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Growth-mediated plant movements: hidden in plain sight Short title: Growth-mediated plant movements

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Abstract

While fast plant movements are spectacular but rare, almost all plants exhibit relatively slow, growth-mediated tropic movements that are key to their survival in the natural world. In this brief review, we discuss recent insights into the molecular mechanisms underlying phototropism, gravitropism, hydrotropism, and autostraightening. Careful molecular genetic and physiological studies have helped confirm the importance of lateral auxin gradients in gravitropic and phototropic responses. However, auxin signaling doesn't explain all tropisms: recent work has shown that abscisic acid signaling mediates root hydrotropism and has implicated mechanosensing in autostraightening, the organ straightening process recently modeled as a proprioceptive response. The interactions between distinct tropic signaling pathways and other internal and external sensory processes are also now being untangled.

Keywords

Tropism; auxin; gravitropism; phototropism; hydrotropism; autostraightening; proprioception

Introduction

The power of movement is so firmly associated with animals that the casual observer might be forgiven for thinking that plants that move are the exception rather than the rule. For example, the fast and spectacular action of a Venus flytrap closing on its prey [1] captures the imagination but leaves the impression that plants that move are rare. In fact, plant movements are ubiquitous and have been noted by close observers at least from the time of Alexander the Great, becoming a topic of consuming interest for great botanists of the 19th century such as Sachs, Pfeffer, and Darwin.

The intensive study of plant movements continues to this day. We now appreciate that all plant movements are ultimately controlled by interactions between intracellular turgor pressure and the plant cell wall. Fast movements such as by carnivorous plants are driven by

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rapid changes in water transport aided by mechanical instabilities in plant structures [2]. In this review, we will examine the basis of the relatively slow plant movements generated by the differential growth of live tissues. These directional growth responses are controlled by anisotropic cell expansion, with the rate and direction of turgor-driven cell growth varying across the cell in a manner determined by local differences in cell wall extensibility and/or elasticity [3]. We will discuss a few recent highlights in the areas of phototropism, gravitropism, hydrotropism, proprioception, focusing on the diverse roles for the growth hormone auxin in these processes (Figure 1).

Phototropism: Bending towards or away from the light

Most plant shoots grow towards a light source while most roots grow away, allowing plants optimal access to light, water, and nutrients. The primary photoreceptors involved in phototropism are the aptly named phototropins. In Arabidopsis, there are two members of this family, phot1 and phot2. As described more fully in recent reviews [4,5], phot1 and phot2 are plasma membrane-associated proteins with a photosensory region, consisting of two Light, Oxygen, or Voltage (LOV) domains, and a protein kinase domain that becomes activated upon blue light exposure. Exposure to blue light causes phototropins to physically interact with NPH3, another plasma membrane-associated protein essential for phototropism [4], which then undergoes dephosphorylation. Despite the ability of the isolated kinase region of phot2 to confer constitutive phototropin signaling [6], full-length phot1 proteins with a mutated, constitutively activate, kinase domain still require a light stimulus to trigger NPH3 dephosphorylation and downstream responses [7]. Subsequent steps in the signaling pathway are incompletely understood, but result in the polar relocalization of auxin transport carriers and formation of a lateral auxin gradient, leading to differential growth of the shaded and lit sides of the organ. Mechanisms used by auxin to control directional organ growth will be discussed in the following section.

Although Darwin established that phototropic cues are sensed at the tip of grass coleoptiles [4], the site of photoreception in dicot shoots has been less clear since *PHOT1* and other signaling components are expressed widely in these plants. Investigators have recently examined the ability of *PHOT1* expressed under various tissue-specific promoters to rescue phototropism in *phot1 phot2* mutants. Light perception in the upper region of the hypocotyl, but not the cotyledons, was found to be necessary and sufficient for phototropic bending [8]. Subsequent studies suggest that normal phototropism depends upon photoreception in the upper hypocotyl, below the shoot apical meristem [9].

Phototropins are also found in green algae, where they have disparate functions such as in regulation of the sexual lifecycle in *Chlamydomonas reinhardtii*. Intriguingly, expression of the *C. reinhardtii phot* gene rescues phototropism in Arabidopsis *phot1 phot2* double mutants [10]. This conservation of function in phototropic bending is however not seen for all algal phototropins. Expression of the single phototropin found in *Ostreococcus tauri* rescues some *phot1 phot2* phenotypes but not phototropic bending [11]. This may be due to its inability to bind to NPH3. In addition, while a fraction of Arabidopsis phot1 is internalized from the plasma membrane upon blue light stimulation, this response is attenuated for the *O. tauri phot* [11]. However, it seems unlikely that this is the cause of the

inability of the *O. tauri* phototropin to mediate phototropic bending: it was recently reported that *Arabidopsis* phot1 constitutively tethered to the plasma membrane mediates phototropic curvature nearly identically to control lines [12].

