PSS *presents:*

Circumnutating Cucurbits: *Weird and Wonderful Winding*

PSS *presents:*

Circumnutating Cucurbits: *Weird and Wonderful Winding*

Gerbode, S. et al. How the Cucumber Tendril Coils and Overwinds *Science* **337** (2012)

Step 1: Circumnutation

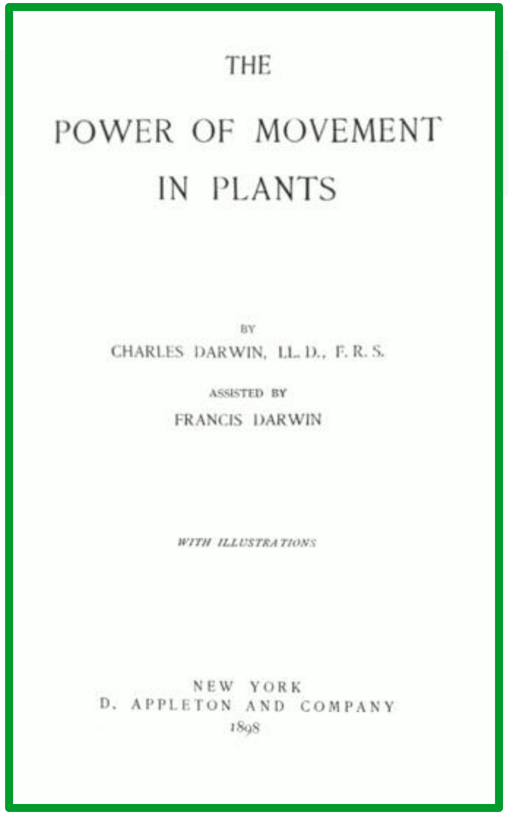
What grows around, comes around

What on Earth?

» Circumnutation
  - *circum- + nutation* : successive bowing or bending in different directions
  - analysed in detail by Darwin (and Darwin)

"My MS. relates to the movements of plants, and I think that I have succeeded in showing that all the more important great classes of movements are due to the modification of a kind of movement common to all plants from their earliest youth."
Darwin to Augustin DeCandolle, May 1880

"I have written a rather big book – more is the pity – on the movements of plants, and I am now just beginning to go over the MS. for the second time, which is a horrid bore."
Darwin to Asa Gray, Oct. 1879


THE
POWER OF MOVEMENT
IN PLANTS

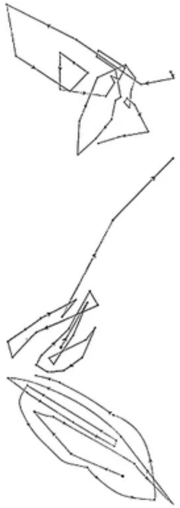
BY
CHARLES DARWIN, LL. D., F. R. S.

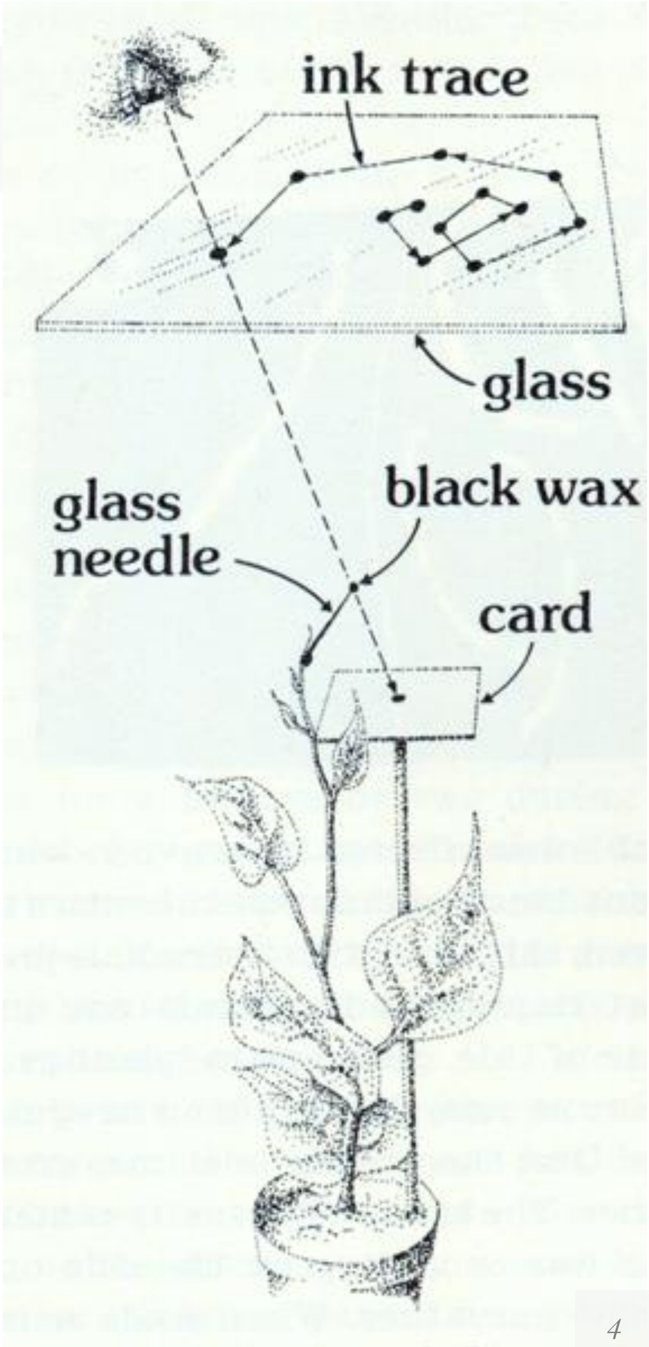
ASSISTED BY
FRANCIS DARWIN

WITH ILLUSTRATIONS

NEW YORK
D. APPLETON AND COMPANY
1898

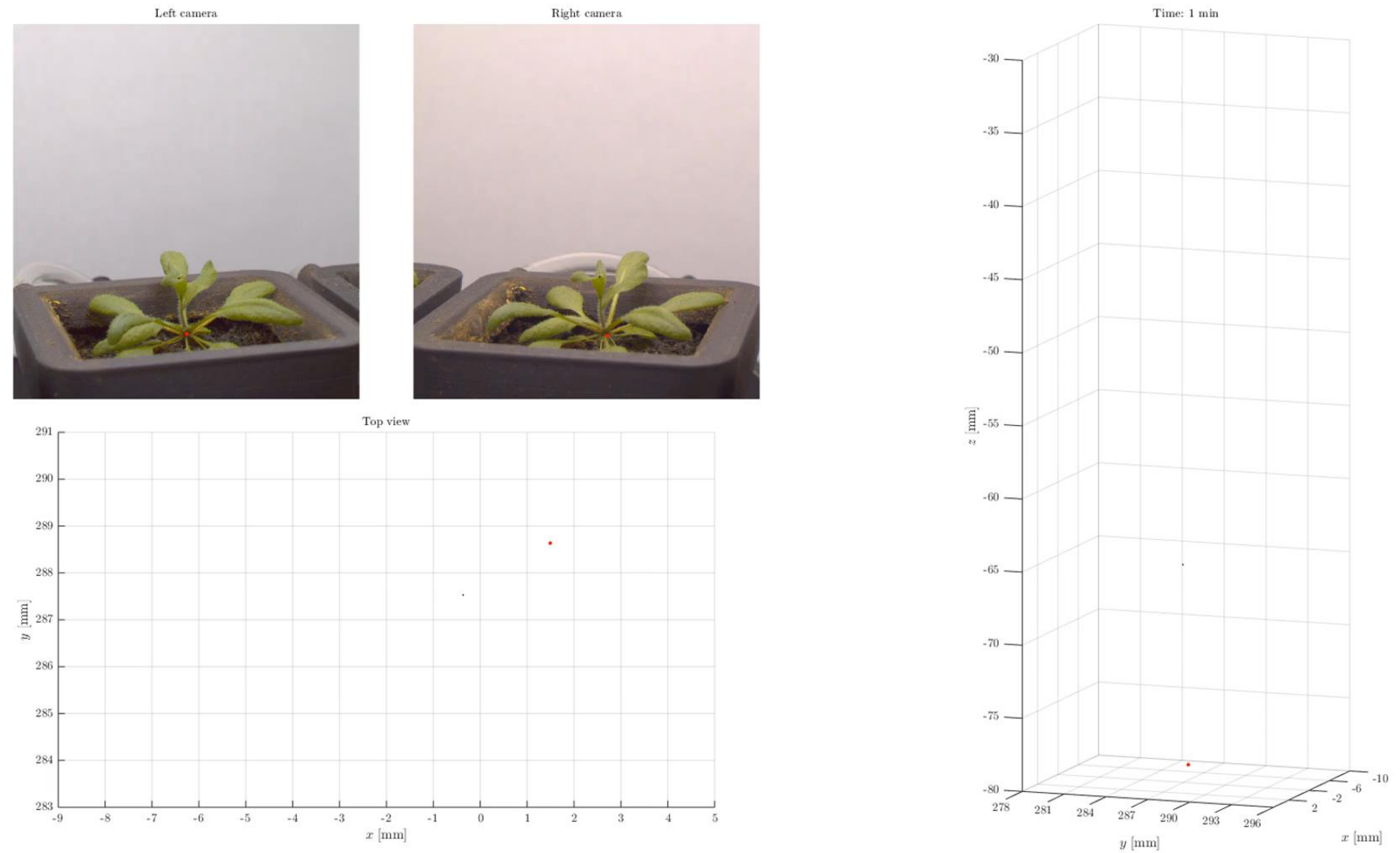

79. Brassica oleracea L.
Wild Cabbage; Y.





What on Earth?

