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## Gravisensing in plants

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# Gravisensing in plants: the contribution of ground and space experiments. Unresolved questions

Valérie Legué



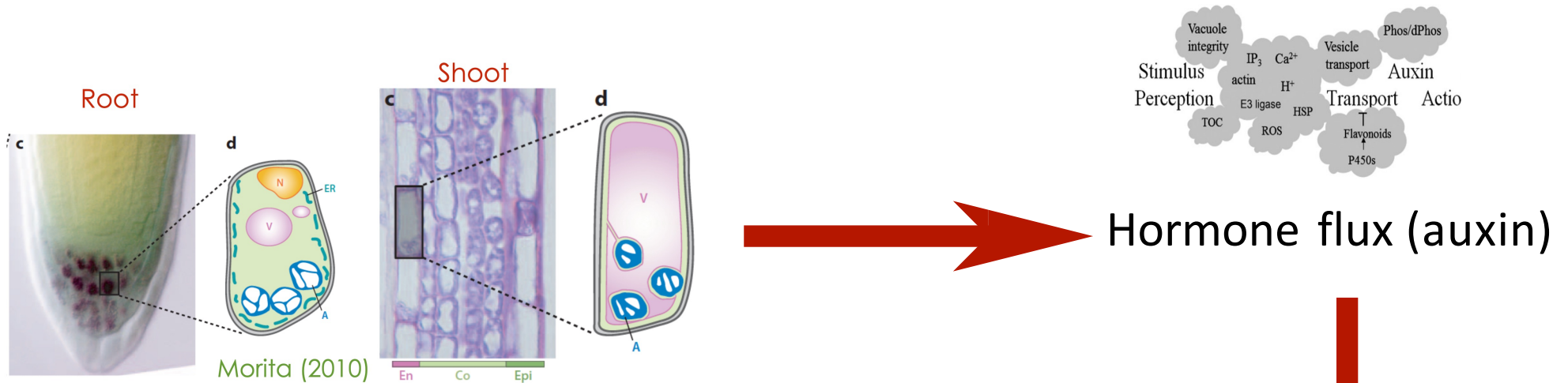
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# At the beginning of gravitropism response...gravisensing



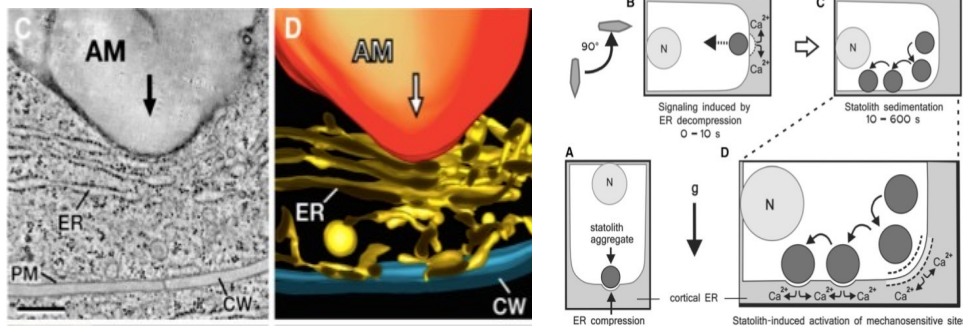
**Amyloplasts: a sensor made of starch-rich grains**

Differential growth and bending of organ

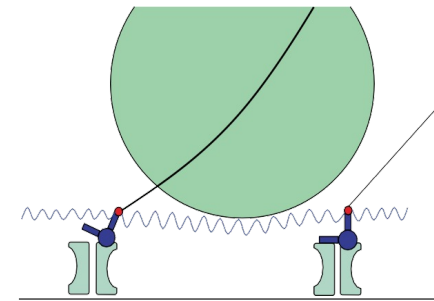
# Amyloplasts: a star in the gravisensing!

A series of successful studies

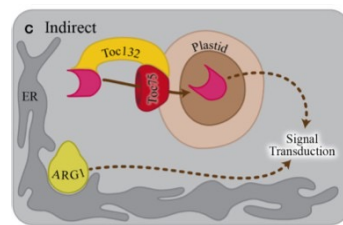
Deformation of the Endoplasmic Reticulum  
(Leitz et al 2009)



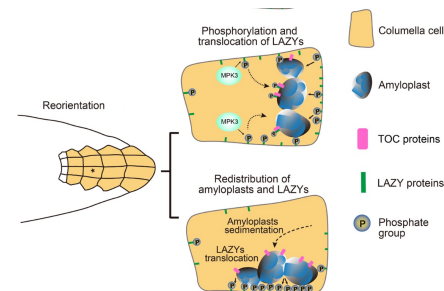
Interaction/Deformation of actin cytoskeleton  
(Perbal and Driss-Ecole, 2003)



Protein interactions and translocation



(Strohm et al 2014)



(Chen et al, 2023; Nishimura et al, 2023)

## Amyloplasts: a star in the gravisensing!

- How does the sensor work? Pressure ? Contact ? Displacement/motion ?
- Role of the granular nature of the sensor?

