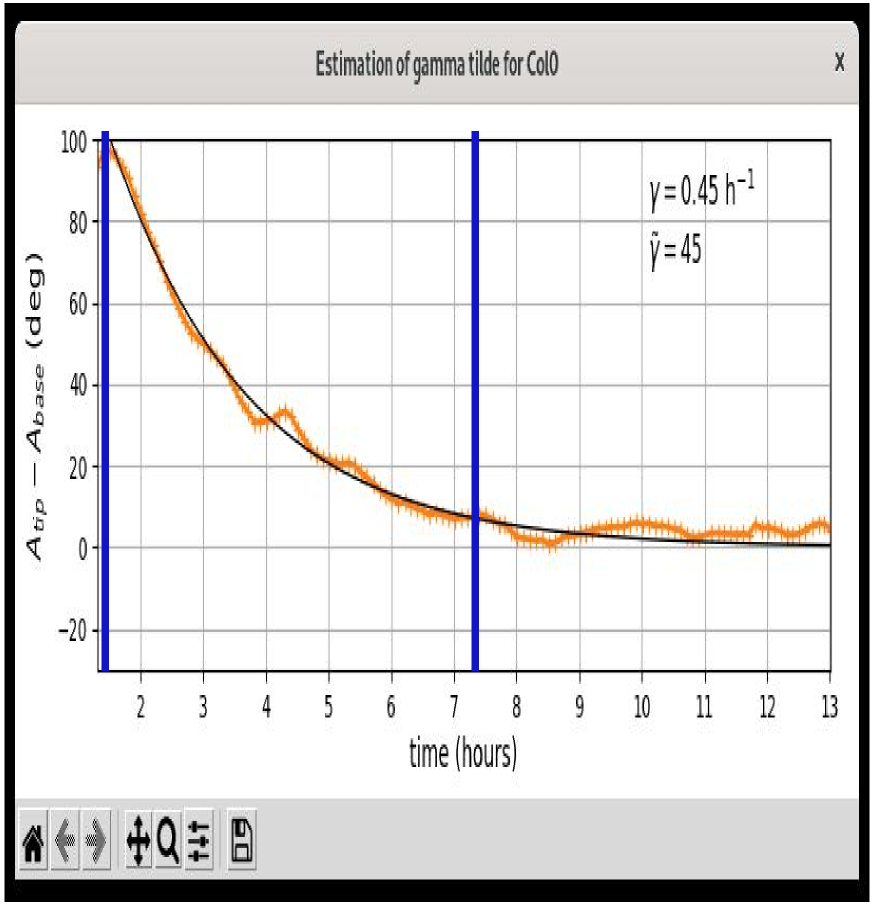


Okamoto et al 2015 Nature Plant, Moulia et al. 2022 Science

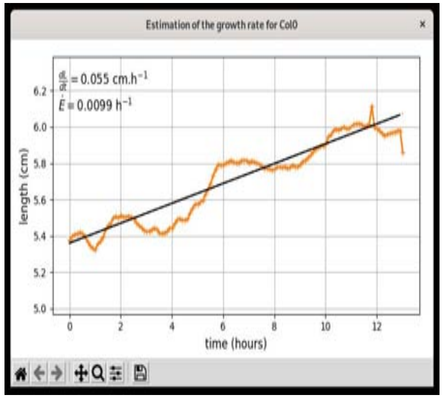
$\tilde{\beta}$: Gravitropic sensitivity