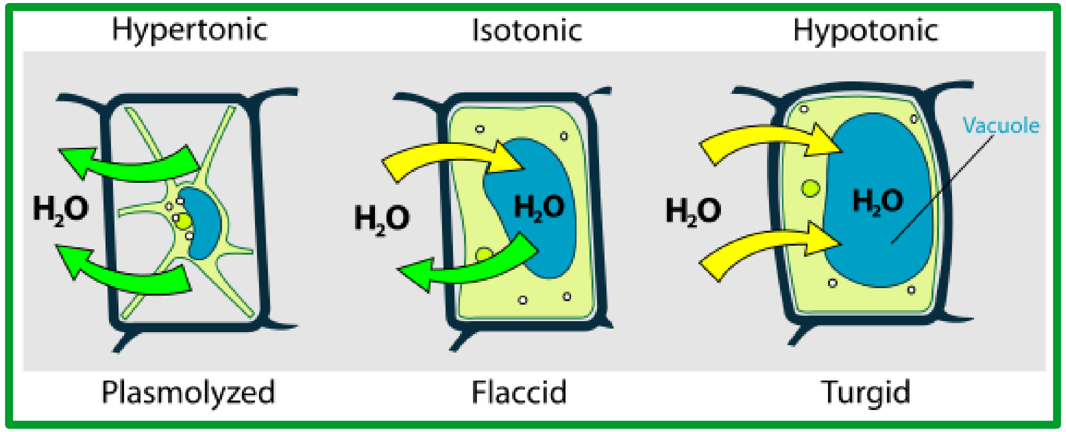
Agostinelli, D., DeSimone, A., and Noselli, G.; Nutations in Plant Shoots: Endogenous and Exogenous Factors in the Presence of Mechanical Deformations *Front. Plant Sci.* ***12*** *(2021)*



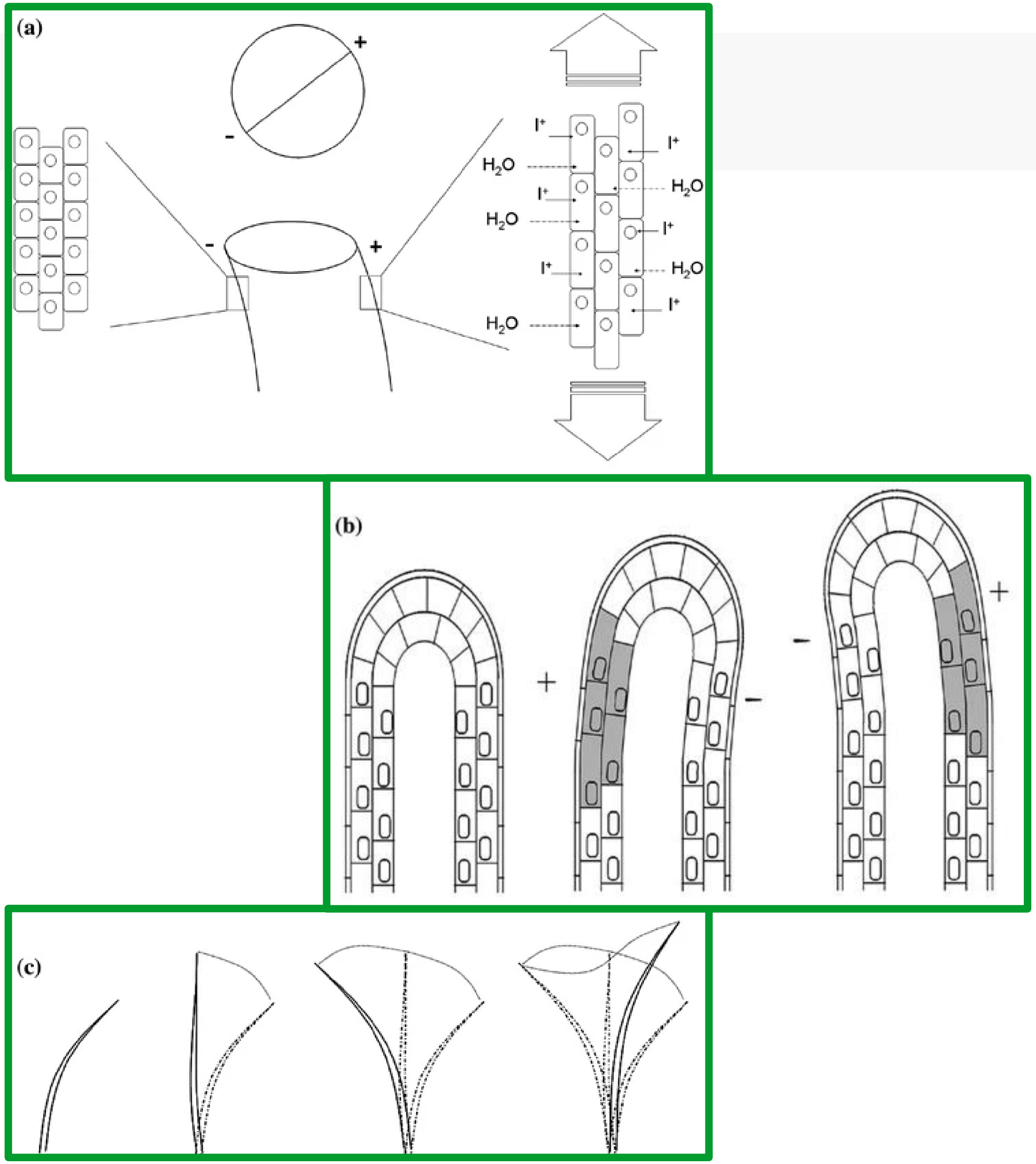
How on Earth?

» Differential growth
  • Okay, but how?

» Turgor pressure / turgidity



» Okay, but ... *how??*



Mugnai, S. et al. (2015) Nutation in Plants
in: Mancuso, S., Shabala, S. (eds) Rhythms in Plants. Springer

Plant growth

» Type of stimulus:

- Chemo-
- Geo- / Gravi-
- Hydro-
- Photo-
- Thermo-
- Thigmo- / Hapto-

» Type of movement

- -tropic (directional)
- -nastic (non-directional)

Circumnutation?

» Type of stimulus:

- Chemo-
- *Geo- / Gravi-*
- Hydro-
- Photo-
- Thermo-
- Thigmo- / Hapto-

» Type of movement

- *-tropic (directional)*
- -nastic (non-directional)

How *in space?*

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Nutation of Helianthus Annuus in a microgravity environment

An experiment to gather evidence to decide between the Darwinian concept of endogenously motivated nutation and the more mechanistic concept of gravity dependent nutation is described. If nutation persists in weightlessness, parameters describing the motion will be measured by recording in time lapse mode the video images of a population of seedlings that were grown at 1-g, but which will be observed at virtual zero gravity. Later, the plant images will be displayed on a video monitor in a laboratory, photographed on 16 millimeter film, and analyzed frame by frame to determine the kinetics of nutation for each specimen tested.

Document ID	19820010391
Document Type	Other - Other
Authors	Brown, A. H. *(Pennsylvania Univ. Philadelphia, PA, United States)*
Date Acquired	August 10, 2013
Publication Date	November 1, 1981
Publication Information	Publication: NASA. Marshall Space Flight Center Spacelab Mission 1 Expt. Descriptions
Subject Category	Life Sciences (General)
Accession Number	82N18265
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1NS101

NUTATION OF HELIANTHUS ANNUUS IN A MICROGRAVITY ENVIRONMENT (1NS101)

Allan H. Brown
University of Pennsylvania, USA

Interest in nutation and in the kind of biophysical mechanism that can account for it is at least partly due to the fact that we do not understand how a plant senses the Earth's gravitational force or other accelerating forces, how it processes the information and transduces it into chemical form, and how the hormonally transmitted signals from sensor to responding tissue are capable of ordering an appropriate differential growth response. If something of basic importance concerning nutation can be learned, such knowledge might have application to the even broader and still vexing question: How does a plant know which way is up?