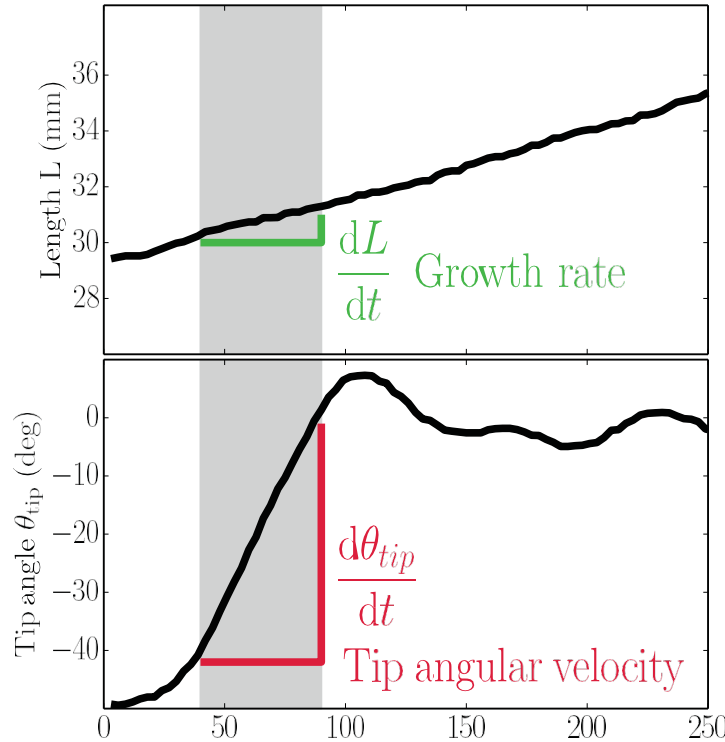
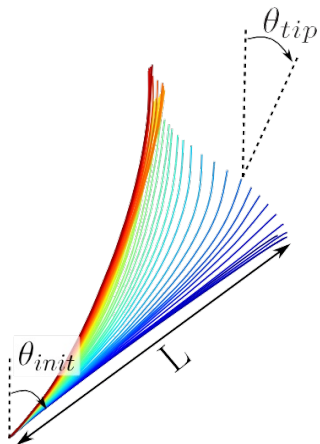


How could the relevant measurements of gravi-response help us for understanding the cellular events of gravi-sensing?

- Using the relevant measurements of gravi-response



# Relevant Measurements of Gravitropic response

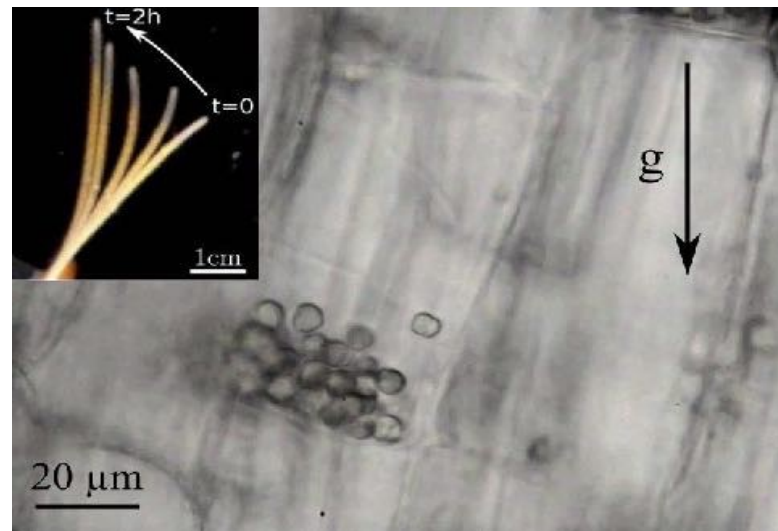


Dynamics of the response:

- Dynamics of Tip angle velocity (linear phase)
- Growth rate
- Radius of organ

The relevant measure for the gravitropic response  $= \frac{\Delta \dot{\epsilon}}{\dot{\epsilon}} = \frac{R}{\dot{\epsilon}} \frac{dC}{dt} \approx R \frac{d\theta_{tip}/dt}{dL/dt}$

What is detected (gravity, angle) at cellular level ?





# One classical result: the sine-law

## At organ scale:

The response is proportional to the sine of the inclination (in permanent inclination)

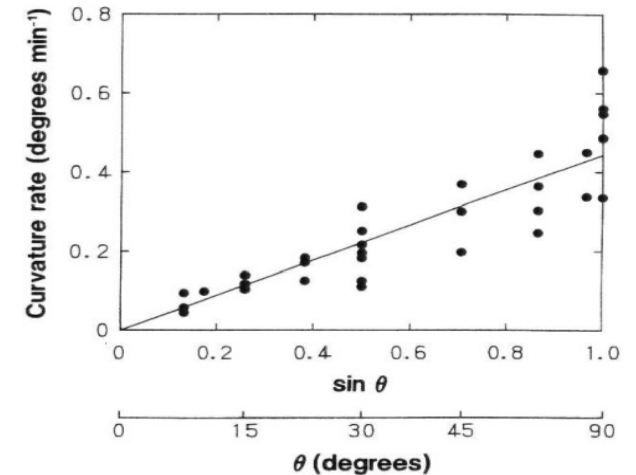
### ➤ The sin-law

see also Sacks 1882, Audus 1964....

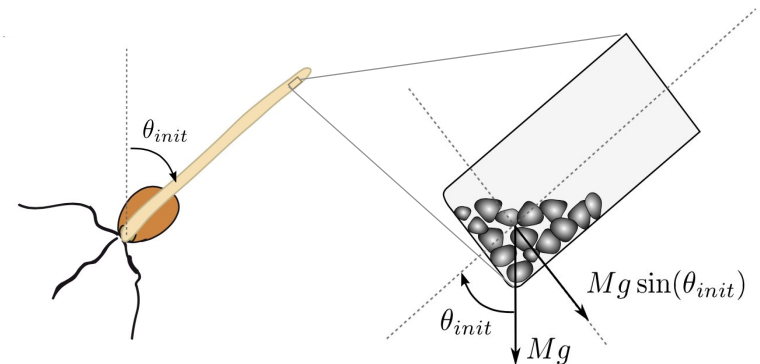
## At cellular scale:

Gravitropic signal comes from the weight of the statoliths on the lateral side of the cell

