as actin assembly regulation. Also, in neuroblastoma cells, cofilin association with the mitochondrial outer membrane is needed for stress-induced release of cytochrome c and consequent apoptosis. In addition, studies of cofilin activity modulation revealed that actin dynamics play important roles at the Golgi in sorting of membrane cargo targeted to neuronal axons or apical membrane of epithelial cells. Vertebrate ADF and cofilin have a nuclear localization sequence which allows them to chaperone actin into the nucleus.

Do these proteins contribute to diseases or developmental abnormalities? In stressed cells, when ATP declines and ADF/cofilin is hyperactivated through dephosphorylation, ADF/cofilin-saturated actin filament bundles may form. In neurons these bundles form within axons and dendrites, block neurite transport and contribute to synaptic dysfunction; similar structures have been identified in the brains of humans with Alzheimer's disease. Mutations in cofilin-2 have been linked to a form of nemaline myopathy in muscle. Cofilin-null mice are embryonic lethal due at least in part to migration defects, but tissue-specific silencing of cofilin in the brain reveals its requirement for the formation of the cortical layers. ADF null mice are viable but go blind about 4 weeks after birth due to corneal thickening.

Where can I find out more?

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Plant tropisms

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When animals are challenged with an environmental stimulus, be it the setting of the sun or the need to find food, behavioral and movement-based responses are the norm. In contrast, plants are sessile — literally rooted to the spot — and so must react to these same challenges through physiological and developmental pathways. These differences in lifestyle can be distilled to the view that while animals move through their environment, plants grow through theirs. This is a fundamental feature of how plants adapt to the challenges of their surroundings and results in plant growth being highly plastic, i.e. being determined to a large degree by environmental stimuli rather than the strict adherence to a genetic blueprint that governs, for example, the extent of human development. One element in the suite of growth responses that plants employ to perform this plastic, environmentally entrained developmental program is directional growth in response to a directional stimulus — a tropism.

In addition to responding to environmental insults such as herbivory and pathogen attack, plants need to explore their environment for the staple nutritional resources that support life. Therefore, plants principally hunt their surroundings for an adequate supply of water, mineral nutrients, light and, in some cases, even physical support. Unfortunately, this is no easy task as these resources are highly variable in distribution in both space and time. For example, mineral nutrients tend to form patches in the soil, water levels and distribution can change dramatically from day to day, and even the available light for photosynthesis will change its direction every minute as the sun tracks across the sky. Being able to monitor the direction of these changes and then grow towards the appropriate resource provides the plant with an enhanced ability to exploit its surroundings. Such tropisms are ubiquitous in plants and are key to their adaptability to the changing world around them.

Indeed, plants exhibit exquisite sensitivity to their surroundings, possessing a wide array of sensory systems needed to monitor the environment and respond appropriately. It is not surprising therefore to see tropic responses to a host of environmental signals. Thus, plants have been shown to be able to elicit directional growth responses to stimuli as varied as gradients in water and mineral nutrient availability, gravity, light, touch, temperature and even electrical fields and gradients in oxygen availability (Figure 1). All are thought to contribute to the adaptive success of the plant by directing growth towards resources or away from potentially harmful environments.

Plant tropisms and auxin
The directional aspect of tropic growth in plants arises from asymmetrical elongation of cells on either side of the responding organ (Figure 2). Because plant cells are inseparable due to their cell walls, they cannot move relative to one
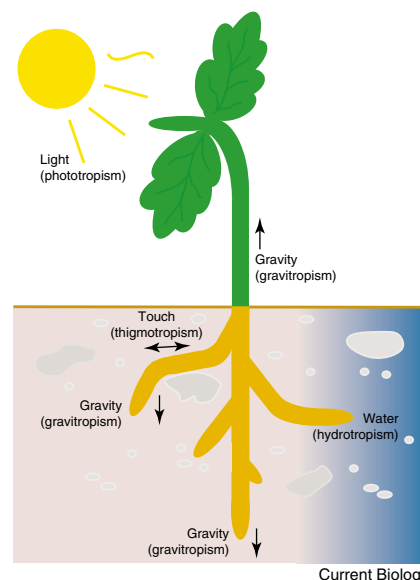

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Figure 1. Plant tropisms.