$\tilde{\gamma}$: Proprioceptive sensitivity



+ Growth and size measurement

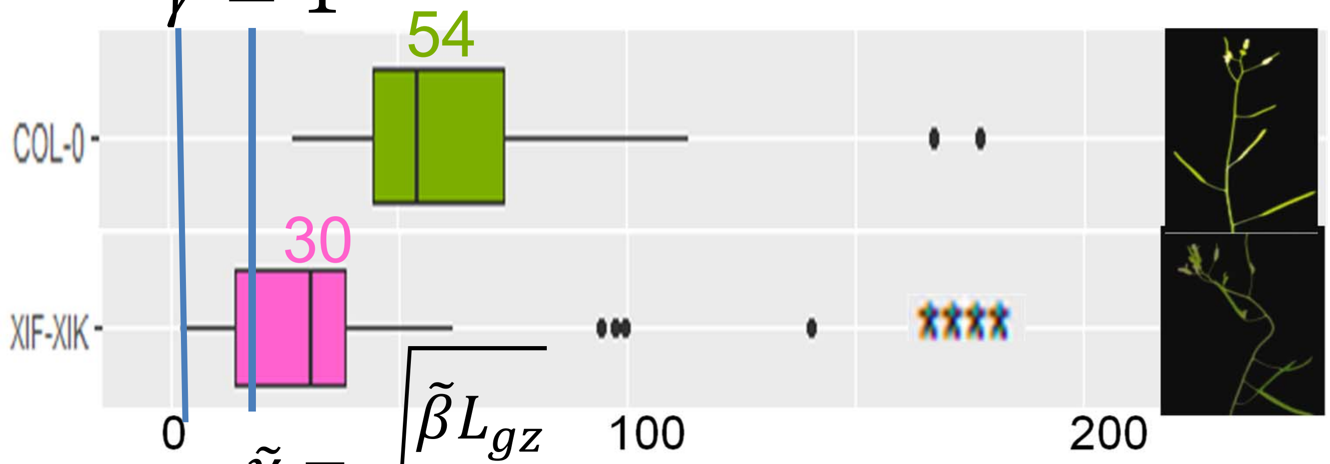


dL/dt, L_{gz}, L, R

Proprioceptive mutants ?

$\tilde{\gamma}$: Proprioceptive sensitivity

$\tilde{\gamma} = 1$



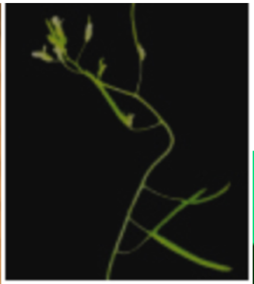
$$\tilde{\gamma} = \sqrt{\frac{\tilde{\beta} L_{gz}}{R}}$$