How *in space?*

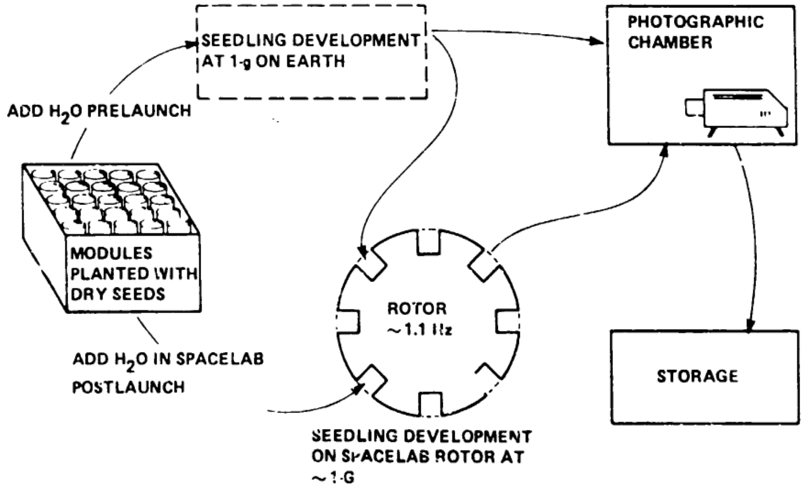


Figure V-11. HEFLEX experiment flow.

V-35

» Endogenous oscillations?

Plant Physiol. (1993) 101: 345–348

Update on Plant Development

Circumnutations: From Darwin to Space Flights

Allan H. Brown*

Gravitational Plant Physiology Laboratory, University City Science Center, 3401 Market Street, Suite 350, Philadelphia, Pennsylvania 19104-3323

the critical test of a putative requirement for gravity to drive nutation was accomplished in 1983 on the first NASA Spacelab mission, during which sunflower circumnutations were initiated and continued in μg (Brown et al., 1990). That result was not predicted by the gravity-dependent model as the exclusive explanation for circumnutational oscillations.

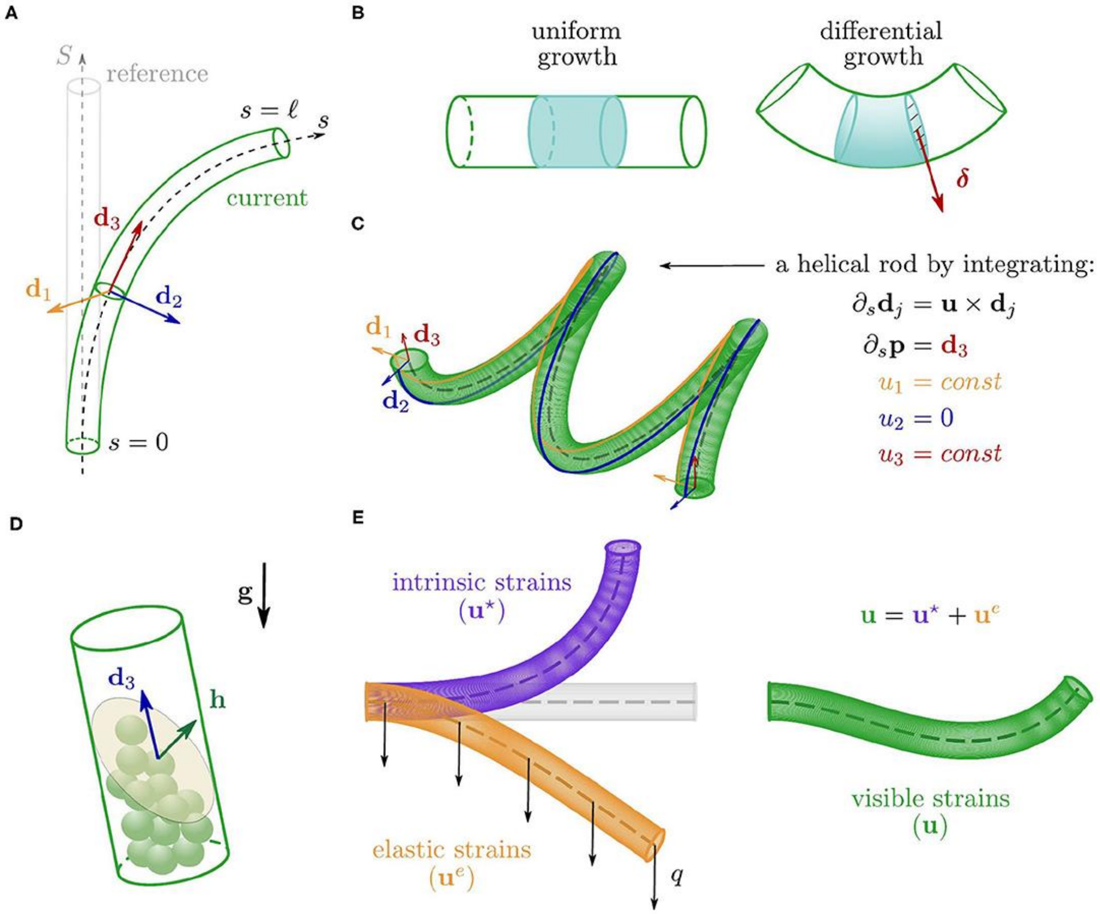
The vigor of oscillations observed in true μg was intermediate between that observed at 1g and that observed at clinostat simulated 0g. The most straightforward interpretation of those results is that gravity does influence both the amplitude and period of nutational oscillations but that it is not a mandatory requirement for circumnutation.

Some maths (finally)

Agostinelli, D., DeSimone, A., and Noselli, G.; Nutations in Plant Shoots: Endogenous and Exogenous Factors in the Presence of Mechanical Deformations *Front. Plant Sci.* ***12*** *(2021)*

» Model the plant stem as a growing, unshearable, elastically inextensible, elastic cylindrical rod with …

- Differential growth
- Endogenous oscillations
- Gravitropic reactions
- Straightening mechanisms



» To get:

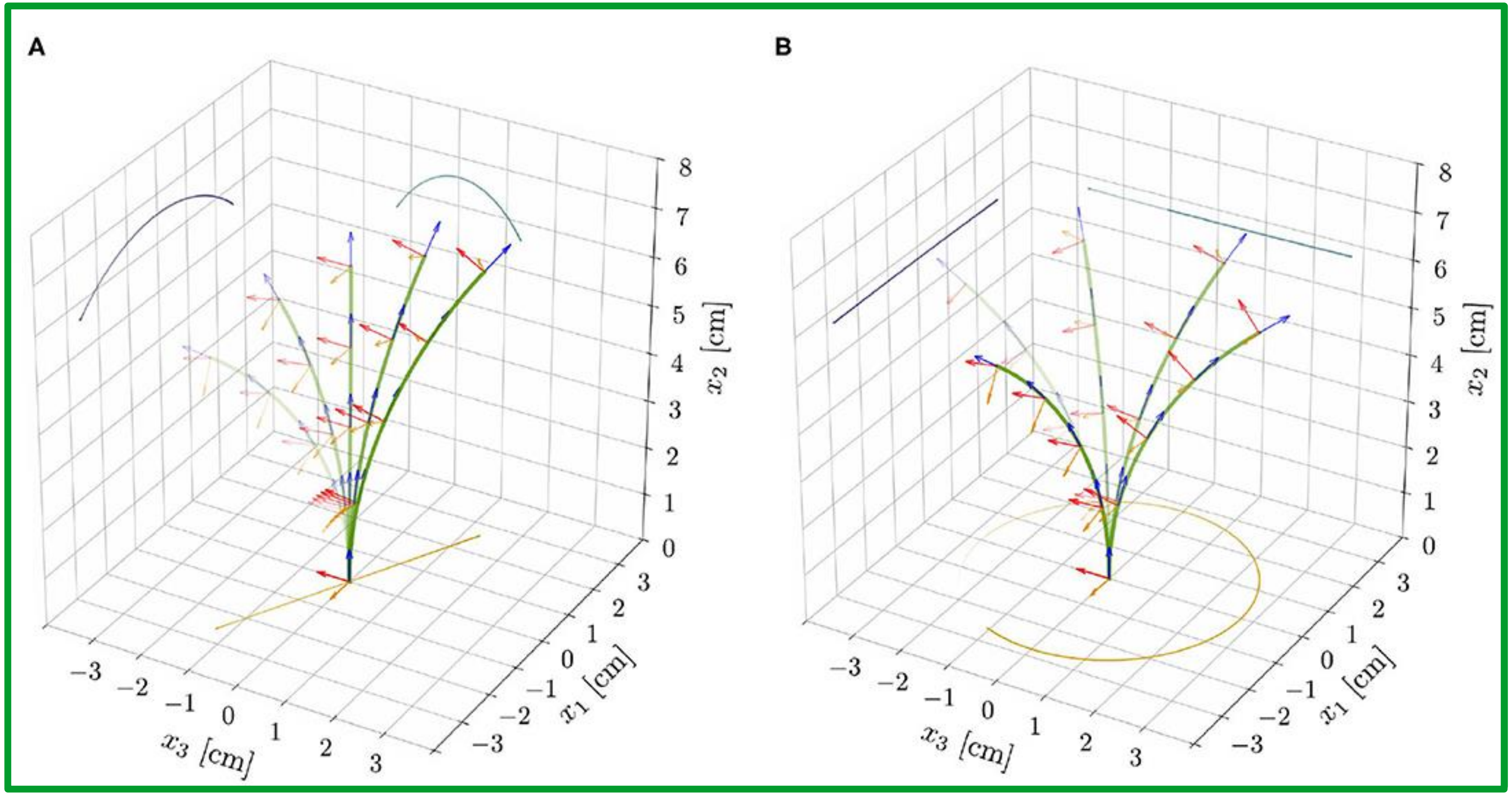
"a coupled nonlinear system [of] … 24 scalar equations in 24 scalar variables"