Plants respond to many directional cues from the environment with directional growth responses called tropisms. The growth response can be towards (positive) or away from (negative) the stimulus as seen in the positive gravitropism of the root and negative gravitropism of the stem. Each organ can simultaneously exhibit several tropic responses, for example, a root encountering a barrier to growth, such as a rock. This root exhibits a thigmotropic response to the touch stimulation to circumvent the obstacle, and then a gravitropic response to restore the downward trajectory of the root tip.
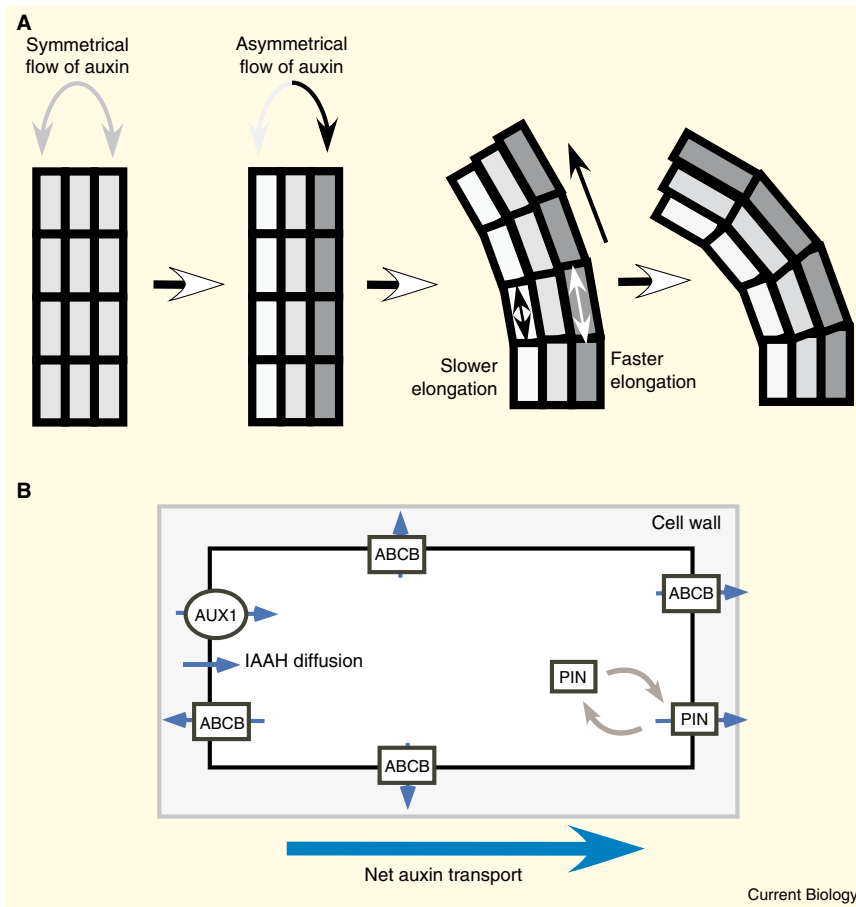
Figure 2. Auxin and directional growth.
(A) Redistribution of the hormone auxin differentially stimulates (in the shoot, shown) or inhibits (in the root, not shown) cell elongation across the organ leading to the bending associated with a tropic response. (B) Flow of auxin (indole acetic acid or IAA) through the plant is governed by the balance between a passive pH-dependent uptake of protonated auxin (IAAH), uptake transporters (AUX1) and efflux transporters (PINs and ABCBs). PIN proteins are known to undergo recycling from the plasma membrane and to relocalize to different faces of the cell. The observation of recycling suggests a possible regulatory point through which tropic stimuli could cause a change in auxin distribution.

another. Thus, the side with the faster elongating cells forces the organ to bend towards the slower growing side. Organs such as roots and shoots are radially symmetrical and can respond with tropic growth in any direction. In addition, the direction of the tropic response is easily reversed when the direction of the stimulus is reversed. Thus, the direction of response is labile and imposed by the sensory systems. The principle regulator of this directional growth response is almost universally accepted to be an asymmetrical redistribution of the plant hormone auxin. In shoots, higher levels of auxin promote cell elongation, whereas in the root higher levels of auxin are inhibitory (Figure 2). Auxin movement is actively regulated by the plant

through control of pH-dependent partitioning into the cell, where the acidic environment of the cell wall promotes formation of the protonated form of auxin (IAAH). The uncharged IAAH permeates the cell membrane and accumulates as the cell-impermeant, charged form (IAA^-) as the H^+ dissociates in the neutral pH conditions found in the cytoplasm. This pH-dependent uptake system is coupled to a series of uptake transporters (AUX and possibly LAX proteins) and efflux transporters (PINs and likely the ABCB proteins, formerly MDRs and PGPs). The sensory systems responding to the myriad signals outlined above must, at some level, feed into the systems that regulate the activity and positioning of these

auxin transporters. The precise molecular link(s) between sensors and the elements of the auxin transport system, however, remains a key open question of critical importance to the tropism field. Interestingly, the PINs are known to show highly dynamic cycling on and off the plasma membrane, suggesting that mechanisms that affect membrane trafficking may be intimately involved in these regulatory processes.