- 44 %

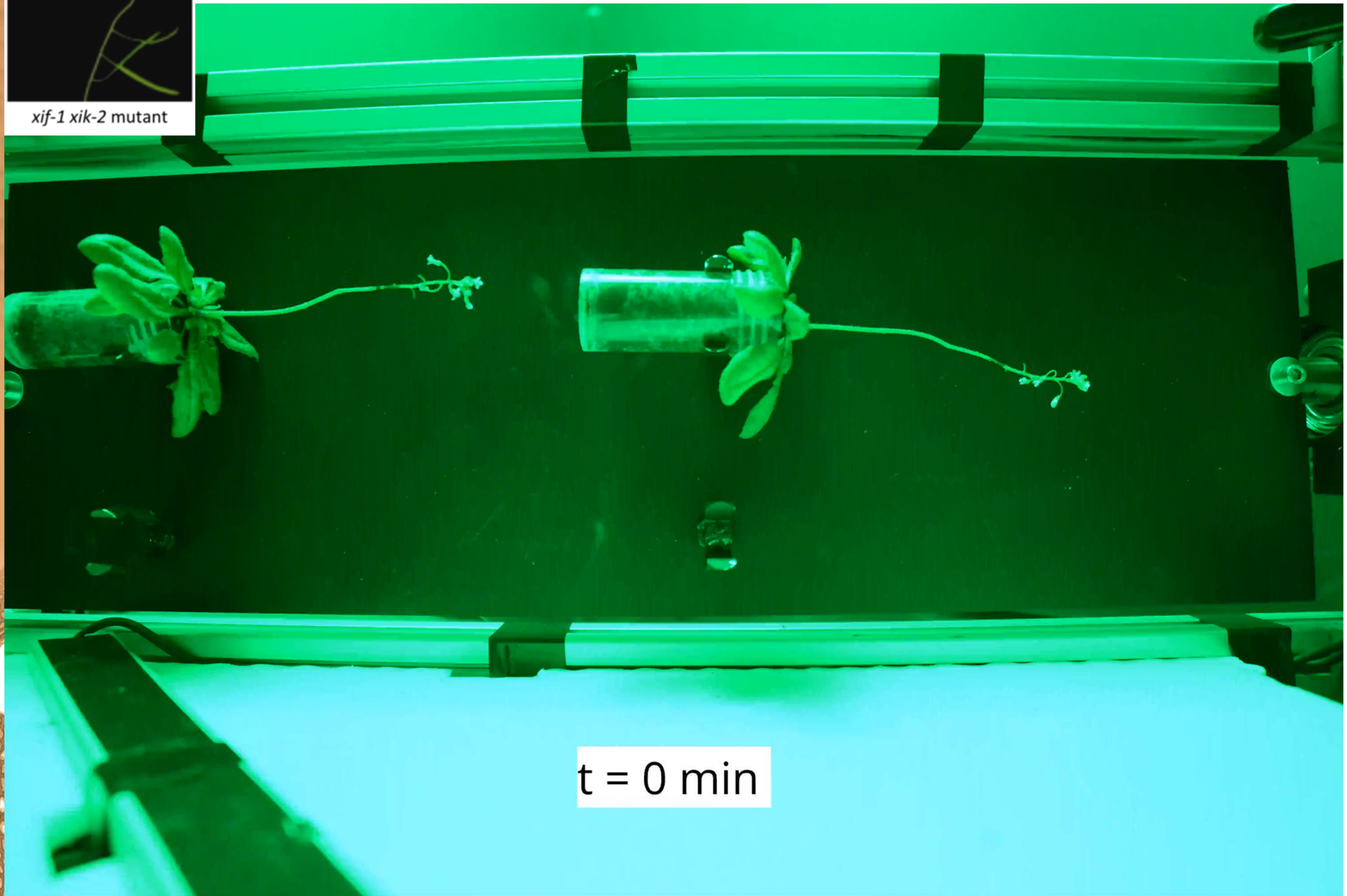
P=9.5 e-07

N= 35 replicates/ genotype

⇨ **proprioceptive drive involves genic regulation (actin*myosin cables)**

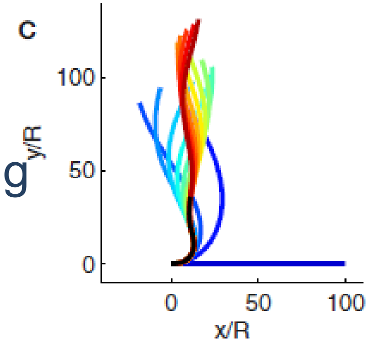


xif-1 xik-2 mutant

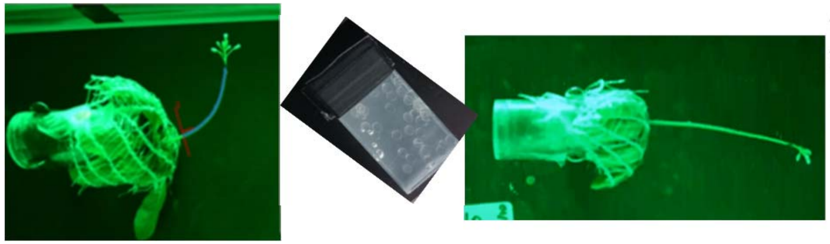


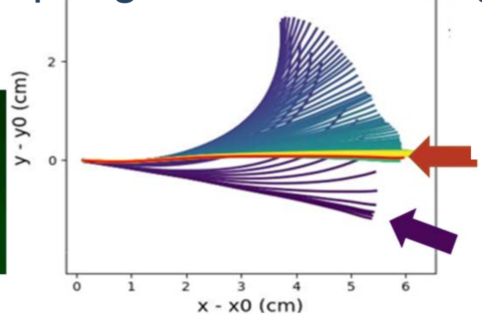
evidences of plant proprioception : graphical abstract

❶ Mathematical demonstration : if not instable :
No posture control and no straightness