### ➤ Statoliths: a force sensor ?



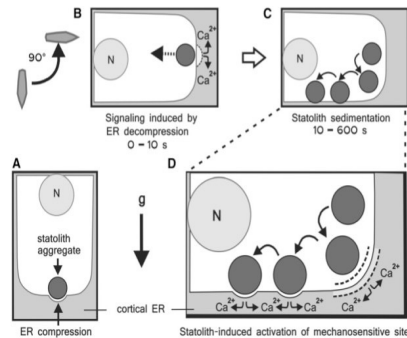
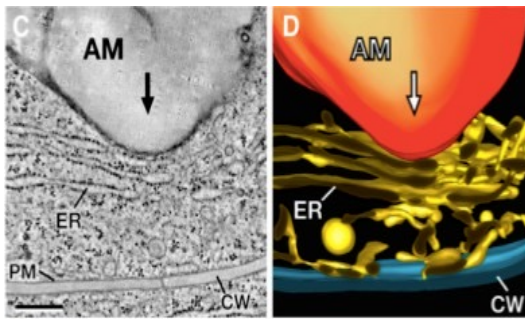
lino et al. 1996



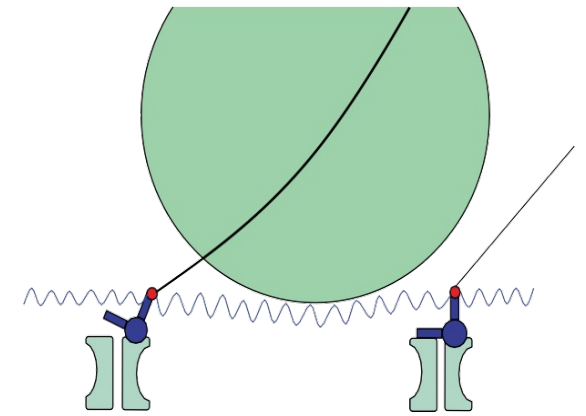
# One classical result: the sine-law

Biological explanation: The statocyte sense the statolith (amyloplast) pressure

Deformation of the Endoplasmic Reticulum  
(Leitz et al 2009)

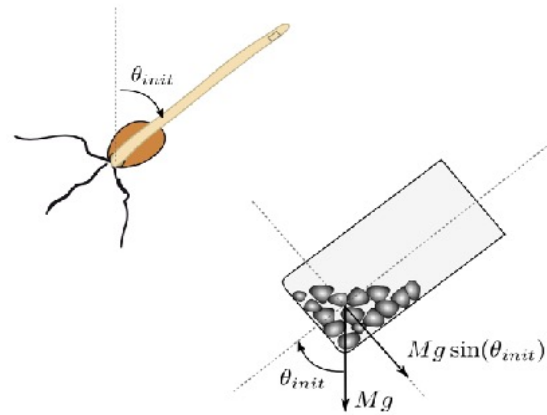


Deformation of actin cytoskeleton  
(Perbal and Driss-Ecole, 2003)



If statolith: a force sensor

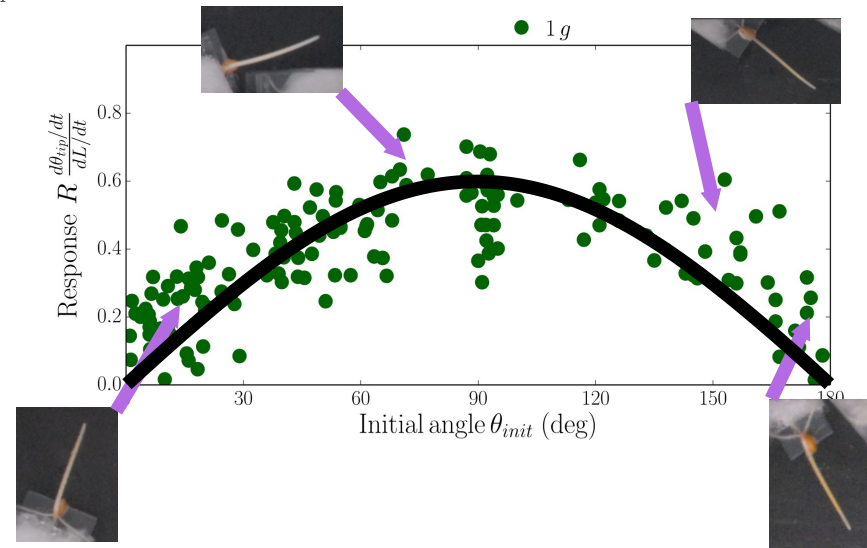
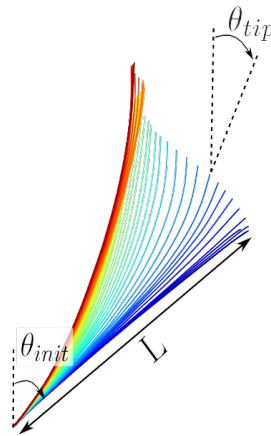
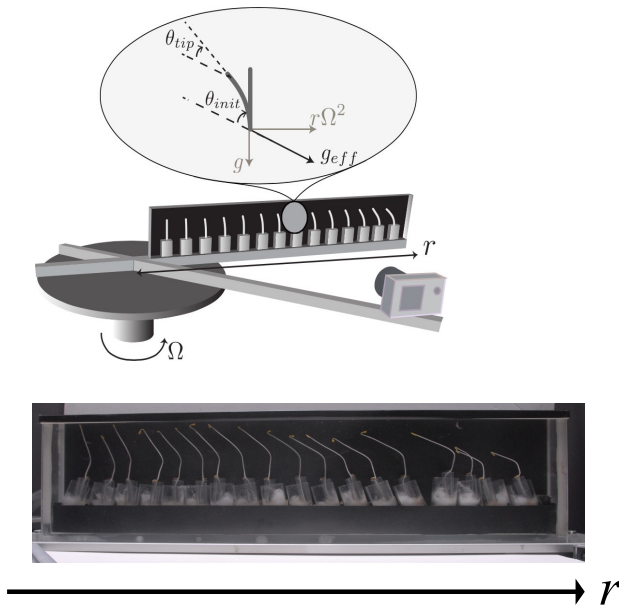
The response should be proportional to the gravity (intensity) ? influence of “g”?