Auxin and directional growth

Auxin has long been implicated in many growth-mediated plant movements [13]. Intriguingly, depending upon its concentration and the plant tissue involved, auxin can either promote or inhibit cell elongation [14–16]. Auxin is primarily produced at the shoot apex and is moved throughout the plant body by specific auxin carrier proteins that shuttle it into and out of cells (auxin influx and efflux carriers). As first conceptualized in the Cholodny-Went model, tropic stimuli can modify auxin transport, causing the lateral redistribution of auxin across a plant stem and localized organ bending in response to this gradient (reviewed in [5]). Mechanisms controlling the intracellular localization and activity of influx and efflux carriers, and therefore the direction of auxin flow and relative levels of auxin across the plant body, are of intense interest and have recently been reviewed [17].

How does auxin cause rapid changes in growth? A possible role for the plasma membrane-localized AUXIN BINDING PROTEIN (ABP) in the control of growth has long been discussed (reviewed in [18]). However, a number of recent publications have put this model into question [18] and a plausible mechanism for the promotion of cell elongation in stems by a nuclear receptor has been proposed. Nuclear-localized TIR1/AFB (TRANSPORT INHIBITOR RESISTANT1/AUXIN SIGNALING F-BOX) receptor proteins bind auxin in conjunction with Aux/IAA (AUXIN/INDOLE ACETIC ACID) co-receptors to initiate a short signal-transduction pathway that regulates expression of hundreds of genes (see [19] for a recent review). Among these genes are the rapidly auxin-induced *SMALL AUXIN UP RNAs* (*SAURs*), which indirectly activate plasma membrane proton pumps, acidifying the apoplast and activating cell wall-loosening enzymes that increase wall extensibility [20,21].

In support of this acid growth model, a recent paper shows that components of the nuclear signaling pathway and induction of gene expression are essential for the acidification of the apoplast and hypocotyl growth in response to auxin [22]. Furthermore, constitutive expression of a normally auxin-induced SAUR is sufficient to confer elongation of aerial organs in *Arabidopsis* and tomato [21–23]. Together, these findings suggest that the nuclear receptor pathway is sufficient to explain auxin promotion of cell elongation in shoots. The role of auxin in the regulation of root growth is more complex, and will be discussed further below.

Gravitropism: multiple pathways at work in roots

In both shoots and roots, gravity is sensed by statocytes. These cells, found in the columella of the root tip and the endodermis of the shoot, contain starch-storing plastids called amyloplasts that upon plant inclination sediment in the direction of gravity and then trigger differential growth. Remarkably, clever experiments with a centrifugal device show the shoot bending response is independent of gravity intensity; furthermore, when plants are subjected to sustained inclination there is no angular threshold of response [24]. These findings

suggest that plants respond directly to organ and statocyte inclination rather than by measuring the force exerted by statoliths upon cellular components. In both roots and shoots, gravistimulation triggers the lateral redistribution of auxin towards the lower side of the organ within minutes to effect directional growth (away from the gravity vector in the case of shoots; towards it in the case of roots; reviewed in [13]). Notably, a recent study has revealed that auxin redistribution is also responsible for the gravitropic responses of woody stems, which cannot undergo elongation growth and instead rely upon asymmetric radial growth to grow away from gravity [25].

The sequence of signaling events downstream of gravity perception is not fully resolved, although auxin signaling is clearly key to responses of both shoots and roots. Recent studies have demonstrated that proteins in the land plant-specific LAZY family act downstream of amyloplast sedimentation in both roots and shoots to generate asymmetric distribution of auxin efflux carriers and higher auxin levels on the lower surface side of the gravistimulated organ [26,27]. Phototropism is normal in *lazy* mutants [26,27], indicating that LAZY proteins act upstream of steps shared between the light- and gravity-sensing pathways in the auxin relocalization process.

In shoots, higher auxin levels promote local acidification of the apoplast and cell elongation, generating upward bending [13]. The role of auxin in the directional growth of roots is more complex. Rapid responses to gravistimulation include increases in cytoplasmic Ca^{2+} levels and changes in apoplastic pH. Increased cytosolic Ca^{2+} levels have been reported to lead to changes in the localization of auxin efflux carriers [28]. Auxin can also induce influx of Ca^{2+} across the plasma membrane in a cyclic nucleotide-gated channel-dependent manner [29]. Mutants in this channel exhibit delays in changes in cell surface pH and in gravitropic bending. Together, these data place calcium signaling both up- and downstream of auxin responses in roots.