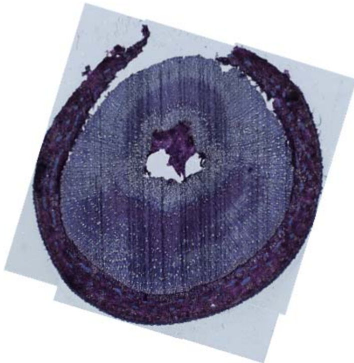


❷ TBTC on primary growth : more than springback : fine tuning

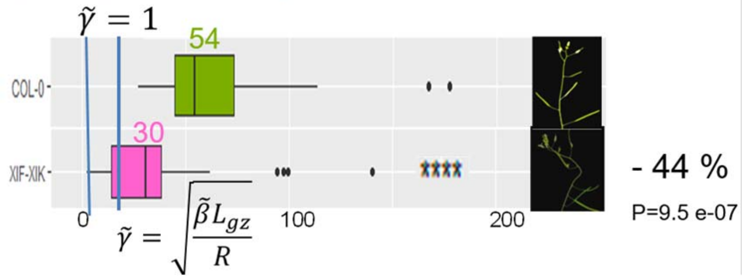




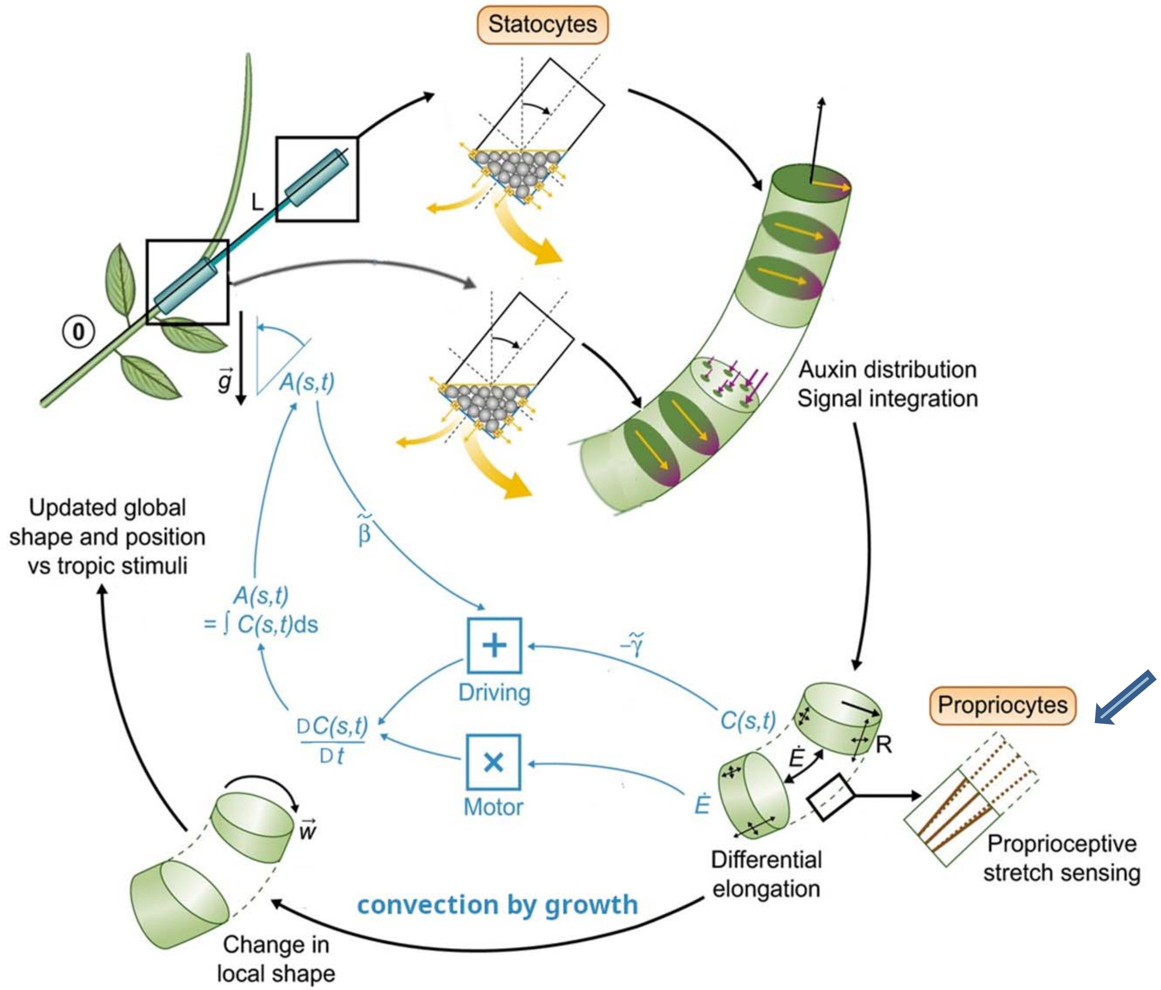
❸ TBTC on secondary growth: active control



❹ Genic regulation $\tilde{\gamma}$: Proprioceptive sensitivity



The gravi-proprio-ceptive loop controlling straight and erected growth



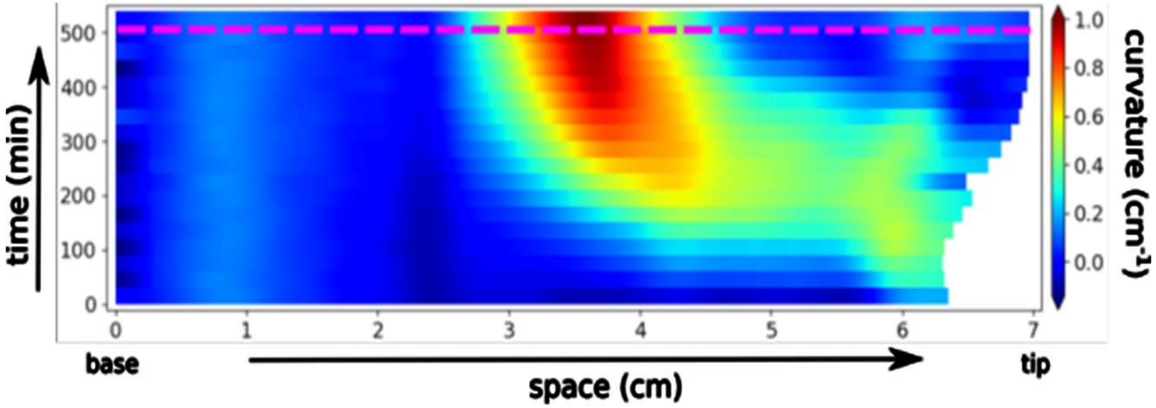
Lavernier et al. 2019, Olivieri et al. 2021 PNAS
Moulia et al. 2022 Tansley Rev. New Phytol