# Test of the Force sensor hypothesis

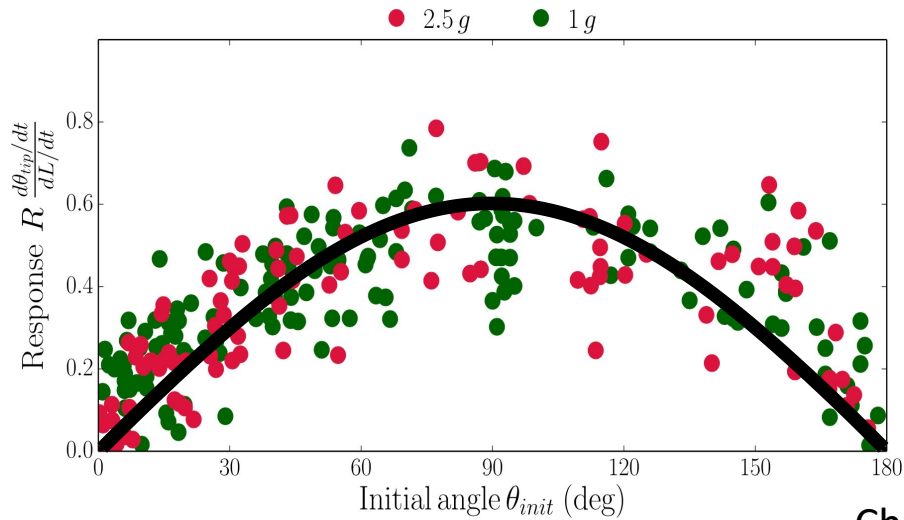
wheat coleoptiles, grown in dark

The relevant measure for the gravitropic response  $= \frac{\Delta \dot{\epsilon}}{\dot{\epsilon}} = \frac{R}{\dot{\epsilon}} \frac{dC}{dt} \approx R \frac{d\theta_{tip}/dt}{dL/dt}$

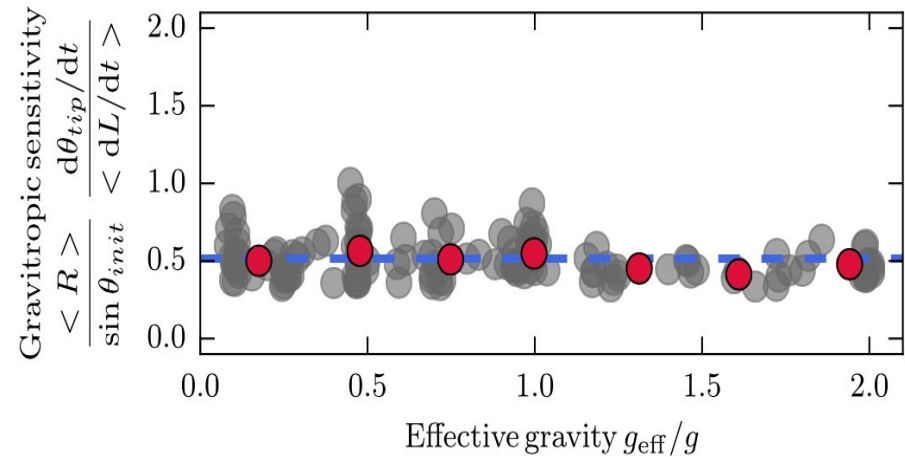


➤ Gravi-sensitivity to permanent inclination: the sine-law

# Test of the Force sensor hypothesis

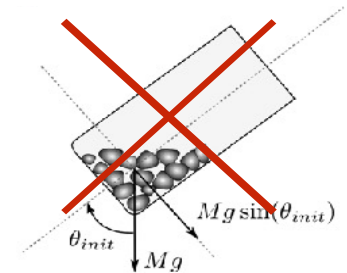


Chauvet et al. 2016



**The sine-law does not depend on g !**

➤ **The plant gravisensor is NOT a force sensor**

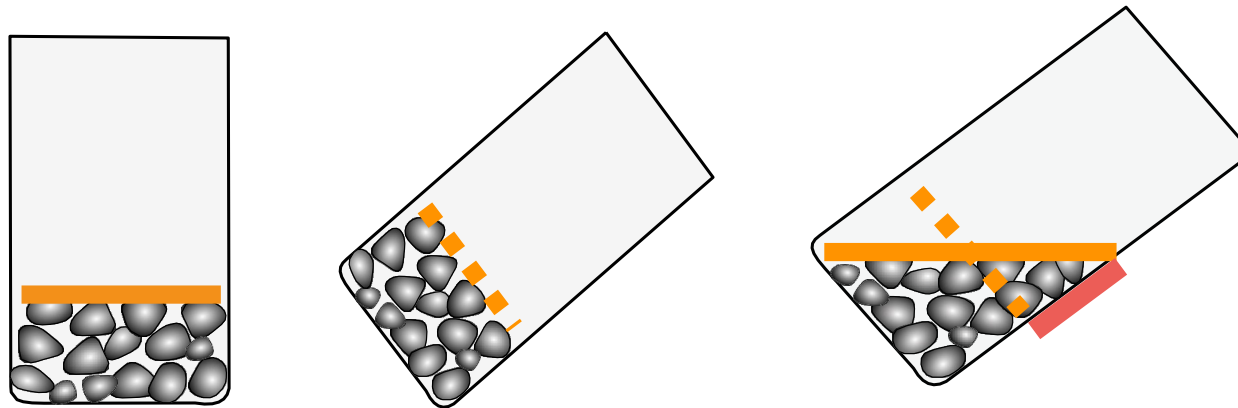


Chauvet et al. 2016

## Another hypothesis:

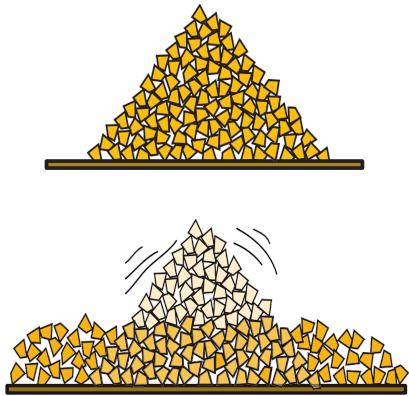
The final position of the statoliths being independent of gravity  
(only inclination)

