



Plants can respond to stimuli by “moving”

Because plants are rooted in one spot, we often perceive them as being relatively immobile. BUT, plants can and do “move”.

Three types of plant movements are:

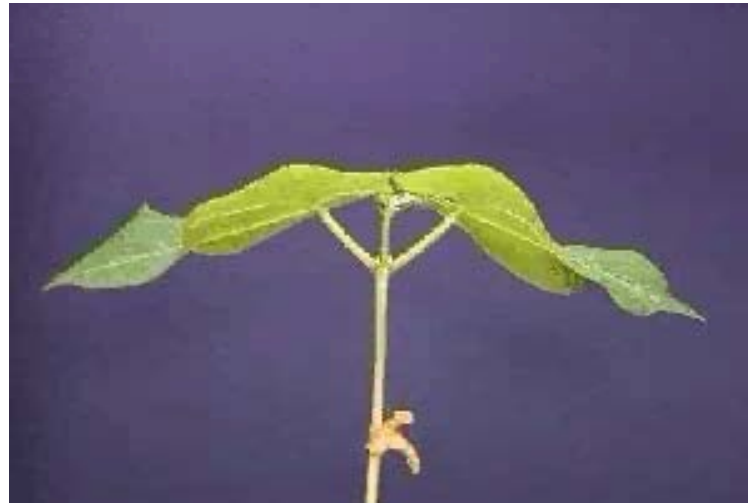
Circadian - movements that occur in response to the time of day.

Nastic - movements that occur in response to environmental stimuli. Nastic movements are not directional in nature.

Tropic - movements that occur in response to a directional stimulus and they involve altering growth to position leaves, roots, and flowers in places where the conditions are the most favorable.

Plants can respond to stimuli by “moving”

Circadian movements occur in response to the time of day. For example, some plants close their flowers or change the positions of their leaves at night. These movements are controlled by a circadian clock that requires input from the environment to stay synchronized with a 24 hr day.



<http://plantsinmotion.bio.indiana.edu/plantmotion/starthere.html>

In this time-lapse movie, beans were grown with 12 hrs of light and 12 hours of dark - this entrained the bean plants circadian clock to a 12 hr diurnal cycle. The movie starts with the plant “waking up” about 3 hrs before the lights would normally come on.

Plants can respond to stimuli by “moving”

Nastic movements occur in response to environmental stimuli, but they are not directional in nature.



<http://plantsinmotion.bio.indiana.edu/plantmotion/starthere.html>

The leaves of the Venus flytrap have hair cells that are sensitive to mechanical stimulation. It is only when the hair cells are touched that the leaf slams shut.

The leaves of the Mimosa plant close shut in response to being touched, shaken, heated, or rapidly cooled. The stimulus induces an electrical signal that moves from cell to cell much like a nerve impulse. When the electrical potential reaches specialized motor cells at the base of each leaflet there is a rapid efflux of K^+ followed by rapid flow of water out of the motor cells which moves the leaflet.

Plants can respond to stimuli by “moving”



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This morning glory vine is “searching” for a support along which to grow. The shoot tip rotates around a central axis as it grows and this is thought to help the plant find a suitable support.

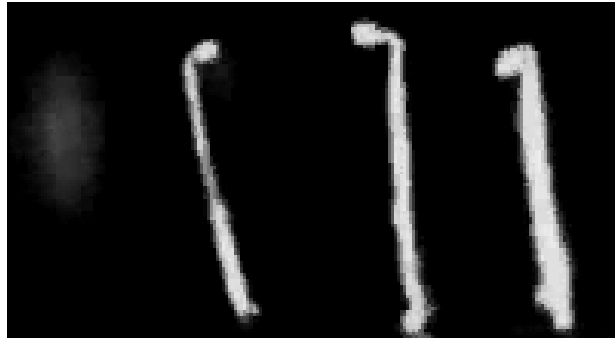
These movements appear to involve growth responses to gravity.

When the shoot rubs against the support, a “touch” response is induced and it causes the shoot to curl around the support.

Plants can respond to stimuli by “moving”

Tropisms are directional growth responses that occur in response to directional stimuli.