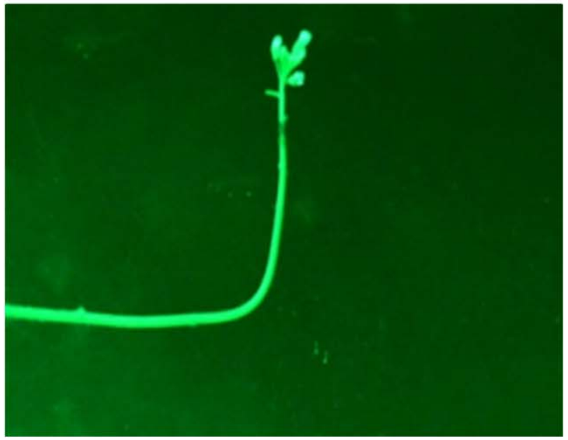
User friendly simulator of ACE model available

Thank you !

- <u>**kinematics : curvature field (ex WT)**</u>

Wild type





⇨ ***Spots where and when the genic regulation leading to posture control is being actuated***

The Balance number : a crucial dimensionless number

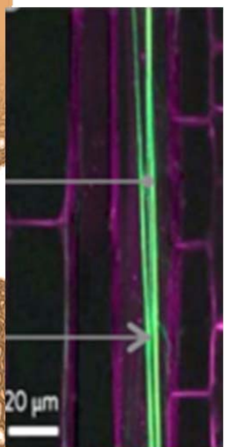
Possible complementation of the macroscopic phenotype though other pathways

⇨ improve analysis

Gravitropic sensitivity

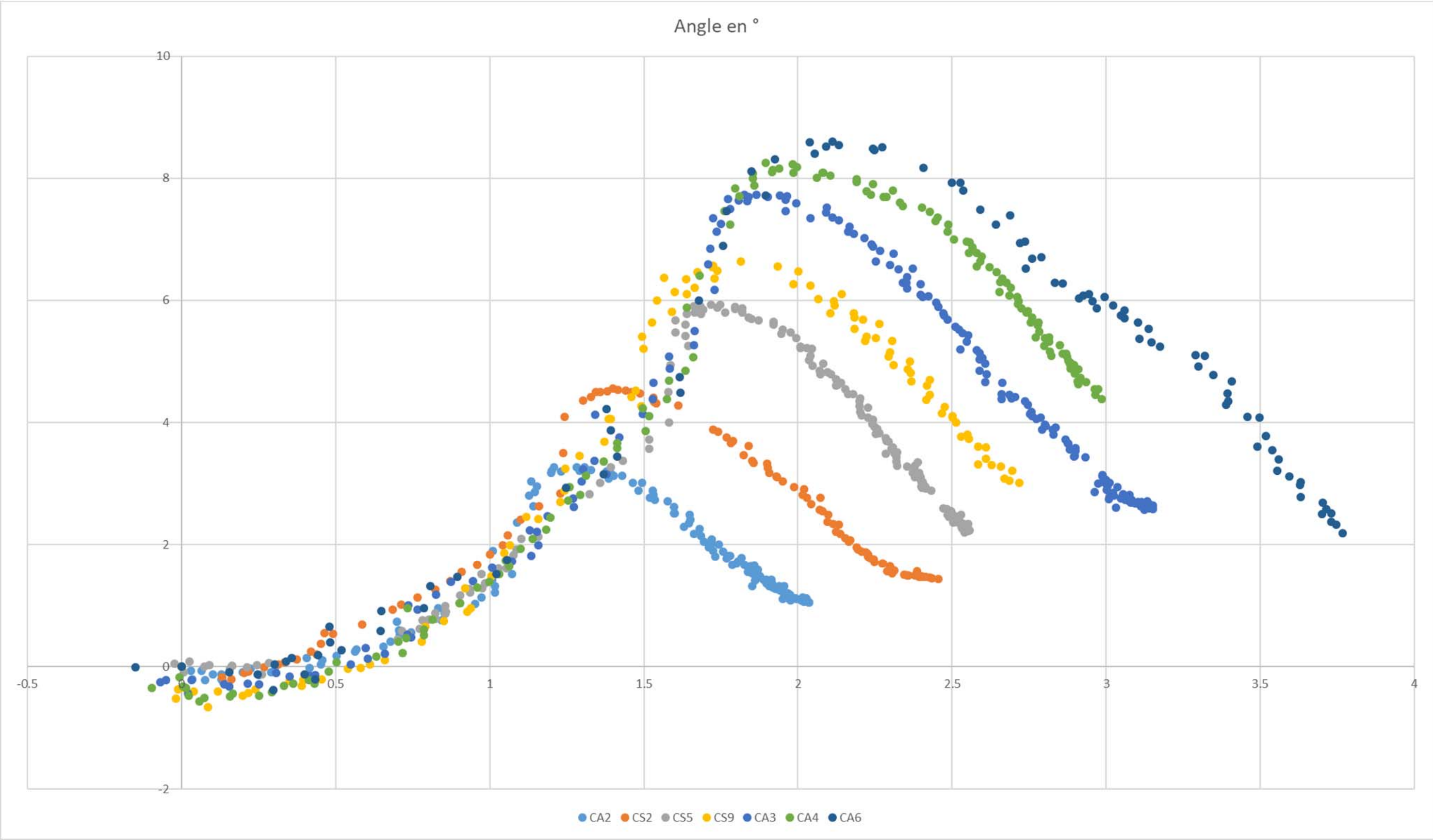
$$B = \frac{\tilde{\beta} L_{gz}}{\tilde{\gamma} R}$$

