

Growth-mediated plant movements: hidden in plain sight

Stacey L Harmer and Christopher J Brooks



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 does not 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.

Address

Department of Plant Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

Corresponding author: Harmer, Stacey L (slharmer@ucdavis.edu)

Current Opinion in Plant Biology 2018, 41:89–94

This review comes from a themed issue on **Growth and development**

Edited by **Gwyneth Ingram** and **Ari Pekka Mähönen**

<https://doi.org/10.1016/j.pbi.2017.10.003>

1369-5266/© 2017 Elsevier Ltd. All rights reserved.

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

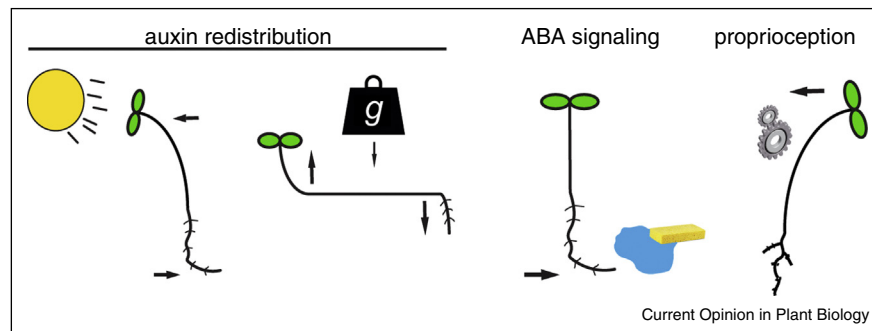
ultimately controlled by interactions between intracellular turgor pressure and the plant cell wall. Fast movements such as by carnivorous plants are driven by rapid changes in water transport aided by mechanical instabilities in plant structures [2]. In this review, we will examine the basis of the 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, and 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

Figure 1



Diverse molecular mechanisms produce tropic movements. Shoot and root gravitropism 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.

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 wild-type protein [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 [14,15,16]. 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 [21,22,23]. 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.

Download English Version:

<https://daneshyari.com/en/article/8380319>

Download Persian Version:

<https://daneshyari.com/article/8380319>

[Daneshyari.com](https://daneshyari.com)