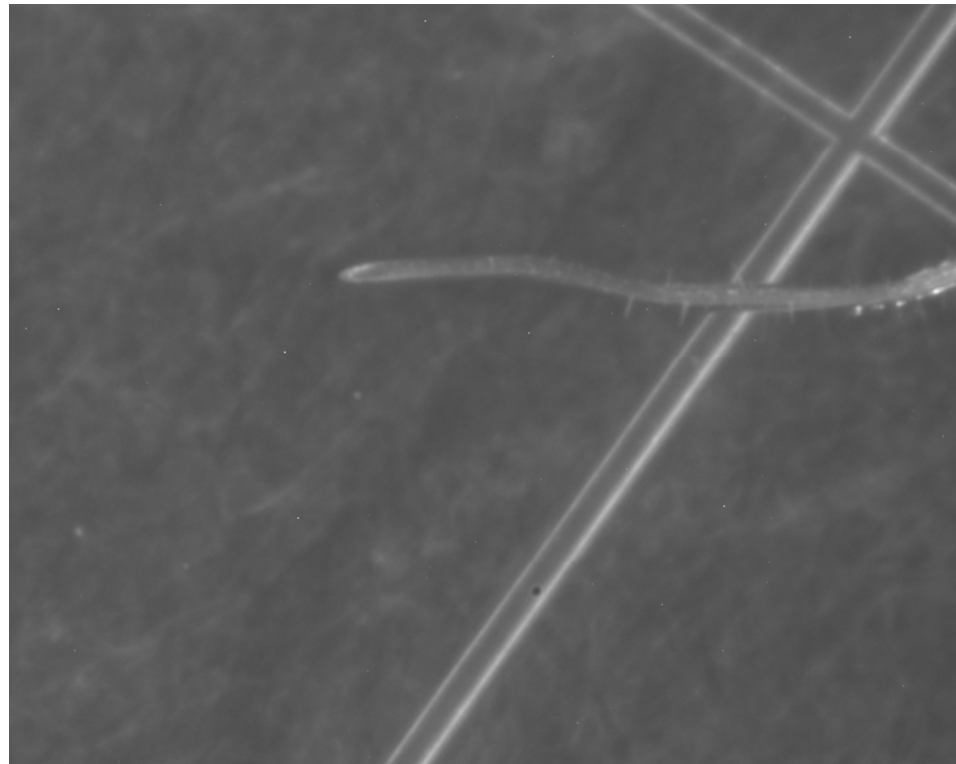
Phototropism occurs when plants direct their growth towards or away from light. It is a blue-light-dependant response that is controlled by blue light photoreceptors called **phototropins**.



These Arabidopsis seedlings were germinated in the dark for about 3 days. Blue light was shone on them from the left side. The movie was taken over a 5 hour period.

<http://plantsinmotion.bio.indiana.edu/plantmotion/starthere.html>

Gravitropism occurs when roots or shoots direct their growth according to the direction of the gravity vector.

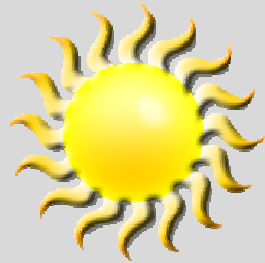


Roots are positively gravitropic - they grow down.

Shoots are negatively gravitropic - they grow upwards against gravity.

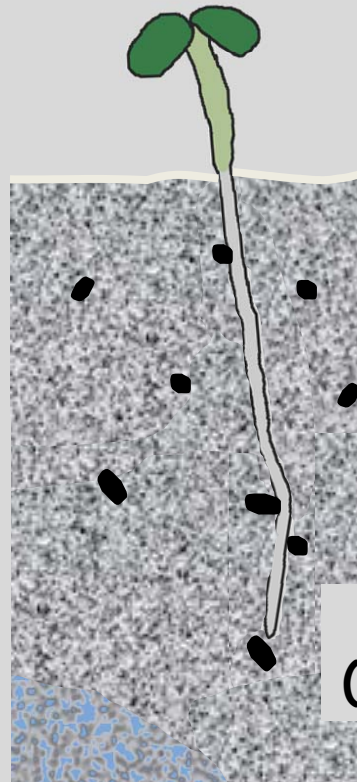
Movie by Stewart Lai,
Bisgrove Lab.

Tropisms



Light
(Phototropism)

Plants can redirect their growth in response to a number of different environmental stimuli.



Moisture
(Hydrotropism)

Gravity
(Gravitropism)



Touch
(Thigmotropism)

Plants are usually being bombarded with multiple stimuli at once. To choose a direction for growth, they must be capable of sorting out and prioritizing competing signals

Tropisms

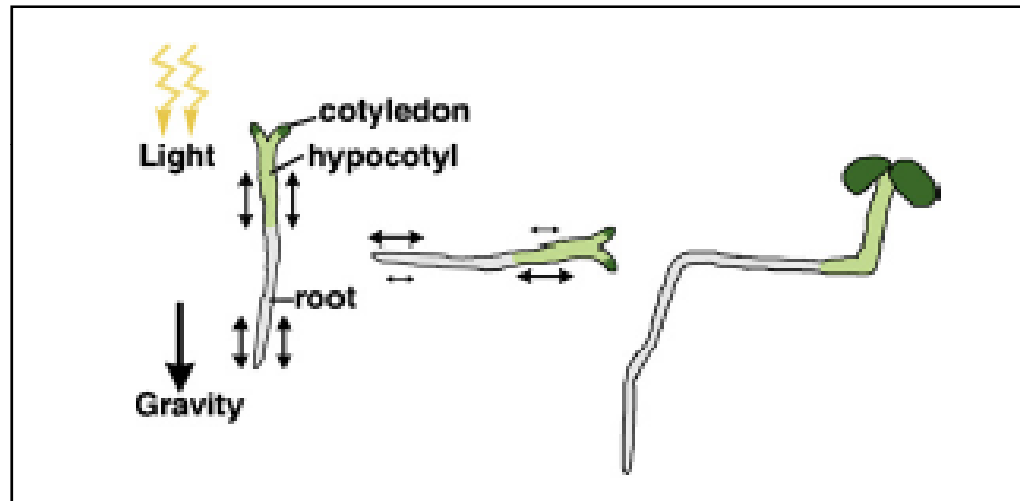
Tropisms involve 4 steps:

Perception of the stimulus

Conversion of a physical signal into a biochemical one

Transmission of the signal to the responding tissues

Growth response



From: Bisgrove, 2008. Plant Sci. 175: 747-755

In stems, gravity is perceived by endodermal cells that are positioned along the stem.