Depending upon the species and the hormone concentration, auxin and apoplast acidification have been reported to inhibit or promote root cell elongation [14–16]. Recent work with a fluorescent reporter enabling the assessment of apoplastic pH at cellular resolution suggests a possible explanation for these conflicting reports [15]. Using genetic tools to manipulate endogenous levels of auxin, Barbez and co-workers concluded that low levels of auxin promote apoplast acidification and root cell elongation. However, their results also suggest that high local levels of auxin, such as those produced upon gravistimulation, cause alkalization of the apoplast and inhibition of cell elongation. Furthermore, they found that auxin-induced apoplast alkalization and normal gravitropism depend upon the plasma membrane-localized receptor-like kinase FERONIA [15]. Thus the effects of auxin on apoplastic pH and root growth are concentration-dependent and are due to the action of multiple signal transduction pathways [15,29].

Hydrotropism: a tropic response independent of auxin relocalization

In addition to responding to light and gravity, plant roots are hydrotropic: they sense differences in water potential in the local environment and direct their growth accordingly. The molecular details underlying this process are just becoming clear. While

pharmacological studies suggest that auxin transport may be involved in hydrotropism in some species, lateral auxin redistribution does not appear to be required for hydrotropism in *Arabidopsis* or *Lotus* [30,31] [32]. The signaling pathways underlying hydrotropism and gravitropism differ in many other ways as well. While gravitropic signals are sensed by root tip cells and cause differential growth at a distance in the elongation zone, it has recently been shown that the cortical cells of the elongation zone both sense and respond to the water potential signal in hydrotropism [33]. Moreover, signaling components downstream of the abscisic acid (ABA) receptor are required for normal hydrotropism, with low concentrations of exogenous ABA promoting both cell division and expansion in the elongation zone [33–35]. Furthermore, while reactive oxygen species are required for gravitropic bending, they inhibit hydrotropism [36]. Thus although root gravitropism and hydrotropism are superficially similar processes, these directional movements are controlled by very different molecular pathways.

Autostaughtening: a proprioceptive response

Plants possess another type of movement response that is currently poorly understood and has variously been called autostraightening, autotropism, or automorphosis (reviewed in [37,38]). There is considerable evidence that plants can sense organ deformation and alter their growth to recover straightness. Thus during phototropism or gravitropism, initial general curving along the entire organ is followed by a period of basipetal straightening, with decurving proceeding from the organ tip so that eventually curvature occurs only at the base of the organ (Figure 2). Mathematical modeling of plant kinematic responses to gravitropic and phototropic signals suggests that the final stable orientation of the plant stem relative to external stimuli depends not only upon the tropic pathways described above, but also upon the concurrent sensing of local curvature via proprioceptive sensing [39,40].

How are proprioceptive cues sensed and transduced into differential growth? Studies using radiolabeled auxin or examining expression of an auxin-responsive reporter gene suggest that autostraightening does not depend upon lateral redistribution of auxin [41,42]. Instead, local curvature appears to be sensed via an actinomyosin-dependent mechanism that triggers autostraightening via an unknown mechanism. An intriguing recent manuscript revealed that *Arabidopsis* plants mutant for either two myosin XI family members or an actin isoform hyperbend both aerial organs and roots in response to gravitropic or phototropic stimuli [43]. These myosin XI genes are preferentially expressed in xylem fiber cells, extremely long cells (~ 1 mm) with actin cables running along their longitudinal axes. It is possible that proprioceptive cues are sensed by the bending of these long actin cables which then activate mechanosensitive channels that produce signals regulating differential growth (reviewed in [44]). These new insights will facilitate studies leading to a better understanding of the molecular mechanisms underlying proprioception and how mechanical cues constrain and inform plant growth pathways.

Future directions

Although plant movements have been intensively studied for decades, many questions remain. Early predictions that phototropic and gravitropic stimuli cause the redistribution of

auxin within roots and stems to generate differential growth across these organs are now well-supported. However, although the proximal receptors have been identified, our understanding of the signaling pathways generating these auxin gradients is still far from complete. Additional, currently unknown receptors may also be involved; for example, the extremely rapid movement of ions across root cell plasma membrane after auxin- or gravistimulation suggests a role for non-nuclear auxin receptors in these processes [29]. Mutant analysis has also revealed the action of opposing response pathways downstream of the same environmental stimulus. For example, the roots of plants mutant for LAZY proteins demonstrate negative, rather than positive, gravitropism [26,27,45]. This growth away from the gravity vector is accompanied by the accumulation of auxin and auxin transporters on the upper, rather than the lower sides, of gravistimulated roots. Thus these mutants reveal a LAZY-independent mechanism for the establishment of an auxin gradient with an opposite orientation to the one generated in wild-type roots in response to gravity.