- Statolith: A position sensor?
- implies that the statoliths have to move and change position to induce a signal.



# Test of the position sensor hypothesis

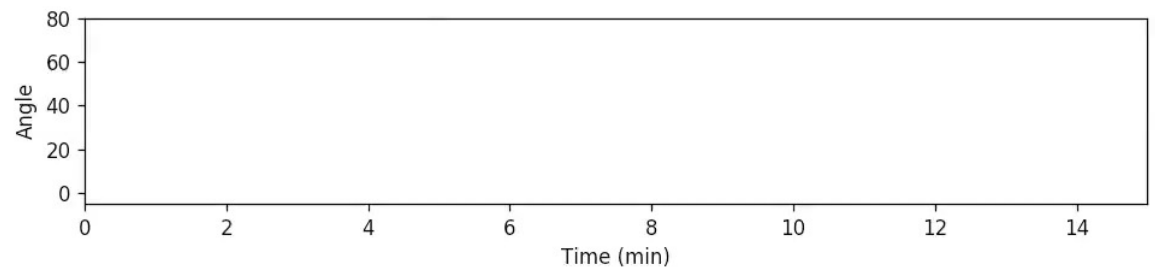
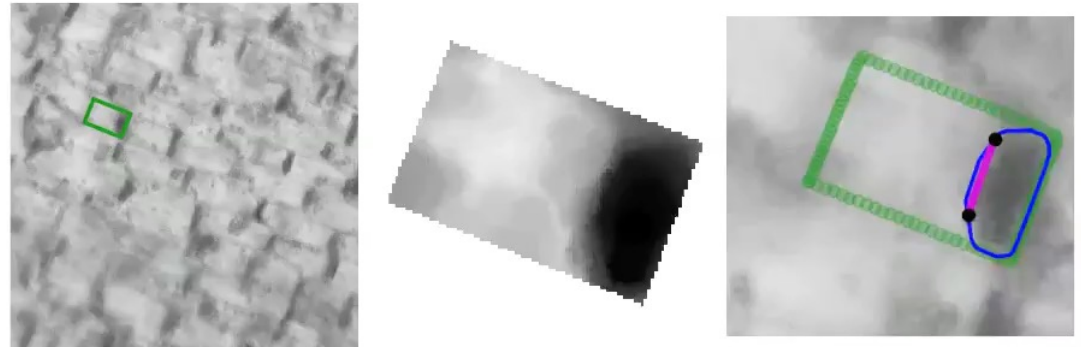
## Visualizing *in vivo* statolith motion



Statolith motion: granular avalanche?

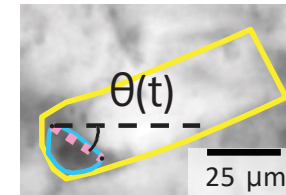
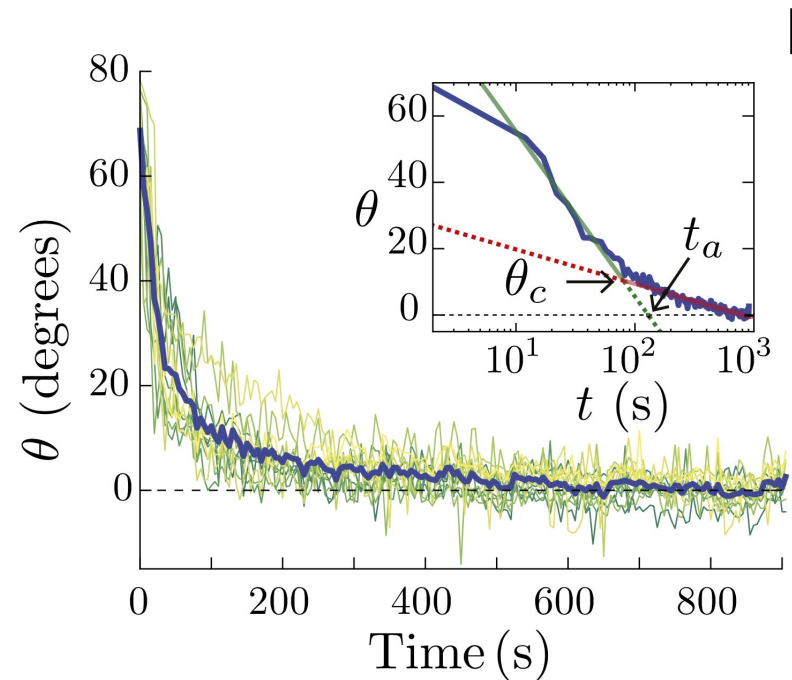