Aspect ratio



Proprioceptive sensitivity

MYOSIN XI –f +k



Angle en °
10
8
6
4
2
0
-2
-0.5
0.5
1
1.5
2
2.5
3
3.5
4
CA2 CS2 CS5 CS9 CA3 CA4 CA6

$$\tilde{\beta} = \beta R / \dot{E} \qquad \tilde{\gamma} = \gamma / \dot{E}$$

$$\beta = \frac{\tilde{\beta}\dot{E}}{R} \qquad \gamma = \tilde{\gamma}\dot{E}$$

$$B = \frac{\tilde{\beta} L_{gz}}{\tilde{\gamma} R}$$

$$T_c = \frac{1}{\dot{E}\tilde{\gamma}}$$

$$T_v = \frac{R}{\dot{E}\tilde{\beta} L_{gz}}$$

Temps pour atteindre la verticale pour la première fois :

$$\frac{DC(s,t)R}{Dt} = \dot{E}(s,t)\left(-\tilde{\beta}A(s,t) - \tilde{\gamma}C(s,t)R\right)$$

Steady state

$$0 = -\tilde{\beta}A - \tilde{\gamma}CR \qquad \tilde{\beta}A = -\tilde{\gamma}CR$$

$$A = -\frac{\tilde{\gamma}}{\tilde{\beta}}CR = -\frac{\tilde{\gamma}}{\tilde{\beta}}\frac{\partial A}{\partial s}R$$

$$-\frac{\tilde{\beta}}{\tilde{\gamma}R}\partial s = \frac{\partial A}{A}$$

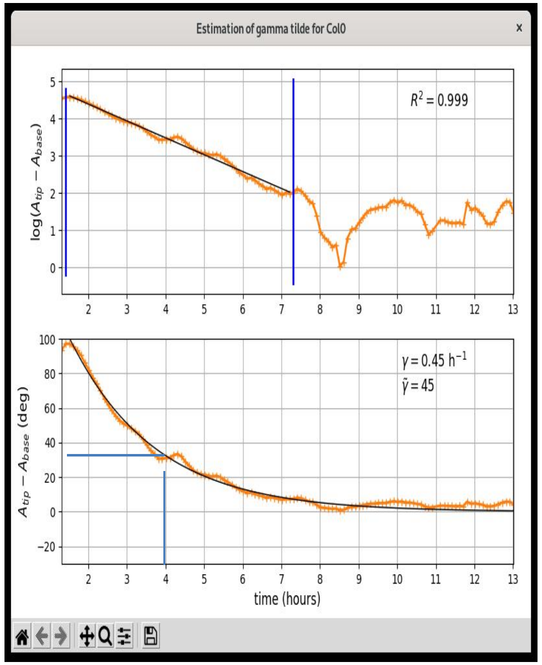
$$\mathrm{A} = A_0 e^{-\frac{\tilde{\beta}}{\tilde{\gamma}}\frac{s}{R}} = A_0\, e^{-\frac{\tilde{\beta}}{\tilde{\gamma}}\frac{L_{gz}}{R}\frac{s}{L_{gz}}}$$