Another important area for future research is how tropic response pathways interact with each other. Although in our above discussion we have generally treated growth-mediated tropic response pathways as though they act in isolation from each other, this is far from the truth. Plants are always subject to multiple, often conflicting, environmental cues. For example, young sunflower plants must maintain an upright posture against gravity while still bending to track the sun from east to west each day and bending back again towards the east each night [46]. To allow plants to cope with such conflicting signals, many tropic response pathways are mutually antagonistic, such as hydrotropism and gravitropism [30,36], and phototropism and gravitropism [47]. Highlighting the complicated relationships between tropic response pathways, it was recently reported that in microgravity conditions, *Arabidopsis* roots exhibit positive, not negative phototropism [48].

Non-directional sensing pathways can also affect tropisms; for example, the red light photoreceptor phytochrome can affect phototropism and gravitropism through control of auxin production and differentiation of plastids, respectively [49,50]. Finally, entirely internal cues can also modulate tropic responses: the circadian clock has been shown to control plant sensitivity to directional light and to gravistimulation [46,51]. Thus a full understanding of growth-mediated plant movements will require not only the unraveling of the complex signaling pathways outlined above, but also how these pathways influence each other.

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Highlights

- Most plant movements are relatively slow and mediated by differential growth
- Lateral gradients in auxin concentration are key for photo- and gravi-tropism
- Activity of nuclear signaling pathways can explain auxin promotion of shoot growth
- However, hydrotropism and autostraightening don't rely on auxin relocalization
- Tropic response pathways don't act in isolation and are often mutually antagonistic

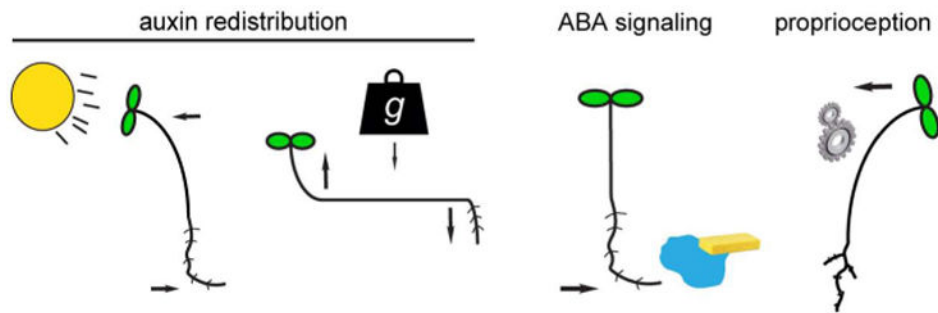


Figure 1. Diverse molecular mechanisms produce tropic movements. Shoot and root gravi- and phototropism rely upon the generation of auxin gradients across these organs. However, the rapid gravitropism of roots requires additional signaling pathways as well. Moreover, root hydrotropism is reliant on ABA signaling while proprioceptive (also called autostraightening) movements may depend upon mechanosensing.

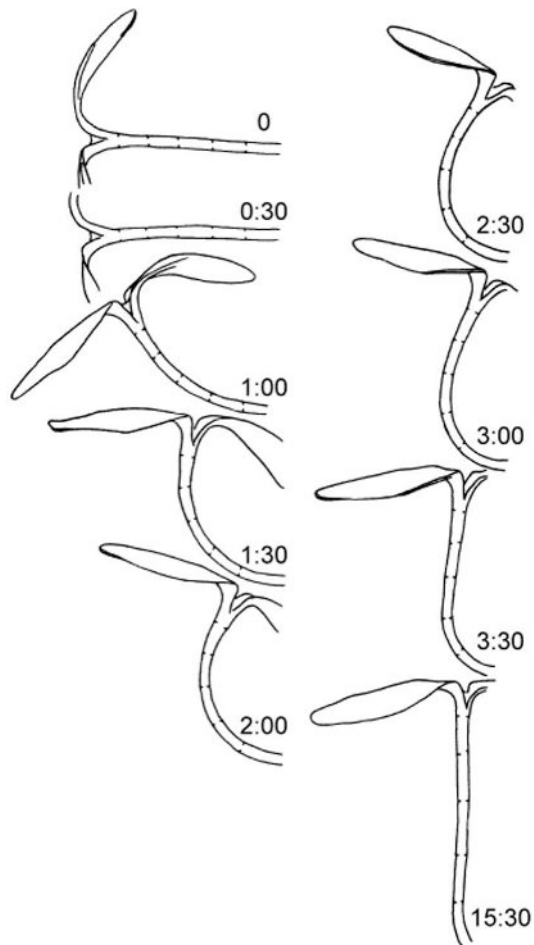


Figure 2. Autostraightening of the hypocotyl of a de-etiolated sunflower seedling subjected to gravistimulation. Hours after the seedling was turned to the horizontal positions are indicated. By one hour after gravistimulation, the hypocotyl exhibits nearly uniform curvature along its length. However, the position of curvature gradually moves basipetally down the hypocotyl until by 3:30 hours the upper portion of the hypocotyl has straightened and curvature is restricted to the base. Re-drawn from Firm and Digby [52].