Wheat coleoptiles cuts and observed on horizontal microscope

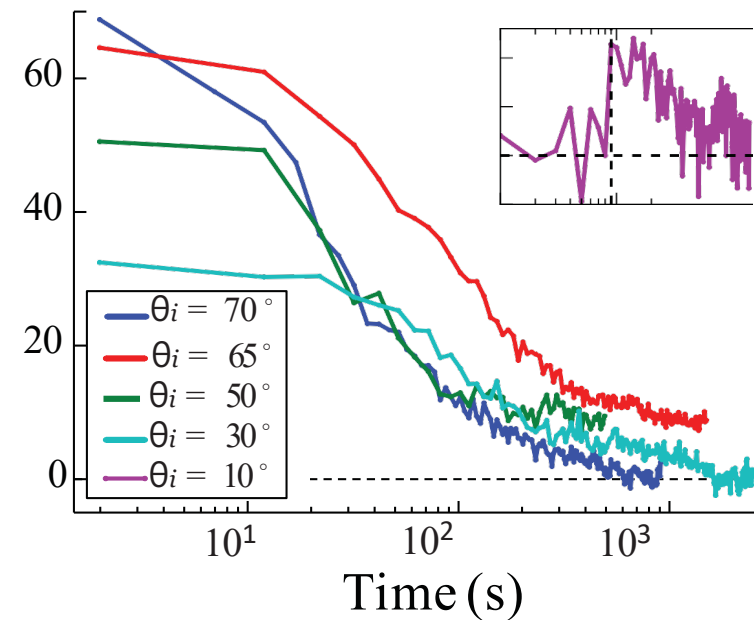


Bérut et al, 2018

# Statolith avalanche dynamics



Bérut et al, 2018



- The statolith pile angle relaxes to zero... as a liquid like-behaviour
- Two different regimes: granular avalanche (2 min) + slow creep (10-20 min)

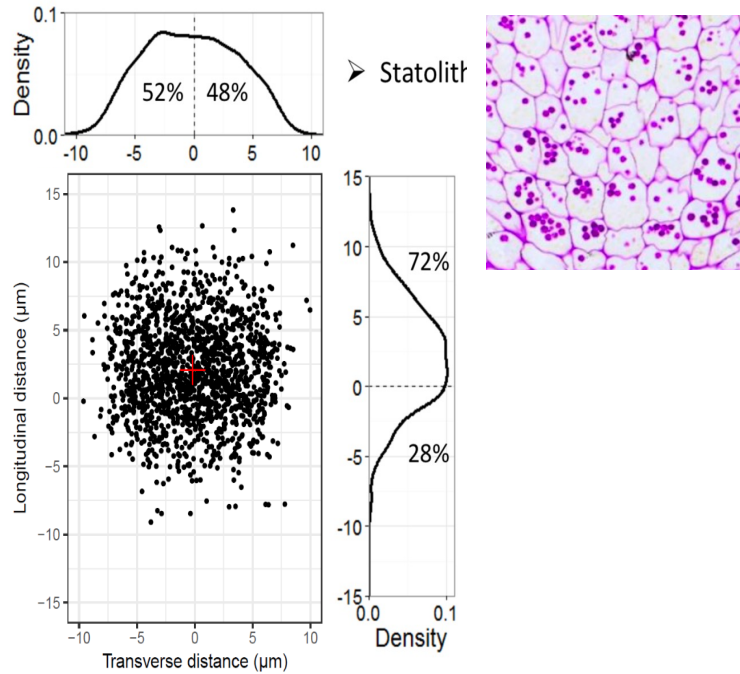
Unlike a classical granular material, statoliths move as **liquid-like behavior on long time**



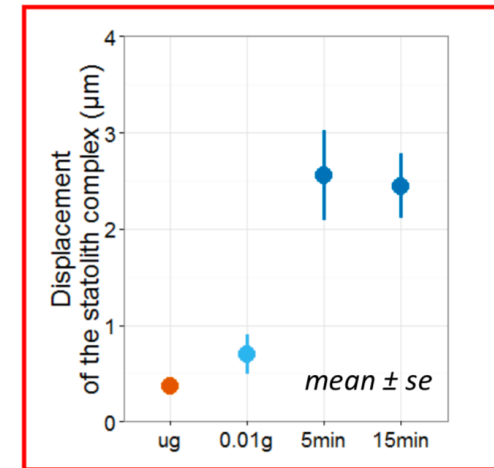
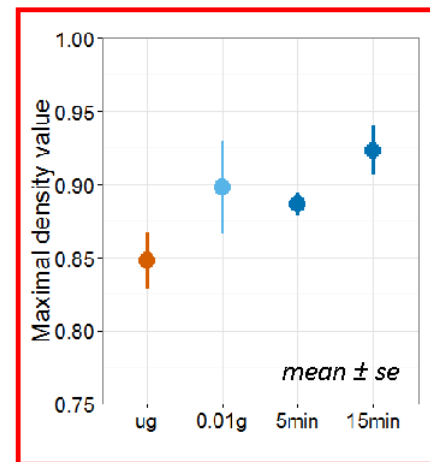
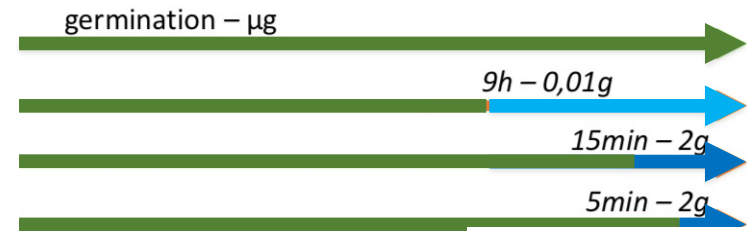
Studies support this hypothesis ?