In roots, the sites of gravity perception and response are spatially separated. Gravity is perceived by cells in the root cap. The signal is then transported to the cells in the elongation zone where the response occurs.

The growth response is a bend that forms when cell elongation rates on the upper and lower flanks of the root are altered. Cells on the outer flank of the bend elongate more than cells on the inner flank = **differential growth**.

Gravitropism

How do plants detect gravity?

Gravity exerts its effects by causing masses to settle. This means that plants must be able to detect the settling or falling of masses.

Two models have been put forth to describe how plant cells sense gravity.

1) The starch-statolith hypothesis:

Proposes that gravity is detected by specialized cells called **statocytes**. In these cells, starch-filled amyloplasts called **statoliths** sediment in the direction of gravity.

2) The protoplast-pressure model:

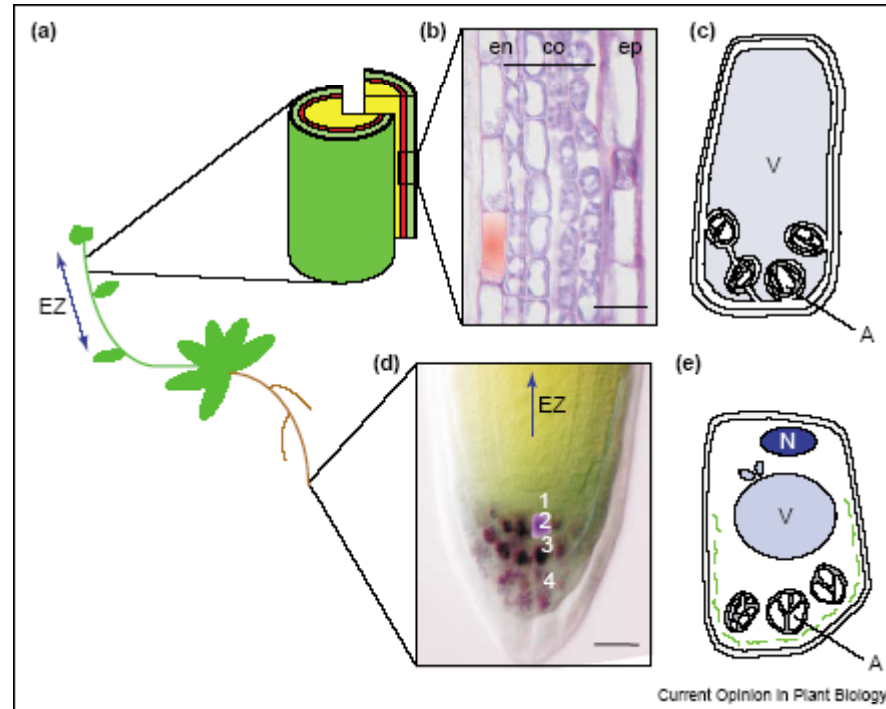
The hydrostatic pressure of the entire protoplast is thought to trigger conformational changes of gravity receptors at the plasma membrane. The direction of gravity would be perceived by sensing the differences in tension and compression between the plasma membrane and the extracellular matrix at the top and bottom of the cell.

Evidence supporting the starch-statolith hypothesis

In higher plants, the ability to detect gravity usually correlates with the presence of amyloplasts.

In stems, endodermal cells contain amyloplasts.

In roots, the columella cells in the root cap are statocytes.



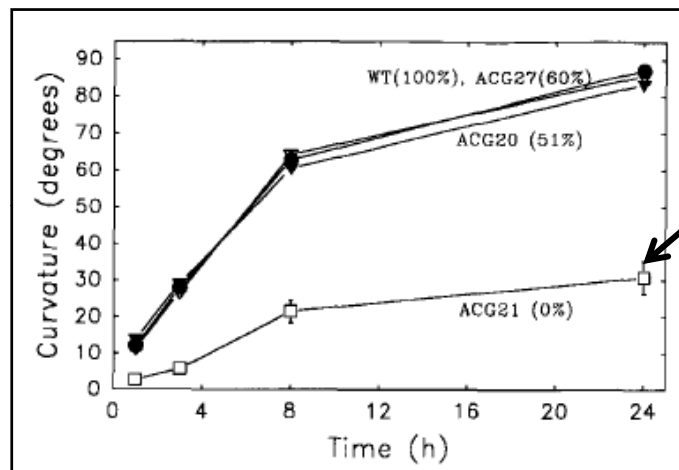
From: Morita and Tasaka, 2004. Curr. Op. Plant Biol. 7: 712-718.

Amyloplasts have also been observed in other tissues that are capable of responding to gravity.

For example, coleoptiles and pulvini of monocots, hypocotyls of germinating seedlings, and inflorescence stems of dicots.

There are *Arabidopsis* mutants that do not synthesize as much starch as wild type plants. One of these is the *phosphoglucosyltransferase* or *pgm* mutant. With reduced starch levels, the amyloplasts in the statocytes don't sediment very well and the mutants have defects responding to gravity.

Amyloplast sedimentation does not appear to be the only way that plants detect gravity



From: Kiss et al., 1996. *Physiol. Plant.* 97: 237-244

This mutant contains no measurable starch in its amyloplasts. Although its response to gravity is reduced, it is still capable of detecting and responding to gravity.

In addition, there are gravity responses that are NOT correlated with the presence of sedimenting statoliths.