"Neglecting elasticity, this reduces to 15 equations in 15 scalar variables"

Some maths

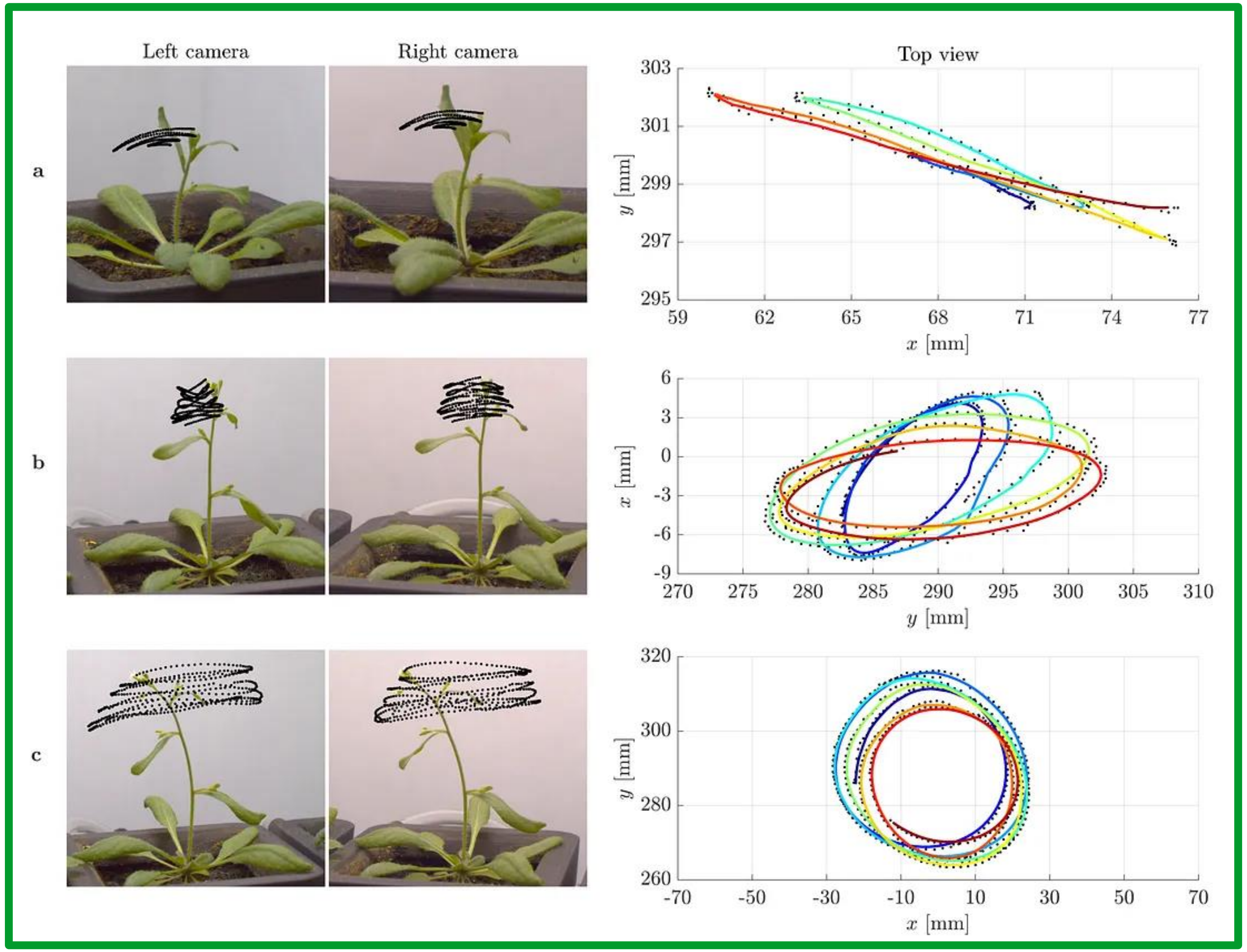
Agostinelli, D., DeSimone, A., and Noselli, G.; Nutations in Plant Shoots: Endogenous and Exogenous Factors in the Presence of Mechanical Deformations *Front. Plant Sci.* ***12*** *(2021)*

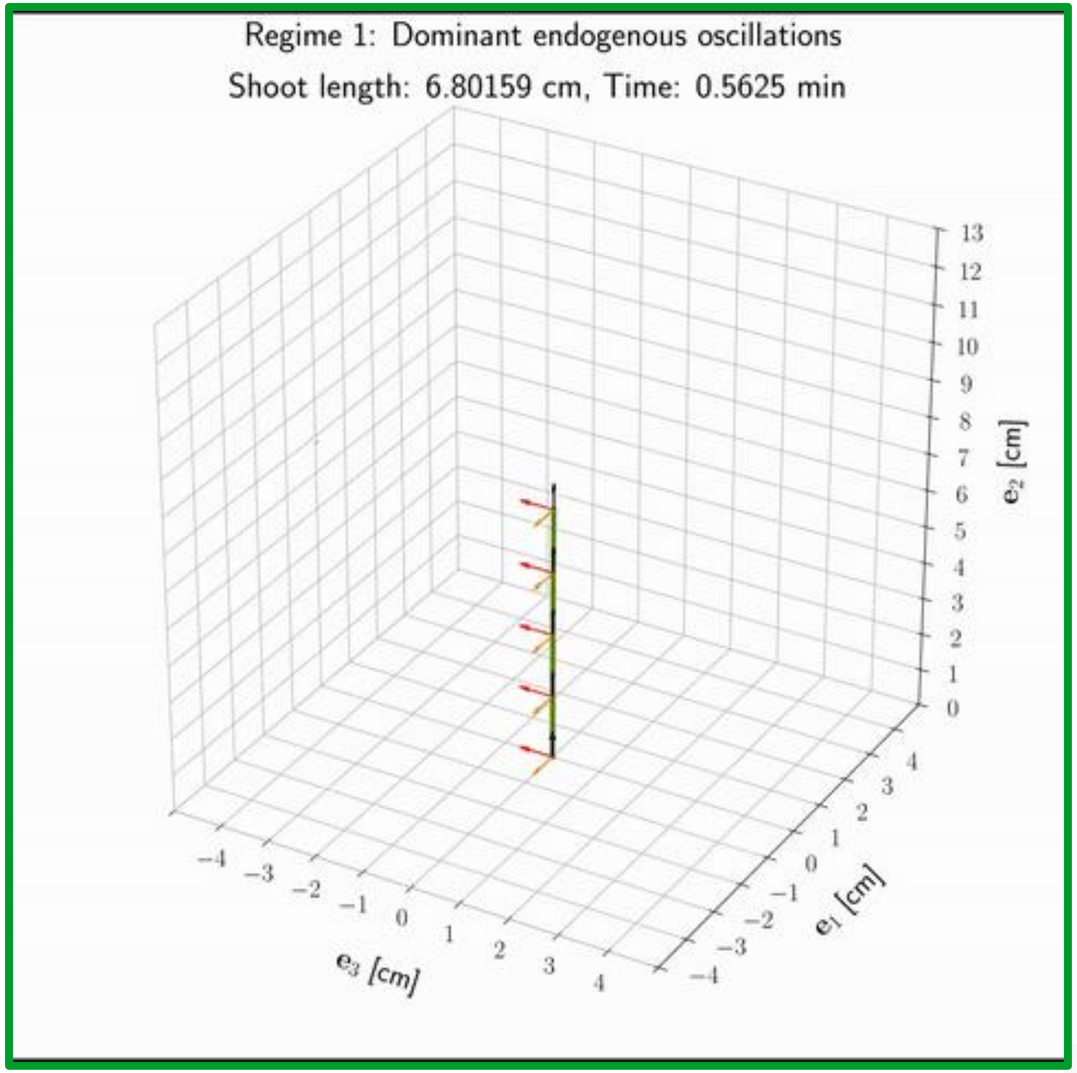
- Look: a bifurcation!
- and, some …
  un-plant-like behaviours?