# Results from microgravity...Analysis of statolith positioning



Microgravity:  
Statoliths form a cluster

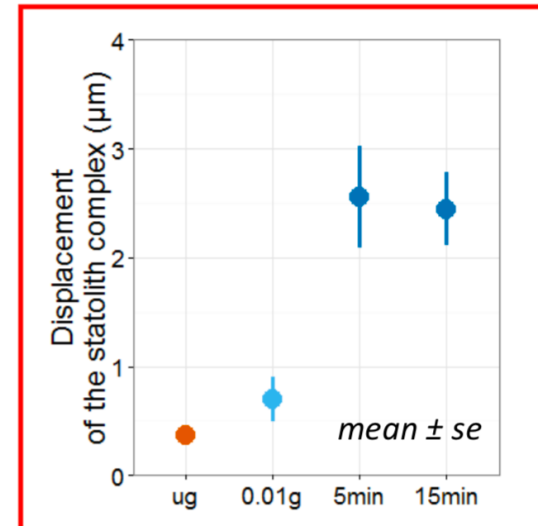


Following gravistimuli:  
Statolith complex occupies an identical space  
and move collectively

# Results from microgravity...Analysis of calcium precipitates

## Density of calcium precipitates

Condition	Number of precipitates /10 $\mu\text{m}^2$
$\mu\text{g}$	$1.0 \pm 0.2$ (6)
$\mu\text{g} + 0.01\text{g}-9\text{h}$	$1.0 \pm 0.2$ (6)
$\mu\text{g} + 2\text{g}-5\text{min}$	$0.9 \pm 0.1$ (12)
$\mu\text{g} + 2\text{g}-15\text{min}$	$1.1 \pm 0.1$ (12)

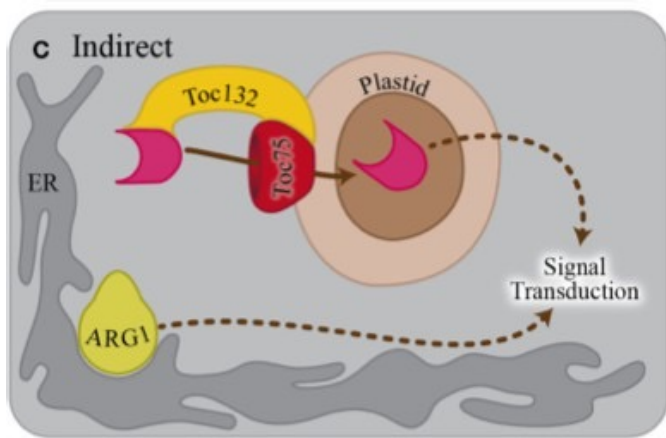


The displacement of amyloplasts-complex:

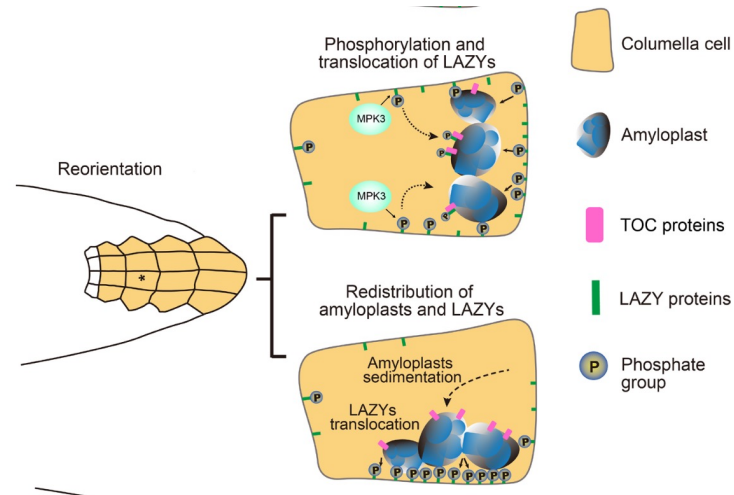
No impact on the number of calcium precipitates density and neither of their localisation

➤ Supports the position sensor hypothesis ?

# Interaction protein on amyloplasts



Protein interactions  
(Strohm et al 2014)



Amyloplast sedimentation repolarizes LAZYs  
(Chen et al, 2023)

LZY translocation from statoliths to the plasma membrane (Nishimura et al, 2023)

« LZY appears to act as a signal molecule that transmits the positional information of statoliths to the PM » (Nishimura et al, 2023)