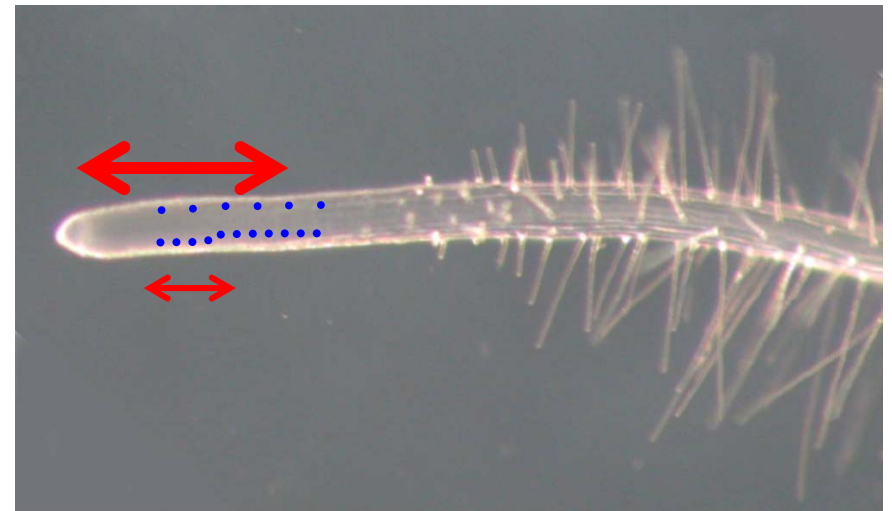
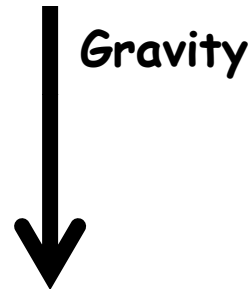
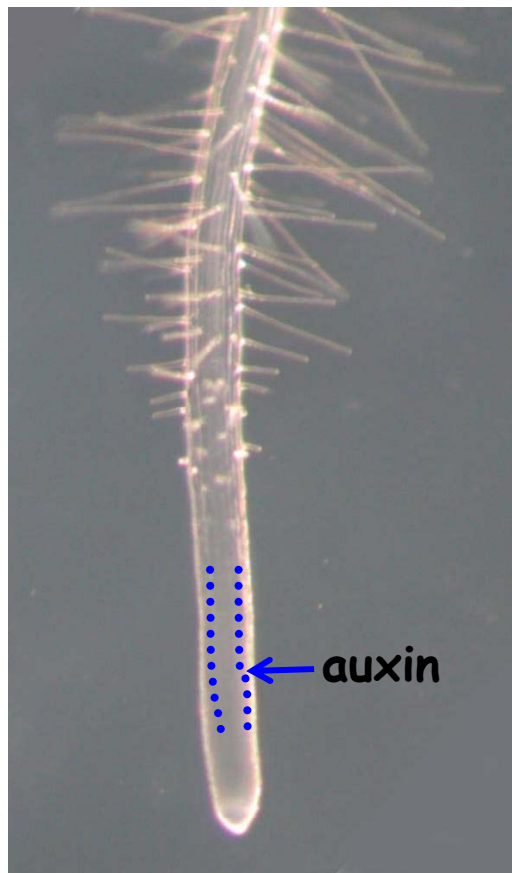
➡ suggests that there are alternative sensing mechanisms that do not involve statoliths.

Higher plants may also be sensing differences in protoplast tension between the top and bottom of the cell.

Root responses to gravity are mediated by auxin

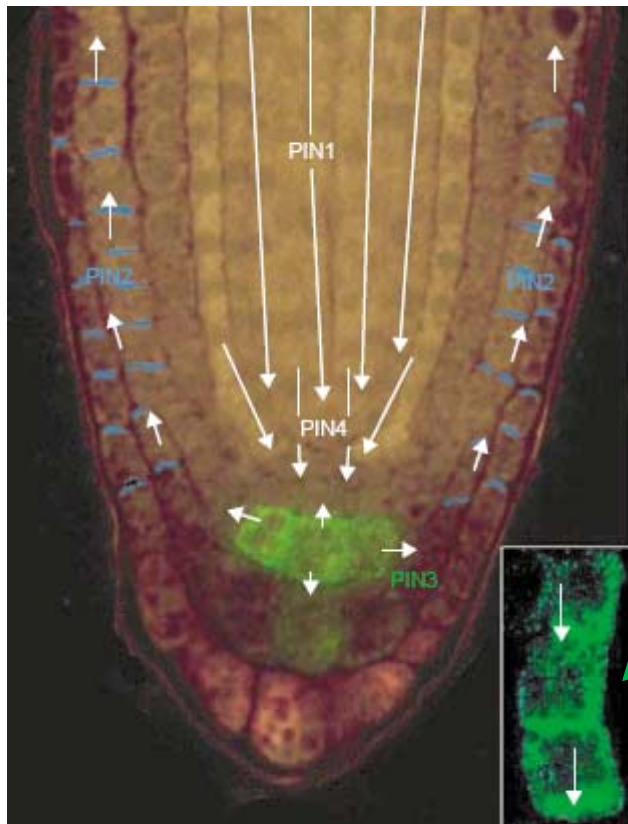
How gravity signals are converted into biochemical signals is unknown. A few proteins that function in the gravity signal transduction pathway have been discovered, although the gravity receptors have not yet been identified.

When a change in gravity is perceived, the stimulus leads to an asymmetric distribution of auxin in responding cells.