clinostat

$$\frac{DCR}{Dt} = \dot{E}(-\tilde{\gamma}CR\ )$$

$$\frac{DCR}{CR \cdot Dt} = -\tilde{\gamma}\dot{E}$$

$$\frac{DCR}{\dot{E}\,CR \cdot Dt} = -\tilde{\gamma}$$



Si convection négligeable

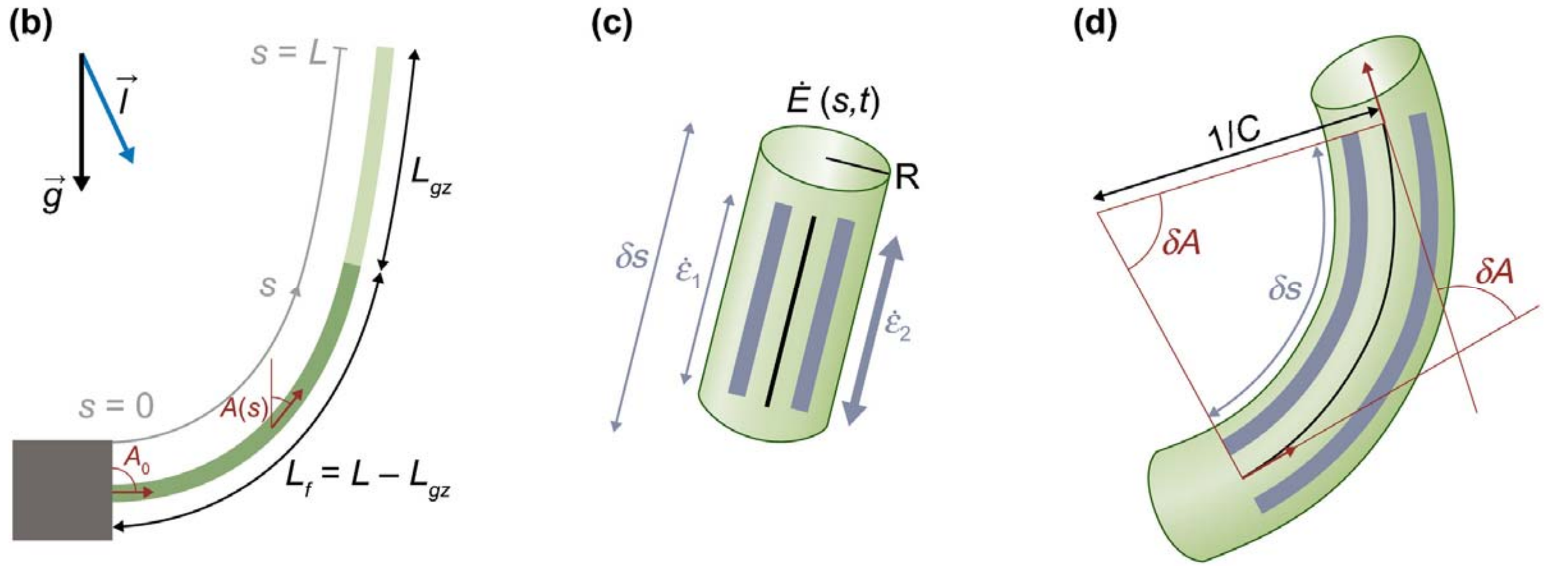
$$\frac{\partial CR}{CR \cdot \partial t} = -\tilde{\gamma}\dot{E} \qquad \int_{CR_0}^{CR} \frac{1}{CR} dCR = \int_{t_c}^{t} -\tilde{\gamma}\dot{E} \cdot \partial t$$

$$\frac{\partial CR}{CR} = -\tilde{\gamma}\dot{E} \cdot \partial t \qquad ln(CR) - ln(CR_0) = -\tilde{\gamma}\dot{E} \cdot (t - t_c)$$

$$CR(t) = CR_0 \cdot e^{-\tilde{\gamma}\dot{E}\cdot(t-t_c)} = CR_0 \cdot e^{-\frac{(t-t_c)}{\tau_a}} \qquad \tau_a = \frac{1}{\tilde{\gamma}\dot{E}}$$

$$(t - t_c) = \tau_a \quad CR(t_c + \tau_a) = CR_0 \cdot e^{-1} = 0.368 \cdot CR_0$$

$$L_f(t) = L(t) - L_{gz} = L_{gz}\dot{E}_0 t$$



Passive angular drift during growth in a elemental segment (of uniiform curvature C