## Origin of the liquid-like behavior? Agitation!

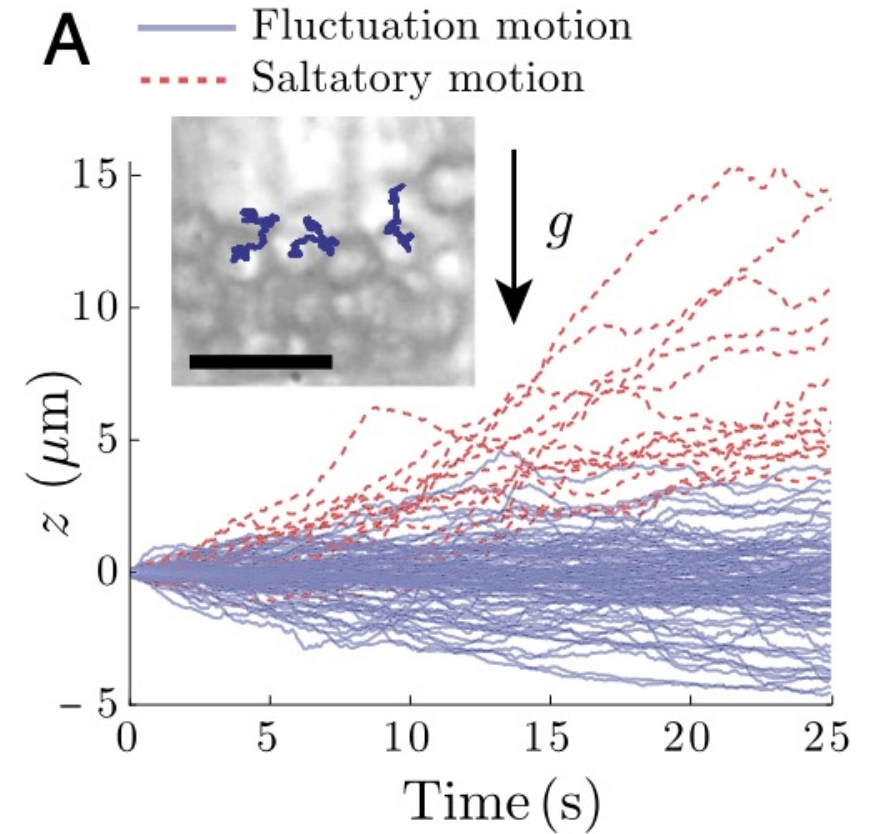
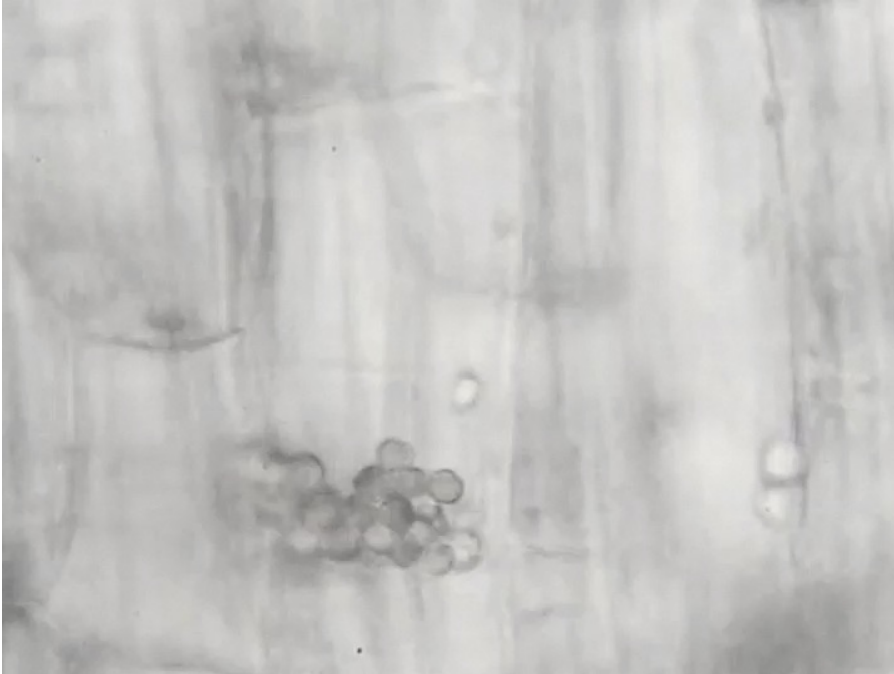


Relaxation of the heap slope to zero angle because of  
the random motion of the statoliths ?

Where does agitation come from ?

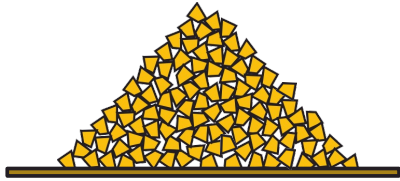


## Individual Statolith agitation

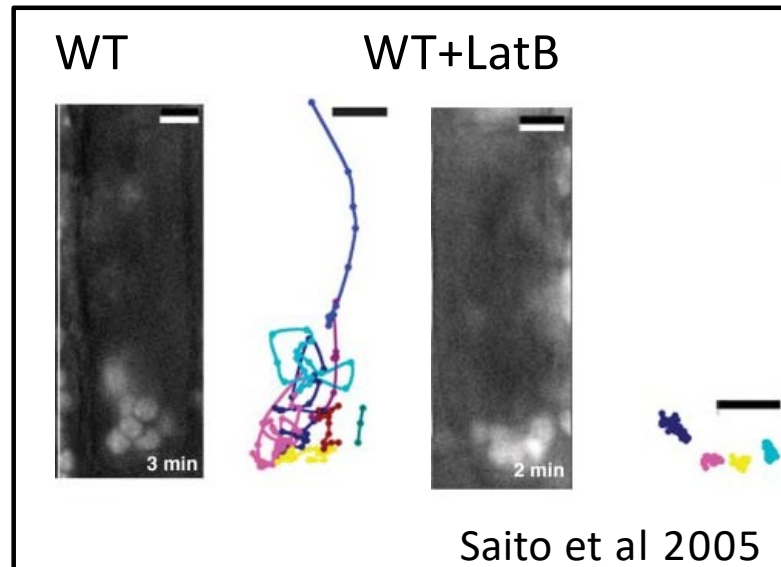
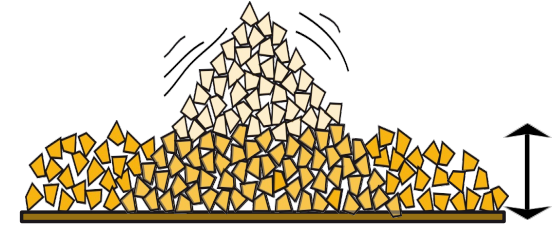


**Individual Statoliths Exhibit Random Motion**

# Origin of the liquid-like behavior? Agitation!



Relaxation of the heap slope to zero angle because of the random motion of the statoliths ?



Cytoskeleton activity ?

## Home message

- Statocyte: a **position sensor** and not a stress/force sensor
  - Sensitivity due to the **agitation** of the statoliths pile induced by the activity of cytoskeleton...
- = a highly sensitive position sensor thanks to the cytoskeleton-induced statolith agitation**



And now

Whats is missing in our gravisensing story ?

## **Link statoliths position to auxin transport**

From proposed models:

Levernier et al Front. Plant Sci. 2021

Meroz's team

## **Permanent and transient stimuli**



INRAE



amU Aix  
Marseille  
Université



Thanks



N. Brunel-Michac, F. Bizet, V. Legué, B. Moulia  
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