In roots, auxin levels increase on the lower flank and decrease on the upper flank. This causes cells on the upper flank to elongate more than the cells on the lower flank.

Root responses to gravity are mediated by auxin

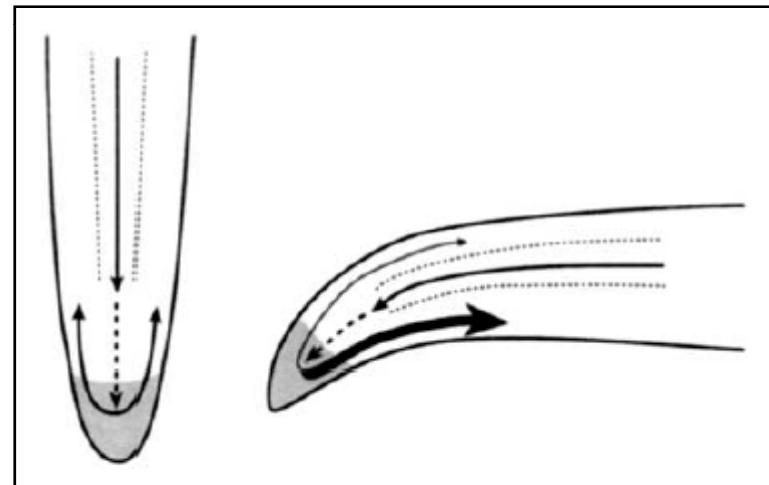


From: Friml 2003, Curr. Op. Plant Biol. 6: 7-12

The PIN3 auxin efflux carrier mediates the lateral redistribution of auxin in the root cap in response to gravity signals

In vertically oriented roots PIN3 is localized symmetrically in columella cells.

When the root is turned 90° PIN3 moves to the bottom membrane of the statocytes.

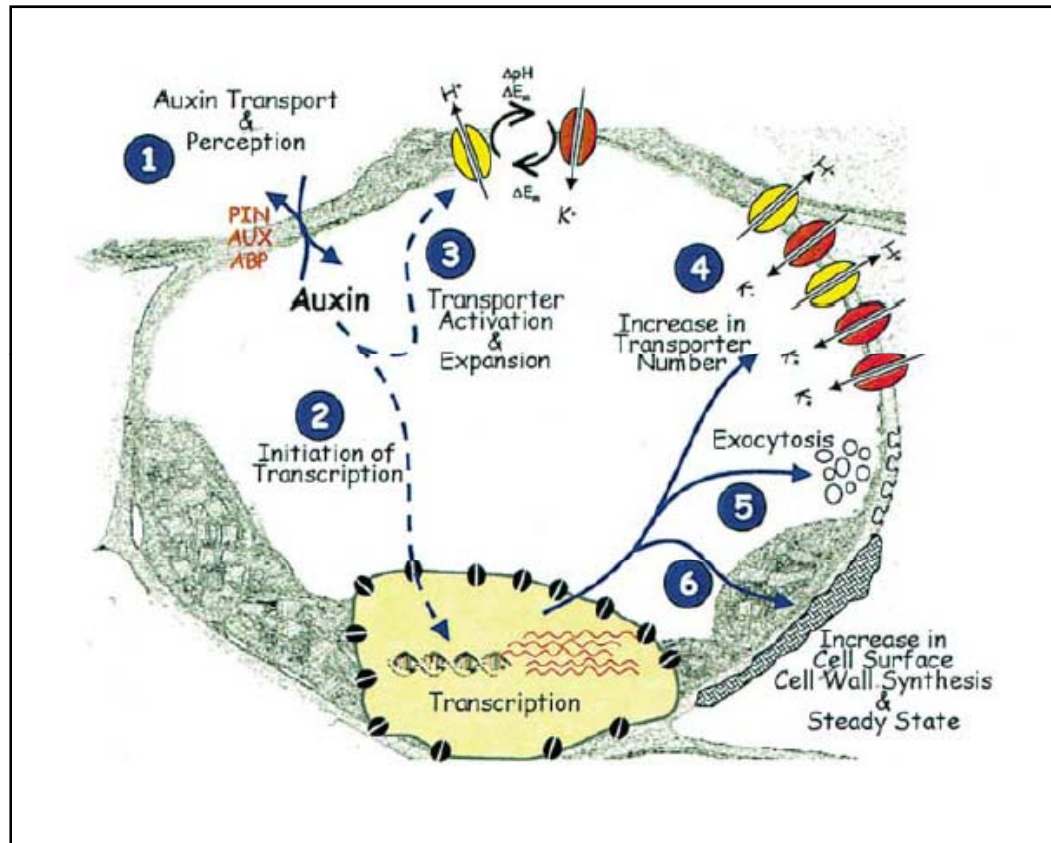


From: Wolverton 2002, J. Plant Growth Reg. 21: 102-112.

Higher levels of auxin accumulate on the lower flank of the root. According to the **Cholodny-Went hypothesis**, the auxin gradient triggers a differential growth response that results in organ bending.

How does auxin alter cell elongation rates?

Acid growth theory of auxin-induced cell elongation:



From: Becker and Hedrich 2002, Plant Mol. Biol. 21: 102-112.

Auxin also alters gene transcription - cell wall loosening enzymes and ion transporters are amongst the genes that are up-regulated. Enhanced exocytotic activity delivers these proteins to their sites of action where they reinforce ion movements across the plasma membrane.