$$\frac{dA'(s,t)}{dt} = \dot{E}(s,t)\left(\Delta(s,t) + C(s,t)R\right)\frac{\delta s}{R}$$

$$\frac{dA'(s,t)}{dt} = \dot{E}(s,t)\left(C(s,t)\delta s\right)$$

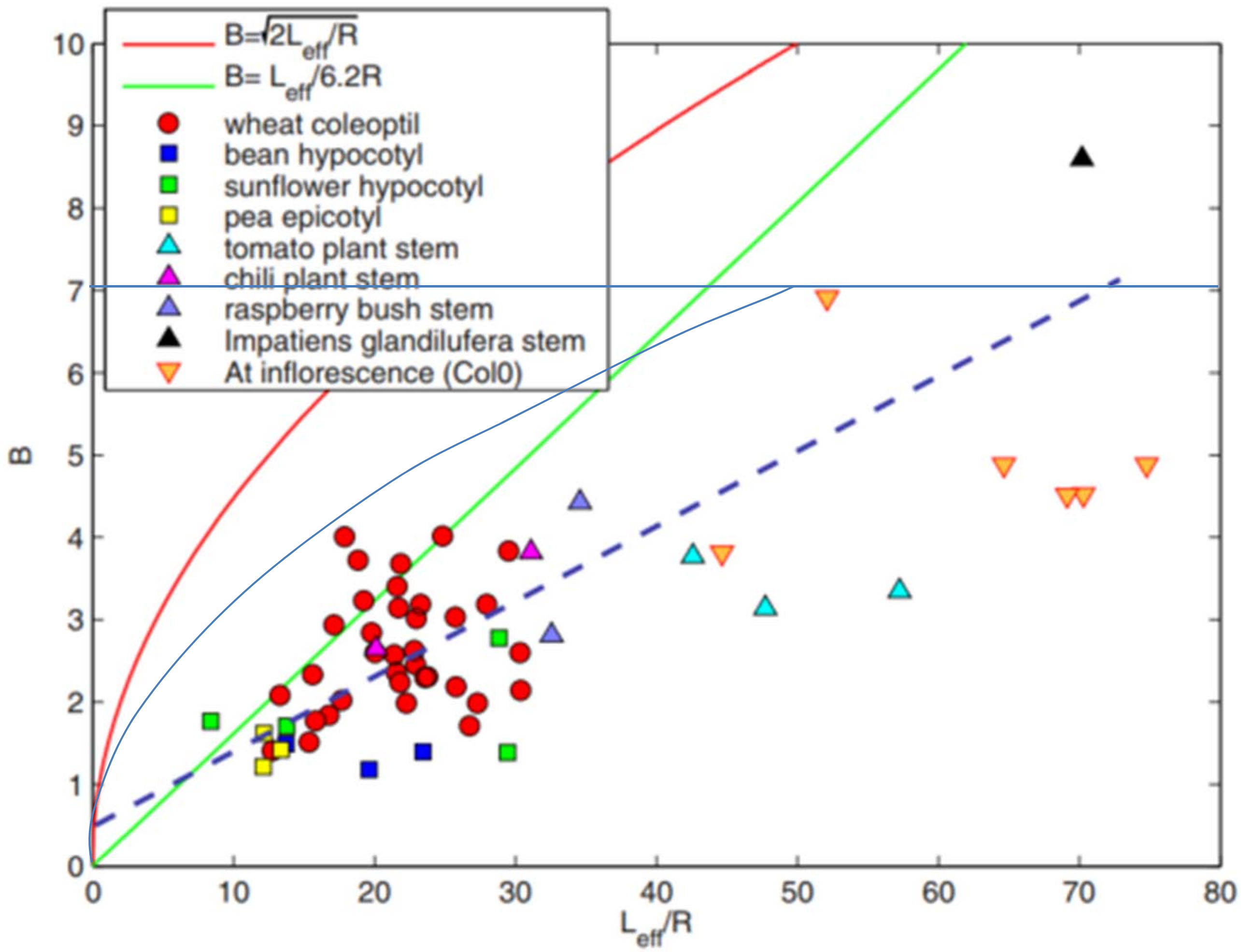


FIGURE 6 | $B = L_{eff}/L_c$ as a function of the effective length of the organ L_{eff}/R. Each point denotes an individual plant. The red line represents $B = \sqrt{L_{eff}/R}$. All the points are under this line $B < \sqrt{L_{eff}/R}$, showing that the destabilizing effects of growth on the whole gravitropic movement are negligible. The green line accounts for $B = L_{eff}/6.2R$. Most of the points are under this line, showing that it is not possible to