Some maths

Agostinelli, D., DeSimone, A., and Noseli, G.; Nutations in Plant Shoots: Endogenous and Exogenous Factors in the Presence of Mechanical Deformations *Front. Plant Sci.* ***12*** *(2021)*





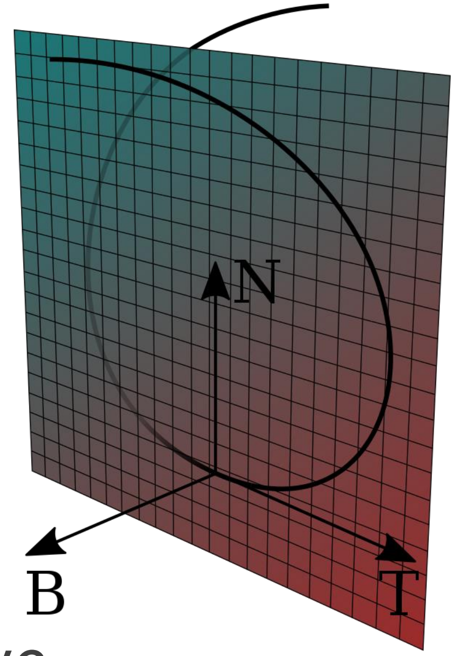
Step 2: Helical Growth

Oh, the Places You'll Grow!

Helices

» A curve in space $\boldsymbol{x}(s) = (x_1(s), x_2(s), x_3(s))$ with constant non-zero curvature and constant non-zero torsion

$$\kappa(s) = ||\boldsymbol{x}''(s)|| \qquad \tau(s) = \frac{\boldsymbol{x}''' \cdot (\boldsymbol{x}' \times \boldsymbol{x}'')}{||\boldsymbol{x}''||^2}$$



» Frenet-Serret frame:

$$\boldsymbol{T} = \boldsymbol{x}' \quad , \quad \boldsymbol{N} = \boldsymbol{T}'/||\boldsymbol{T}'|| \quad , \quad \boldsymbol{B} = \boldsymbol{T} \times \boldsymbol{N}$$

$\kappa = \boldsymbol{T}' \cdot \boldsymbol{N}$ is the rate of change of direction of the curve

$\tau = -\boldsymbol{B}' \cdot \boldsymbol{N}$ is the rate of rotation of the binormal vector

Helices

» A curve in space $\boldsymbol{x}(s) = (x_1(s), x_2(s), x_3(s))$ with constant non-zero curvature and constant non-zero torsion

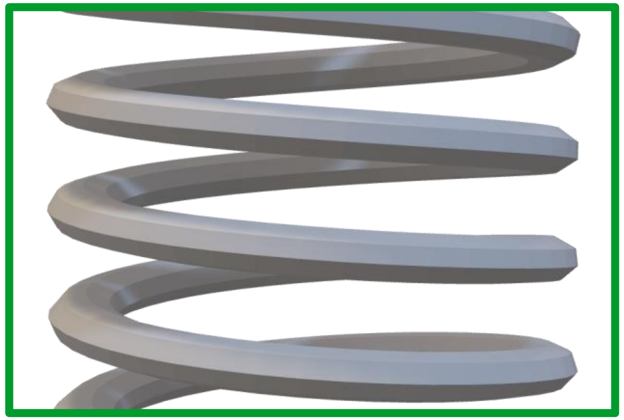
$$\kappa(s) = ||\boldsymbol{x}''(s)|| \qquad \tau(s) = \frac{\boldsymbol{x}''' \cdot (\boldsymbol{x}' \times \boldsymbol{x}'')}{||\boldsymbol{x}''||^2}$$

$\tau < 0$ $\tau = 0$ $\tau > 0$

Helices – left or right?

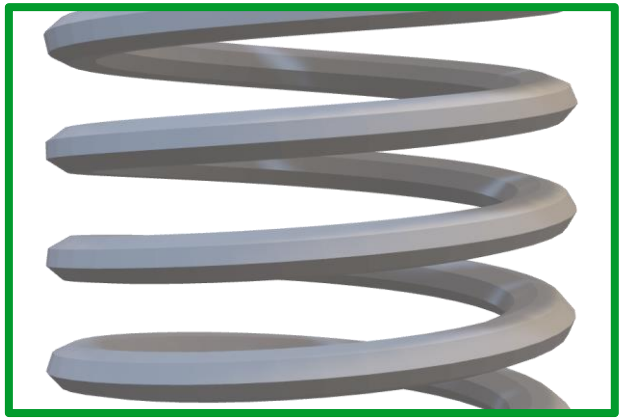
» "With the line of sight along the helix's axis, if a clockwise screwing motion moves the helix away from the observer, then it is called a right-handed helix; if towards the observer, then it is a left-handed helix." – Wikipedia

'Left'



$\tau < 0$

'Right'



$\tau > 0$

Helices – left or right?

» "Professor Miller has suggested to me that as the tendrils of the vine are right-handed screws and those of the hop left-handed, the two systems might be called those of the vine and the hop respectively. The system of the vine, which we adopt, is that of Linnaeus, and of screw-makers in all civilized countries except Japan."

J. C. Maxwell, *A Treatise on Electricity and Magnetism*, 1892


(grape) vine

hop (bine)


Helical growth – left or right?

Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2007) **16**, 795–800

RESEARCH PAPER

The global trend in plant twining direction

Will Edwards[1*], Angela T. Moles[2,3] and Peter Franks[1]

[1]*School of Tropical Biology, James Cook University, Cairns, QLD 4878, Australia,* [2]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia,* [3]*School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand*

ABSTRACT

Aim To examine, at a global scale, patterns in the direction in which climbing plants twine. We tested three hypotheses: (1) that twining direction is determined randomly; (2) that twining direction is determined by apices following the apparent movement of the sun across the sky; and (3) that twining direction is determined by the Coriolis effect.

Location Seventeen sites spanning nine countries, both hemispheres and 65° of latitude.

Helical growth – left or right?

Results Ninety-two per cent of the 1485 twining stems we recorded grew in right-handed helices, i.e. they twined in an anticlockwise direction. This is significantly ($P < 0.001$) different from random. The proportion of stems twining right-handedly (anticlockwise) was independent of both latitude ($P = 0.33$) and hemisphere ($P = 0.63$). These data are inconsistent with the idea that twining direction is determined by either the relative passage of the sun through the celestial sphere or by the Coriolis effect. Thus, we reject all three of our hypotheses.

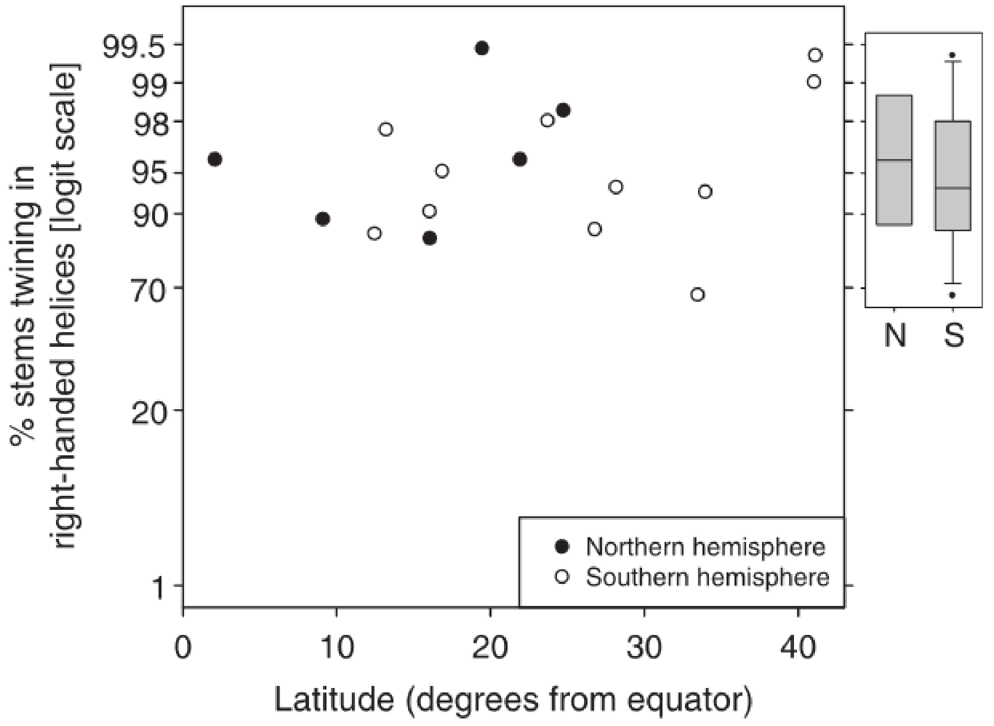


Figure 2 Scatterplot of the percentage of plants producing right-handed helices (logit scale) versus latitude for each of the 17 study sites. Also shown are boxplots for the distribution of the percentage of right-handed helices in each hemisphere. There was no effect of latitude or hemisphere on twining direction.

Helical growth – left or right?