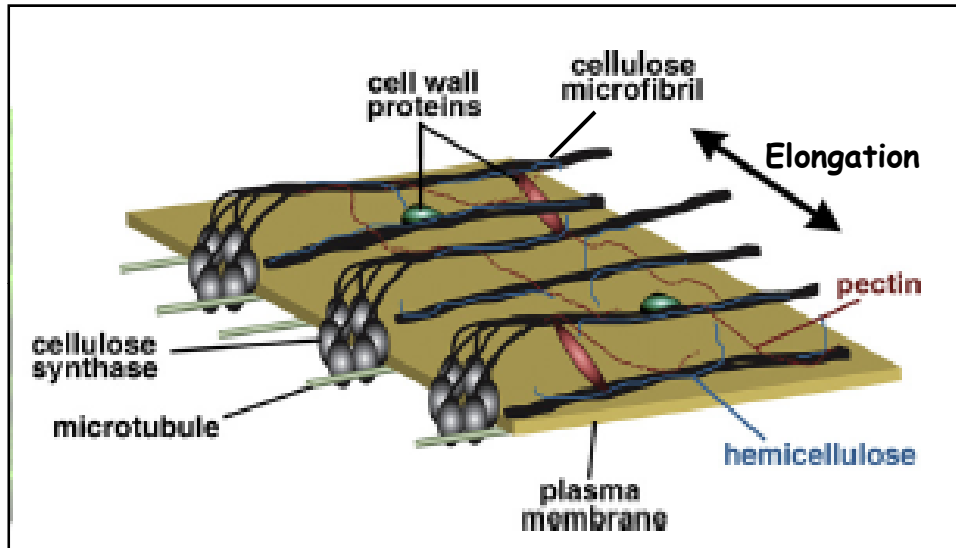
Changes in ion transport is one of the first cellular responses to auxin that occurs. Proton ATPases at the plasma membrane are activated and they pump protons out of the cell. This acidifies the cell wall and activates enzymes that loosen the wall making it more extensible.

As protons are pumped out of the cell, the membrane becomes hyperpolarized - the resulting voltage and proton gradients activate K⁺ channels and K⁺ flows into the cell.

There is an increase in turgor pressure, and this combined with the loosening of the cell wall drives cell expansion.

How does auxin alter cell elongation rates?

Cell elongation:



From: Bisgrove, 2008. Plant Sci. 175: 747-755

The wall of expanding cells is composed of cellulose microfibrils that are arranged in parallel arrays that encircle the cell.

Cellulose microfibrils are held together by matrix polysaccharides - these are the load bearing elements in the wall.

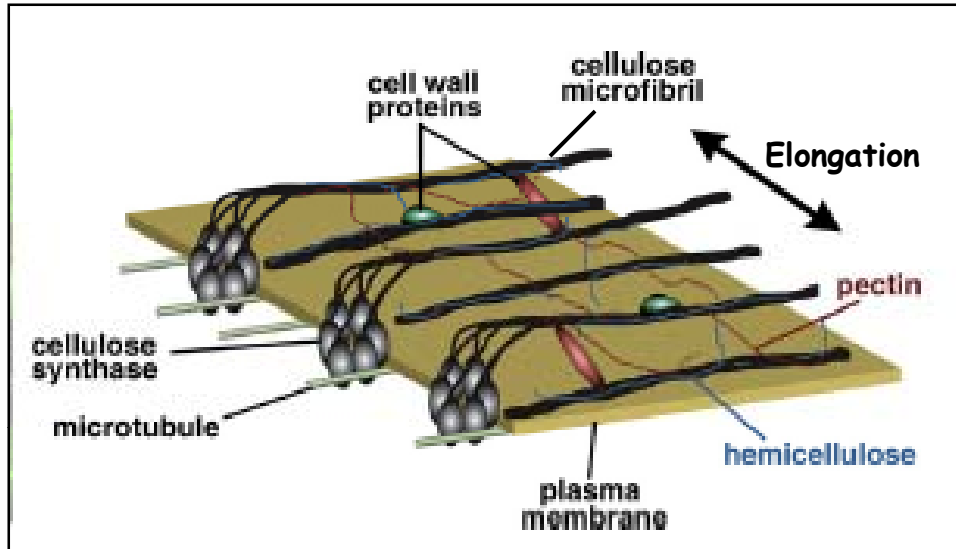
Turgor pressure provides the force that drives cell elongation. Because microfibrils are very strong along their lengths, turgor pressure exerted on the wall causes the microfibrils to move apart from one another and the wall expands perpendicular to the microfibrils.

The rate of cell elongation can be altered by selectively loosening the load-bearing linkages between cellulose microfibrils.

Expansins are activated at low pH and their expression is induced by auxin. These proteins induce dissociation and slippage of the cellulose binding glycans in the matrix.

How does auxin alter cell elongation rates?