Receptor systems
The receptors for tropic stimuli have really only been defined for the response to the direction of light (phototropism). Plants discriminate between the various wavelengths of light, generally growing towards blue light. The phototropins are the blue-light sensory receptors for this response and are well understood at a molecular level. Although red light generally does not induce a phototropic response, the phototropin system does appear to interact with a pathway dependent on the red-light sensor phytochrome to enhance the overall blue-light response. Phototropism is widespread amongst plants, being seen in mosses, ferns, seed plants and even in algae. It is most easily observed in stems and leaves, with leaves often showing complex diurnal patterns of movement as they track the sun throughout the day to maintain the angle of the blade to the incident sunlight. However, phototropic responses are also seen in roots and have been proposed to help orient root growth with respect to the upper regions of the soil where light can still penetrate. As early as the 1880s, Charles Darwin conducted seminal experiments on maize seedlings to show that the light-perceptive machinery was likely to be localized to specialized regions of the plant. Thus, for maize, he determined that the apex of the coleoptile (a sheath enclosing the seedling shoot) was required for phototropic sensitivity, suggesting that the sensory apparatus that drives tropic growth may be localized to receptive regions of the plant. Similarly, for the response to gravity (gravitropism), specialized sensory cells are located either in the root tip or close to the vascular tissue in the shoot. The directional information of the gravity vector is thought to be translated to a biochemical signaling cascade through

the sedimentation of starch-filled amyloplasts in the cytoplasm. How the movement of these organelles is translated to a biochemical signaling pathway remains a mystery, however, despite the intensive research of many labs. Similarly, for touch it is thought that a Ca^{2+}-related signaling network triggers a cellular response, but the sensor (likely a mechanically sensitive ion channel) and the downstream components that respond to the Ca^{2+} change are largely undefined. Receptors for stimuli such as water gradients or patches of nutrients also remain to be discovered. Current approaches to isolating these elusive receptors and signaling components lean heavily on the isolation of mutants that are altered in the degree of tropic response. A large number of auxin transport–response mutants have been derived from these screens, reinforcing the central role played by auxin in regulating the growth aspect of these tropic systems.

Integrating responses

Considering the barrage of environmental information that the plant must process to yield the appropriate growth response, it is not surprising that evidence is accruing that the various tropic response systems interact and their information is integrated by the plant. For example, in the case of responses to light and gravity, it is known that red light represses shoot gravitropism. Conversely, in some maize varieties, gravitropic responses are actually dependent on prior activation of the red-light signaling system. Similarly, tropic responses to both touch (thigmotropism) and water (hydrotropism) have been shown to downregulate gravitropism. It is likely that part of the integration lies in shared elements of the response system, i.e. all tropic signaling systems have to modulate plant cell expansion at some point. Therefore, it seems highly probable, although not proven, that the various tropic signaling systems are modulating the same cellular machinery that controls cell growth. In addition, data suggest that the various tropic stimulus–response systems can actually compete with each other for ultimate control. The final tropic response would therefore represent the various contributions of each signal dictated by a hierarchy of tropic

response systems under a given developmental and environmental state. Sharing control of the components driving cell growth would provide an obvious site where each signaling pathway could compete for influence on the same cellular regulators, although interaction at the level of modulating receptor sensitivity is also known. For example, under severe drought, finding water is of critical importance for the plant and, under these circumstances, hydrotropic stimulation is known to repress gravitropic signaling. This repression is thought to occur through degradation of the starch-filled amyloplasts that form the core of the gravity-sensing apparatus. Such desensitization of the gravitropic sensor allows the root to concentrate on growth towards its currently most important resource, water. Mechanical stimulation of the root has a similar effect of repressing the gravitropic response, although the mechanism here does not seem to operate through starch degradation. Again, reducing the influence of gravitropism allows the root to respond to its currently most important environmental stimulus, in this case permitting the downward course of growth to be temporarily diverted sideways, allowing rapid circumnavigation of obstacles in the soil. The interactions between other stimuli, such as the influence of mechanical signaling on hydrotropic response, have yet to be determined.

In addition to the effects of multiple environmental stimuli, the precise tropic response from an organ is also highly dependent on its developmental program at that particular time. For example, in the case of the root system, the main root can often show growth dominated by the gravitropic response, growing vertically downward. Should lateral roots show the same response, the developing root system would never expand sideways and so would explore only a small volume of the soil. The lateral roots therefore actually show a gravitropic response that takes them out at an angle from the main axis. This developmentally programmed angle changes as the lateral roots grow and has an important impact on the development of the root system architecture as a whole. Similarly, in the aerial organs, the angle that a branch grows relative

to gravity is highly controlled and differs between different branches throughout development. These angles are so precisely regulated that the characteristic silhouette of a tree can even be used for species identification. Such observations have led to the idea that organs possess their own poise as far as tropic responses are concerned, with developmental, physiological and environmental history all contributing to the response that any particular stimulus can elicit.

Recent progress

Many of our most recent major advances in understanding the molecular mechanisms behind tropic responses have come from using models such as *Arabidopsis*. Thus, researchers have been able to capitalize on the power of access to a sequenced genome and rapid mutant identification coupled to a comprehensive array of insertional mutants across the genome. However, in parallel, our increased understanding of the developmental and environmental effects on particular tropisms has been an important conceptual advance. It has highlighted the care required both in defining the conditions under which tropic analyses are to be performed and in placing each individual tropic response into the context of the network of stimuli to which the plant must sense, integrate and respond. The more we are able to combine molecular and physiological analyses with increasingly sophisticated measurements of tropic behavior, the more we can appreciate the complexity of the calculations the plant must perform in deciding where to grow.

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