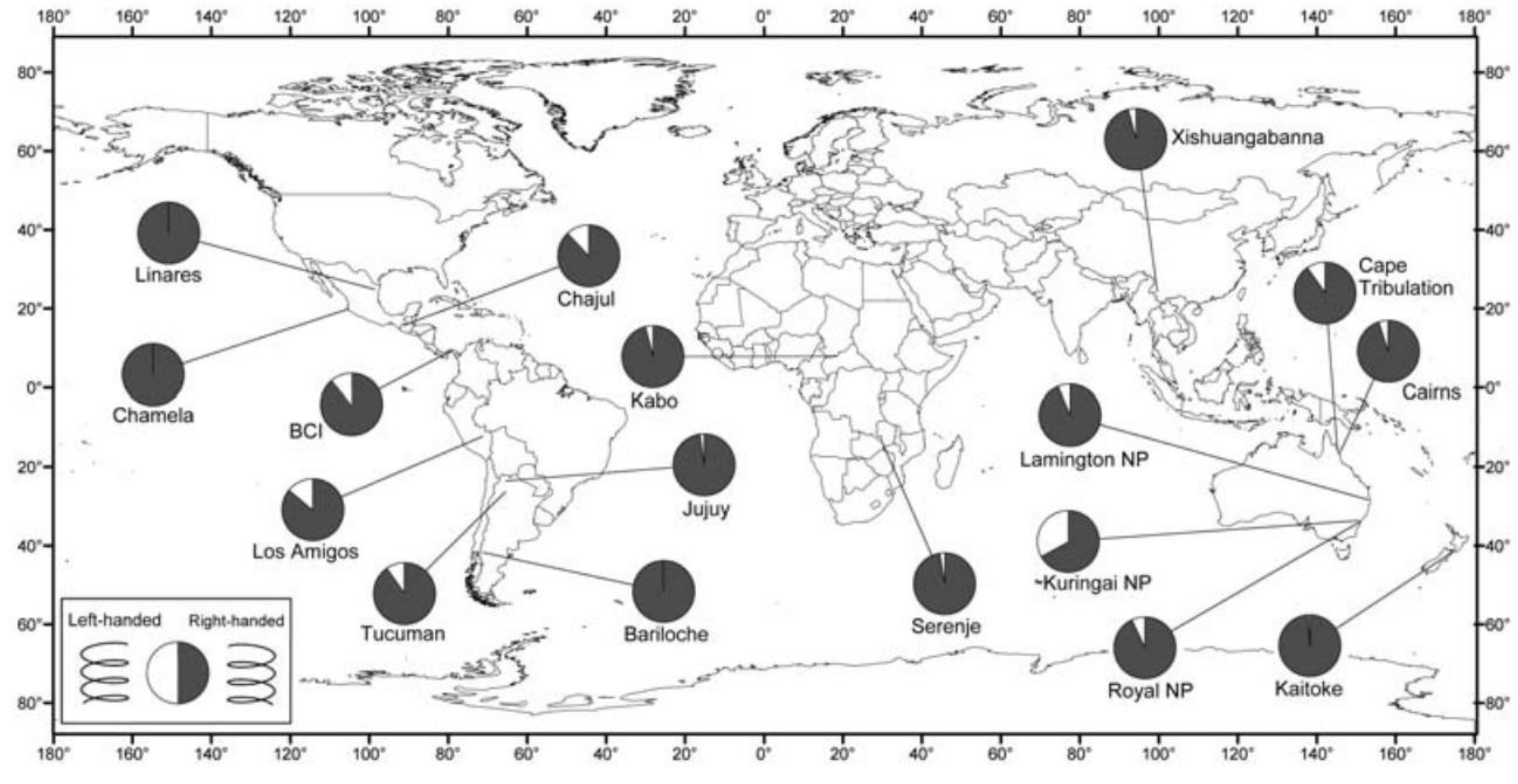


Figure 1 Global distribution of the 17 study sites, and the percentage of plants producing either left- (open segment) or right-handed (filled segment) helices at each site. Right-handed growth is recognizable as an increase in height from left to right (see legend).

Step 3:

Tendril Perversion

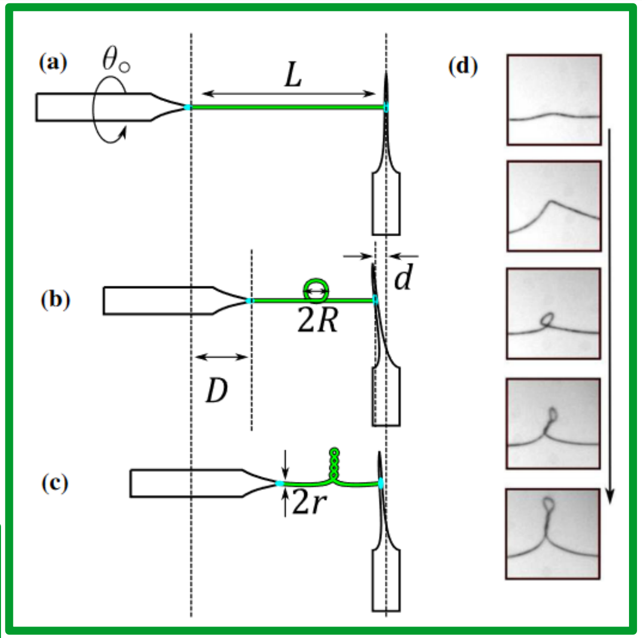
Step 3: Tendril Perversion

Just grow with it

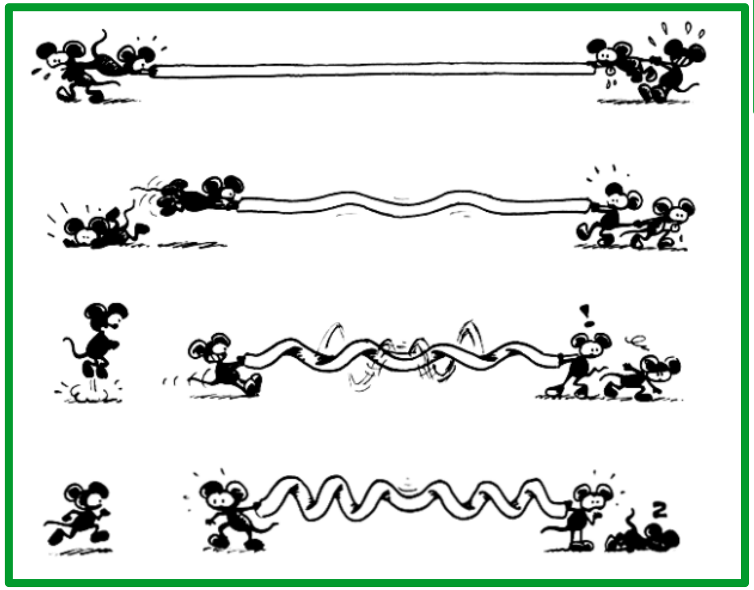
Instabilities of elastic filaments

» Demo. 1: twist-to-writhe (plectoneme)

Fortais, A., Loukiantchenko, E., Dalnoki-Veress, K.;
Writhing and hockling instabilities in twisted elastic fibers
Eur. Phys. J. E ***44*** *(2021)*



» Demo. 2: curvature-to-writhe (perversion)

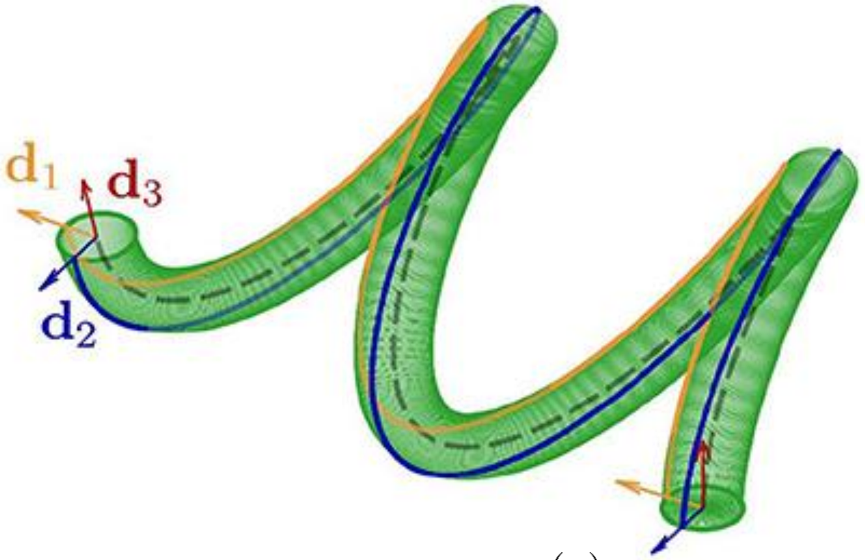


McMillen, T., Goriely, A.;
Tendril Perversion in Intrinsically Curved Rods
J. Nonlinear Sci. ***12*** *(2002)*

The mathematics of tendril perversion

- Centreline $\boldsymbol{x}(s,t)$ with orthonormal director basis $\{\boldsymbol{d}_1(s,t), \boldsymbol{d}_2(s,t), \boldsymbol{d}_3(s,t)\}$
- Fix $\boldsymbol{d}_3 = \boldsymbol{x}'$ and $\boldsymbol{d}_2 = \boldsymbol{d}_3 \times \boldsymbol{d}_1$
- Orthonormality implies twist $\boldsymbol{\kappa}$ and spin $\boldsymbol{\omega}$ vectors:

$$\boldsymbol{d}_i' = \boldsymbol{\kappa} \times \boldsymbol{d}_i \quad , \quad \dot{\boldsymbol{d}}_i = \boldsymbol{\omega} \times \boldsymbol{d}_i$$