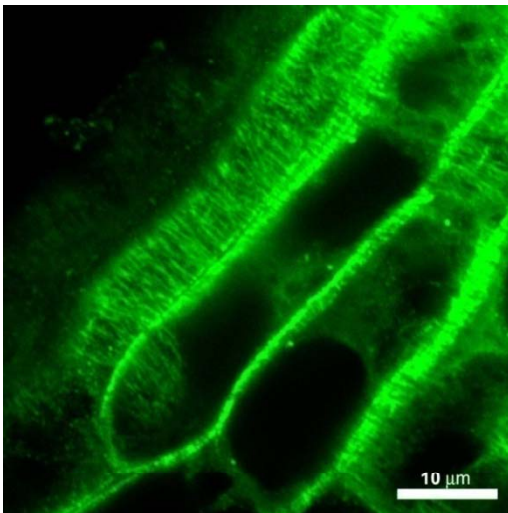
Cell elongation:



The orientation of cellulose microfibrils in the wall determines the direction of cell elongation.

Cellulose microfibrils are deposited into the wall by large transmembrane cellulose synthase complexes.

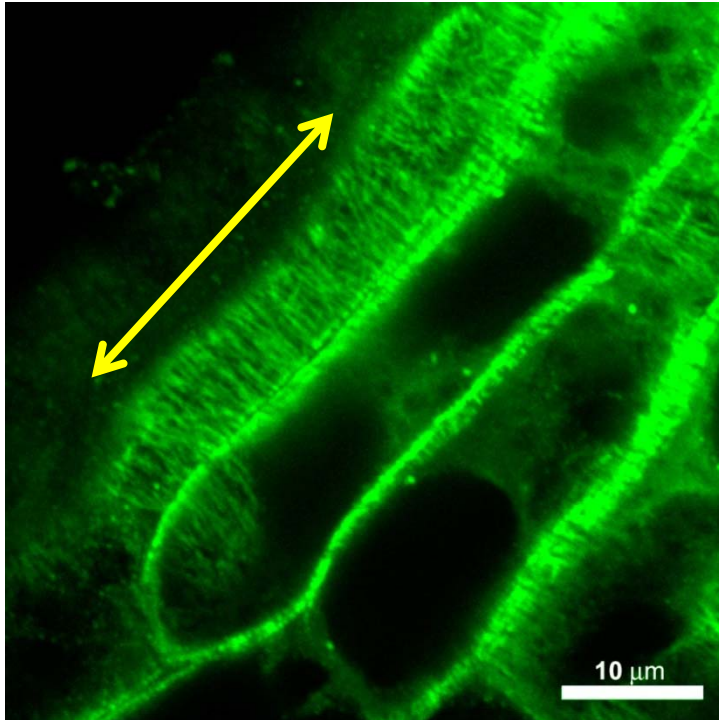
Cellulose microfibrils in the wall are co-aligned with microtubules that are located in the cortex of the cell closely associated with the plasma membrane.



Microtubules are thought to act as tracks that guide the cellulose synthases as they move through the plasma membrane.

Auxin also alters the orientation of microtubules in elongating cells. Since microfibril deposition parallels the orientation of the microtubules, a switch in microtubule orientation would also change the orientation of the microfibrils. It has been proposed that this change in microtubule/microfibril orientation could alter cell elongation enough to facilitate bend formation in stems and roots.

Do microtubules have a role in tropisms?



The idea that auxin-induced microtubule reorientations might play a role in organ bending is controversial.

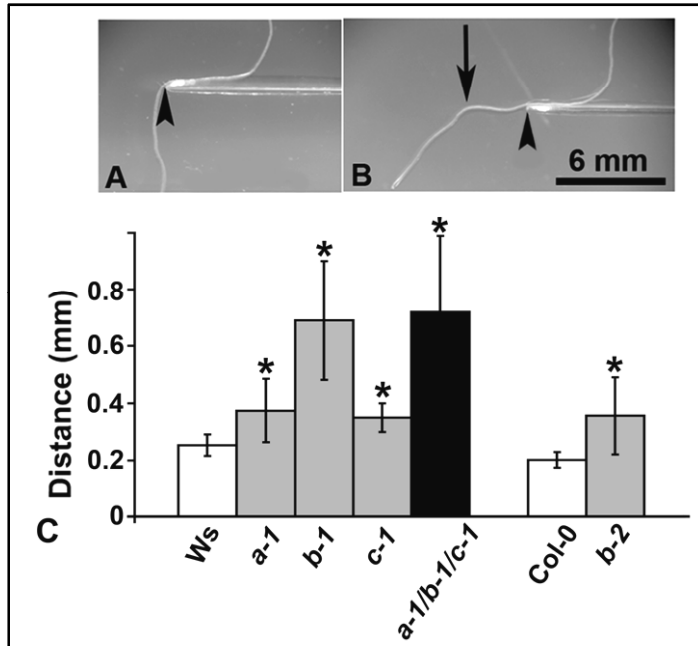
When plants are treated with chemicals that depolymerize microtubules, gravitropic bending is not consistently inhibited.

Physical strain can cause microtubule reorientations and some have argued that the reorientations that occur during organ bending may result from bend formation rather than cause it.

Issues have also been raised with respect to the timing of the microtubule reorientations. bend formation. Microtubule reorientations that preceded organ bending are not consistently observed; in some cases organ bending was initiated before microtubules reoriented.

Do microtubules have a role in tropisms?

The microtubule associated protein END BINDING 1 (EB1) appears to have a role in plant responses to gravity and/or touch stimuli.



From: Bisgrove et. al., 2008. Plant Cell

We are trying to assess whether EB1 functions in response to gravity or touch or both.

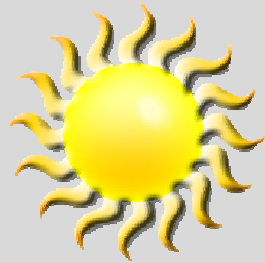
We would also like to know how EB1 is involved in bend formation.