- Static Kirchhoff model of an elastic rod:

$$\boldsymbol{F}'' = \boldsymbol{0}$$

$$\boldsymbol{M}' + \boldsymbol{d}_3 \times \boldsymbol{F} = \boldsymbol{0}$$

$$\boldsymbol{M} = (\kappa_1 - \kappa_1^{(u)})\boldsymbol{d}_1 + (\kappa_2 - \kappa_2^{(u)})\boldsymbol{d}_2 + \Gamma(\kappa_3 - \kappa_3^{(u)})\boldsymbol{d}_3$$

for total force $\boldsymbol{F}(s,t)$ and moment $\boldsymbol{M}(s,t)$ on the centreline, Γ constant, and intrinsic curvature $\boldsymbol{\kappa}^{(u)}$

- Set $\boldsymbol{\kappa}^{(u)} = (K, 0, 0)$ and consider the stationary solution of a straight twistless filament under tension $\boldsymbol{F} = (0, 0, \varphi^2)$

The mathematics of tendril perversion

- Linear stability analysis – expand *all the things* – about $\boldsymbol{\mu}^{(0)} = (\boldsymbol{f}^{(0)}, \boldsymbol{\kappa}^{(0)}) = (0,0,\varphi^2,0,0,0)$

$$\begin{aligned}
\boldsymbol{d}_i' &= \boldsymbol{d}_i^{(0)} + \varepsilon\boldsymbol{\alpha}^{(1)} \times \boldsymbol{d}_i^{(0)} + \mathcal{O}(\varepsilon^2) \\
\boldsymbol{F} &= \varphi^2\boldsymbol{d}_3^{(0)} + \varepsilon\varphi^2(\alpha_2^{(1)}\boldsymbol{d}_1^{(0)} - \alpha_1^{(1)}\boldsymbol{d}_2^{(0)} + \boldsymbol{d}_3^{(0)}) + \mathcal{O}(\varepsilon^2) \\
\boldsymbol{\kappa} &= (\boldsymbol{\alpha}^{(1)})' + \mathcal{O}(\varepsilon^2)
\end{aligned}$$

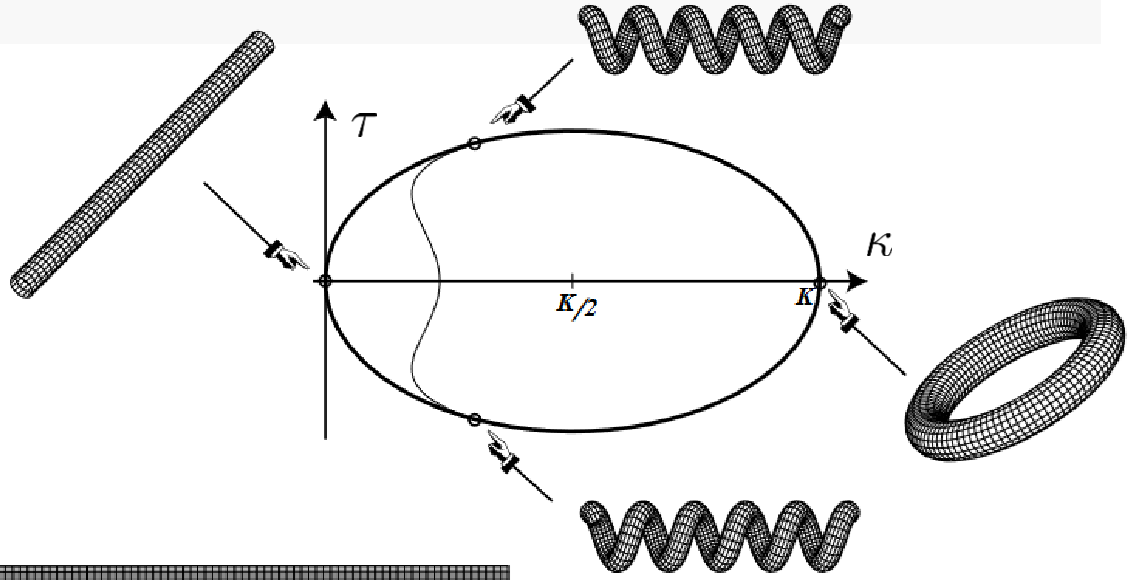
- Get a linear system for the leading order correction $\mathcal{L}(\boldsymbol{\mu}^{(0)}) \cdot \boldsymbol{\mu}^{(1)} = 0$

- Decompose into modes $\boldsymbol{\mu}^{(1)} = \sum_n e^{\sigma(n)t} A_n x_n e^{ins} + \text{c.c.}$ to get a dispersion relation $\Delta(\sigma(n), n) = 0$

- Onset of instability at $\Delta(0,n) = 0$: $\quad K^2 - \Gamma n^2 = \Gamma\varphi^2$

- For a finite filament of length $2\pi L$, first unstable mode $n = L^{-1}$ at $\varphi_c = K\Gamma^{-\frac{1}{2}}$

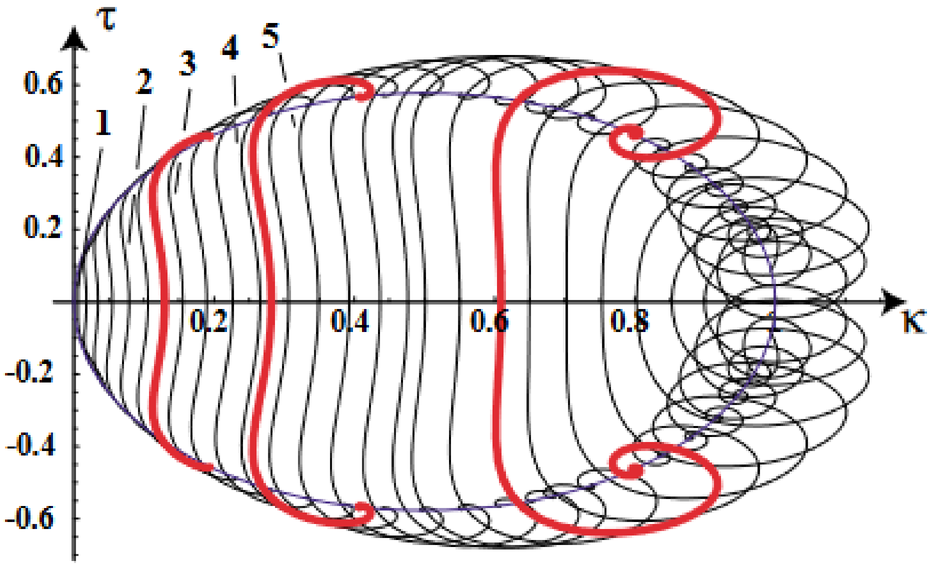
The mathematics of tendril perversion

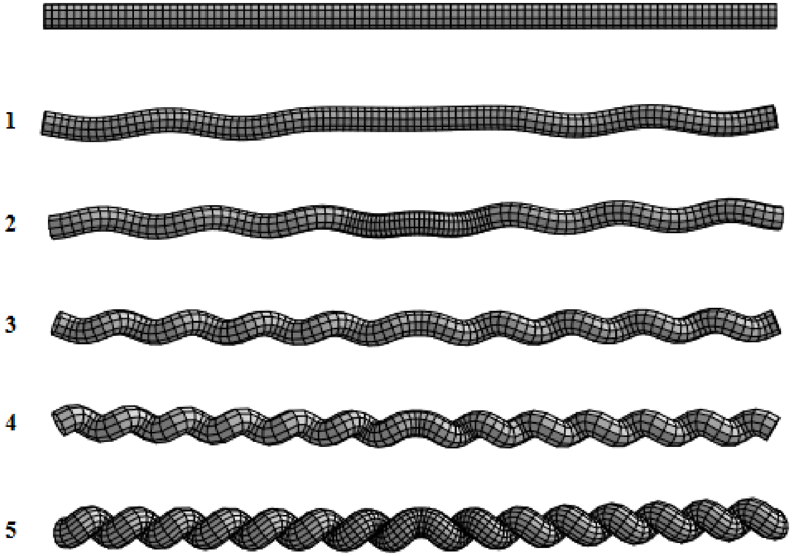


- Asymptotic analysis: minimising energy $\mathcal{E} = \boldsymbol{M} \cdot (\boldsymbol{\kappa} - \boldsymbol{\kappa}^{(u)})$

$$\Gamma\tau^2 = \kappa(K - \kappa)$$

- Put the two together (magic):





McMillen, T., Goriely, A.;
Tendril Perversion in Intrinsically Curved Rods
J. Nonlinear Sci. ***12*** *(2002)*

The biophysics of tendril perversion

» Intrinsic curvature via differential growth?

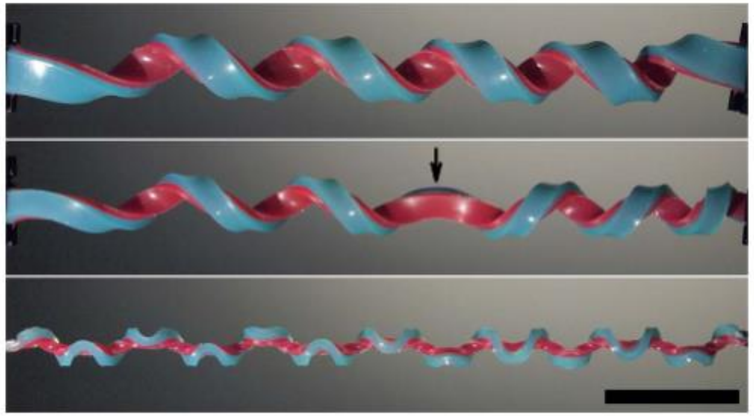


Figure 1. Illustration of a helix (top), a hemihelix with one perversion marked by an arrow (middle) and a hemihelix with multiple perversions (bottom).

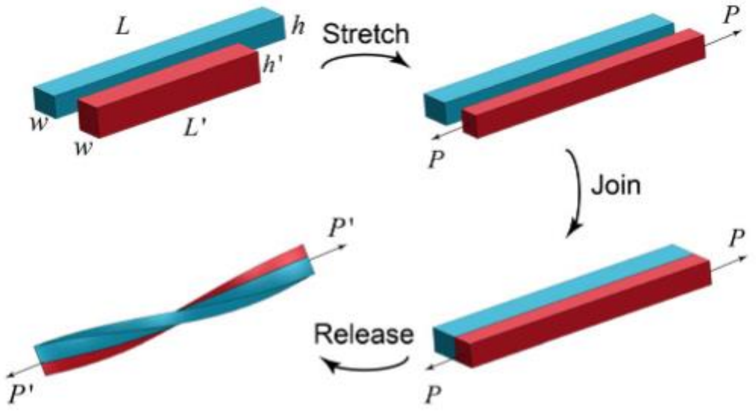


Figure 2. Sequence of operations leading to the spontaneous creation of hemihelices and helices. Starting with two long elastomer strips of different lengths, the shorter one is stretched to be the same length as the other. While the stretching force, P, is maintained, the two strips are joined side-by-side. Then, as the force is slowly released, the bi-strip twists and bends to create either a helix or a hemihelix.

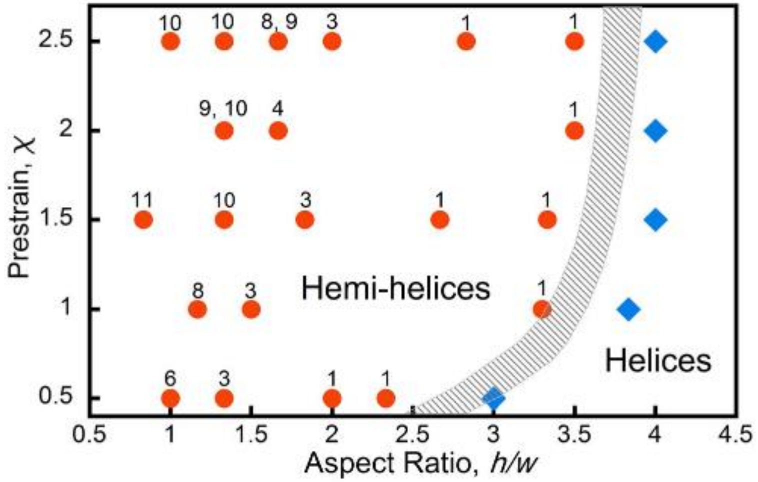


Figure 3. The number of perversions observed as a function of both the prestrain and the cross-section aspect ratio, h/w.

Liu, J., Huang, J., Su, T., Bertoldi, K., Clarke, D.; Structural Transition from Helices to Hemihelices *PLOS One* **9** (2014)

The biophysics of tendril perversion

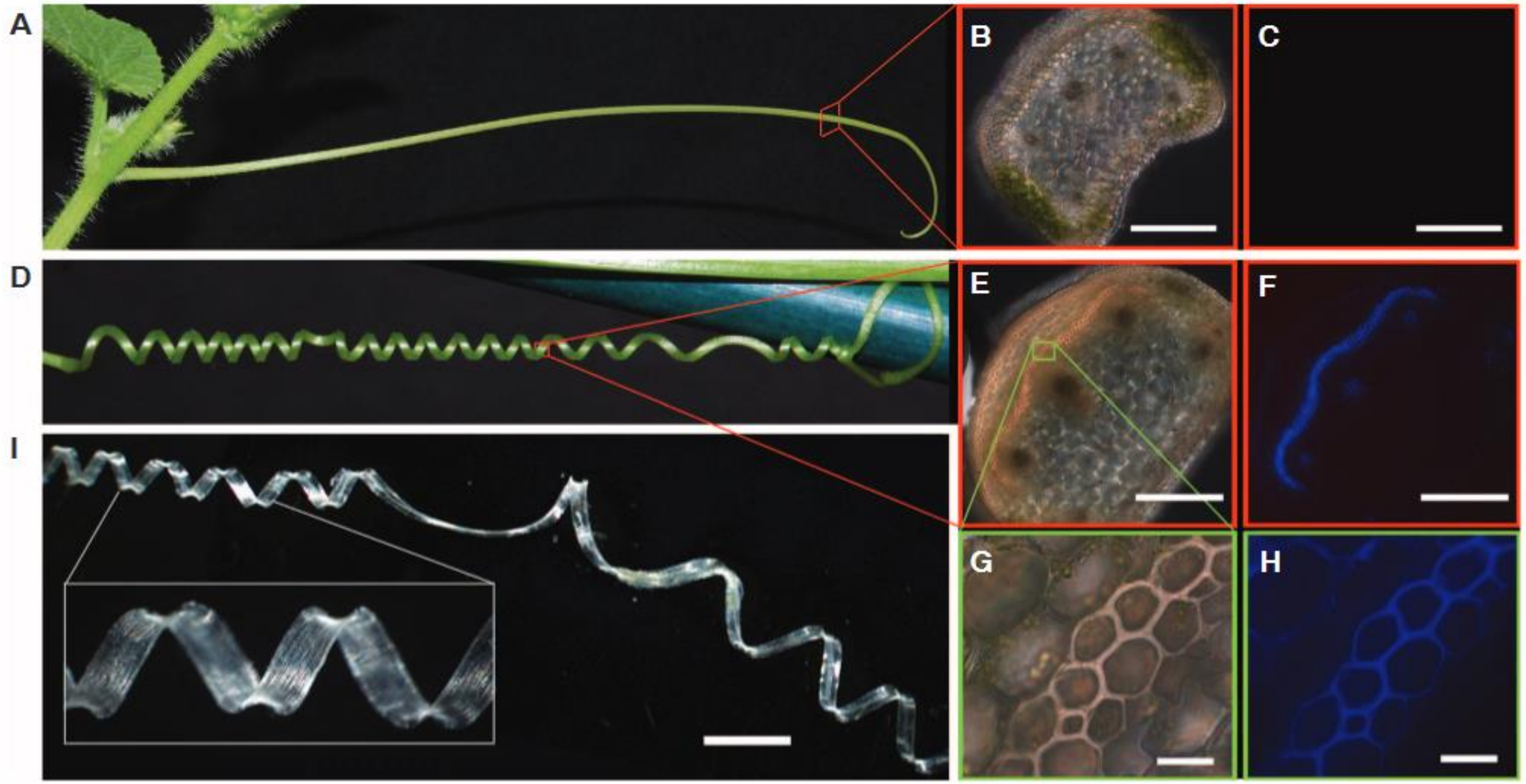


Fig. 1. Tendril coiling via asymmetric contraction. During coiling, a strip of specialized structural gelatinous fiber cells (the fiber ribbon) becomes lignified and contracts asymmetrically and longitudinally. (**A** to **C**) A straight tendril that has never coiled (A) lacks lignified g-fiber cells. In the tendril cross section, darkfield (B) and UV autofluorescence (C) show no lignin signal. (**D** to **H**) In coiled tendrils (D), the fully developed fiber ribbon consists of ~2 layers of highly lignified cells extending along the length of the tendril. In the tendril cross section, darkfield (E) and UV autofluorescence (F) show strong lignification in the fiber ribbon. In (G) and (H), increased magnification reveals that ventral cells (top left) are more lignified than dorsal cells. (**I**) The extracted fiber ribbon retains the helical morphology of the coiled tendril. (Inset) Higher magnification shows the orientation of g-fiber cells along the fiber ribbon. Scale bars, (B) and (C) 0.5 mm, (E) and (F) 100 μm, (G) and (H) 10 μm, (I) 1 mm.

Gerbode, S., Puzey, J., McCormick, A., Mahadevan, L.; How the Cucumber Tendril Coils and Overwinds *Science* **337** (2012)

PSS *presents:*

Circumnutating Cucurbits: *Weird and Wonderful Winding*

or:

How I Learned to Stop Worrying and Love the Tendril Perversions