Does it function early, during the signal perception or transduction events that lead to auxin gradient formation?

Or, does it function later to facilitate root bending?

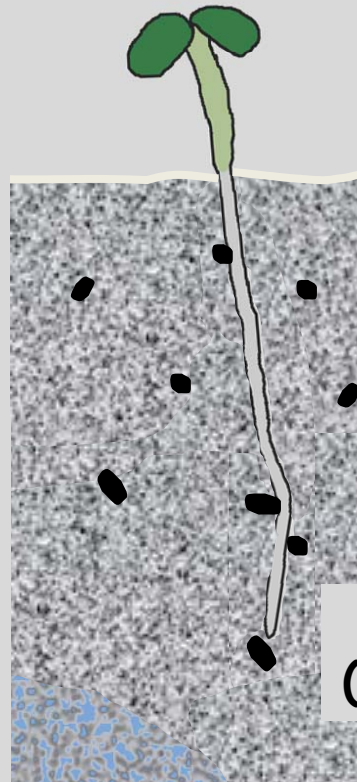
So far touch/gravity are the only stimuli that we have looked at - we would also like to know whether EB1 has a role in growth responses to other environmental stimuli.

How do multiple signals influence tropisms?



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(Phototropism)

Plants can redirect their growth in response to a number of different environmental stimuli.



Gravity
(Gravitropism)



Moisture
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Touch
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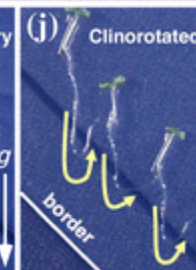
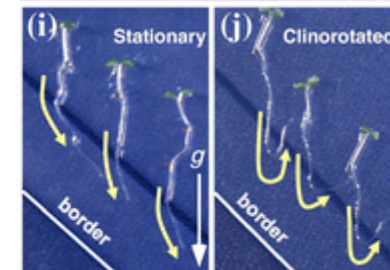
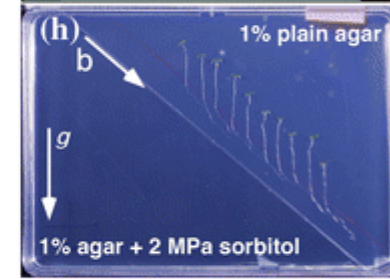
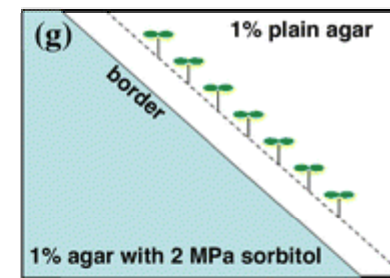
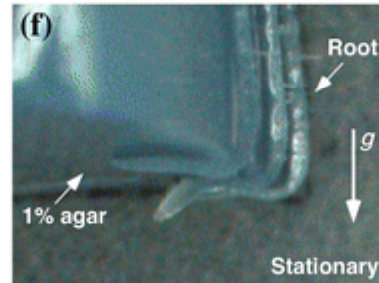
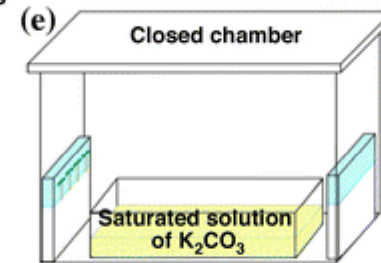
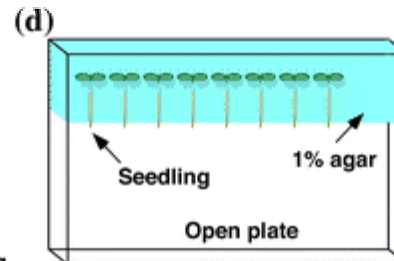
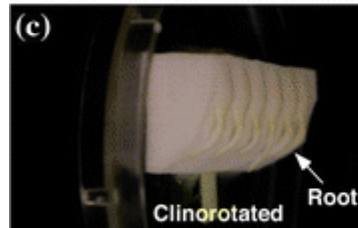
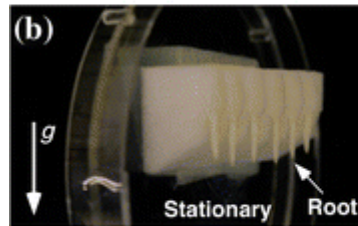
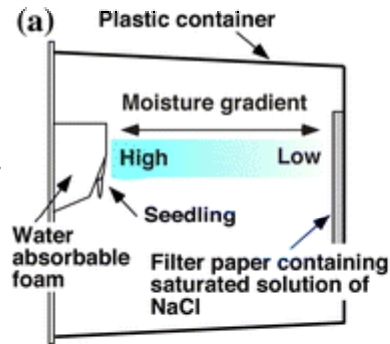
Plants are usually being bombarded with multiple stimuli at once. To choose a direction for growth, they must be capable of sorting out and prioritizing competing signals

How do multiple signals influence root growth?

Hydrotropism vs gravitropism.

To study hydrotropism, plant physiologists expose roots to moisture gradients.

Seedlings are germinated perpendicular to the moisture gradient.



This apparatus can be placed in a clinostat to reduce the effects of gravity.

How do multiple signals influence root growth?

Hydrotropism vs gravitropism.

More to come