PLANT RESPONSES TO GRAVITY - INSIGHTS AND EXTRAPOLATIONS FROM GROUND STUDIES
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ABSTRACT

Formal investigations on the effects of gravity on plants started 300 years ago, but many aspects of gravitropism remain elusive. Despite remarkable progress analyzing the gravity-induced growth response of shoots and roots, the perception of gravity is still enigmatic. The interaction of gravity with competing, intracellular activities (noise) complicates the identification of the primary gravity signal and questions the exclusive role of starch-filled amyloplasts because starch-free mutants are able to respond to gravity. Nonetheless, a reliable response to reorientation relative to the gravity vector must be related to movable masses. The sedimentation of dense intracellular particles such as amyloplasts or protein crystals is reduced by cellular activity; however, the same activity may lead to repeated stimulation of sensitive cellular structures. This concept of dynamic gravisensing has the ability to integrate different cellular organelles as gravity sensors. The transduction of the gravistimulus to a biochemical signal requires a mechano-transducing element such as the cytoskeleton. This cellular system either produces secondary signals such as calcium waves and pH changes but also integrates temperature, light, and other parameters. Biochemical modifications are manifested as subsequent differential elongation, which is controlled largely by the redistribution of auxin efflux carriers and lateral auxin gradients. Efflux carrier redistribution depends on the activation of various kinases and possibly the cytoplasmic auxin gradient itself. Auxin accumulation inhibits elongation of roots but promotes elongation of shoots. The network of physiological interactions forms a graviresponse system that functions continuously for gravitational loads between microgravity and hypergravity of several hundred g-equivalents. The increasing availability of gravitropic mutants will provide answers but also pose many new questions. Together with a plethora of unanswered problems, these challenges will stimulate numerous branches of biology and ensure that gravitropism remains a fascinating topic.

INTRODUCTION

Undoubtedly, the effects of the environment on plant growth have been observed ever since humanity cultivated crops. Among the most conspicuous and important aspects is the emergence of shoots above the ground and the infallible descent of roots into the substrate. Despite age-old knowledge of these facts, methodic investigations of what now is known as gravitropism, have only started in 1700 by the French botanist Denis Dodart. Gravity as cause of the growth responses was identified a century later by Knight (1806), systematically investigated by von Sachs (1879), Ciesielski (1872), and Charles and Francis Darwin (1880). The identification of statoliths and sensing tissue (root cap and shoot endodermis) dates back to studies by Némec (1901) and Haberlandt (1903). A comprehensive treatise by Rawitscher (1932) summarized quantitative aspects of gravitropism and the definition of the gravitropic set-point angle by Digby and Firn (1995) put into context many different growth orientations that once were viewed as separate responses. This brief historical reminder should not obscure the fact that the last decades of research on plant gravitropism brought amazing insights in the biology of plant responses to gravity. However, many aspects of perception, transduction and subsequent growth responses are still not understood, a sentiment that is lamented by most reviews of this topic (see Björkman, 1988; Sack, 1991; Konings, 1995; Kiss, 2000; Tasaka et al., 2001; Blancaflor and Masson, 2003, Palme et al., 2006). Nonetheless, the similarity of responses to gravity and other types of mechanostimulation have prompted attempts to develop ‘a unified hypothesis of mechanoperception in plants’ (Teleswski, 2006). This paper illustrates recent accomplishments allows the formulation of a model of grav- and mechanosensing that integrates some overlooked information; this information should help develop a better understanding of the plant growth response known as gravitropism.

The fundamental significance of gravity for terrestrial growth but reduced importance for aquatic organism suggests that a reliable gravity detection mechanism was necessary for land plants. However, many algae, especially those that are viewed ancestral to land plants, such as the Characeae, have a sophisticated gravisensing and response mechanism (Braun and Limbach, 2005). Complicated interactions between the (aquatic and terrestrial) environment, (thermal and mechanical) loads and stresses, and additional requirements such as the spatially correct orientation of flowers (Shimizu et al., 2005) required adaptations and specialized sensory structures. Hence, many gravisensing mechanisms have evolved (Barlow, 1995). The inter-connectivity among various effects of gravity as a mechanical force resulted in structures that respond to mechanosensing and serve as gravisensors (e.g., flagella of algae, Høder et al., 2005). This paper attempts to summarize principles and interactions that make up a seemingly redundant but robust network of sensory pathways that contribute to the gravity response in plants.

The often-cited progression of the chain of events that comprise gravitropism starts with the perception of a
stimulus by a susceptible structure, transduction (translation of a mechanical into a biochemical signal), and a subsequent, measured response. Although these stages are logical, the true nature of these steps is still elusive.

**Signal perception**

The biggest mystery concerns the process of gravity perception. It has not been possible to identify all relevant gravity-susceptible structures or their interaction with the cellular machinery that constitutes transduction. Although earlier theoretical speculation all but ruled out that individual cells could sense gravity because of its relative weakness compared to other cellular forces (Albrecht-Buehler, 1990), the principle that gravity acts on mass has identified statoliths as perceiving elements of sensory cells. While the term statolith is generic, higher plants rely on starch-filled amyloplasts, Chara BaSO₄-enriched vesicles (Hemmersbach et al., 1999) and fungi such as Phycomyces protein crystals (Schimek et al., 1999) to perform this function. However, fungi may sense gravity ‘inversely’ through the buoyancy of lipids (Grolig et al., 2006).

Despite the diversity of statoliths, their distribution is neither universal nor essential as starchless mutants also respond to gravity, albeit slower (Caspar and Pickard, 1989; Kiss et al., 1989). The lack of statoliths can be compensated by enhanced acceleration such that Arabidopsis roots lacking amyloplasts, regained wild-type level response when hypergravity (5 g) was applied (Fitzelle and Kiss, 2001). The fact that the amount of starch and the number of statoliths correlates positively with gravisensitivity (Kiss and Sack, 1989, 1990; Vitha et al., 2007) does not preclude that other structures or processes can effectively substitute starch-filled amyloplasts. The challenge then is to identify mechanisms that are applicable to cellular processes, compatible with cellular organization and sensitive enough to explain a low sensitivity threshold (about 10⁻⁴ g in roots, Shen-Miller et al., 1968). If starchless mutants respond to gravity (Caspar and Pickard, 1989), but more statoliths in Chara (Kiss, 1994) or starch-loaded amyloplasts provide faster and stronger response [in Arabidopsis stems], one can conclude that ‘only large changes in starch content relative to the WT affect gravitropic sensitivity’ and argue that ‘wild-type sensing is not saturated’ (Vitha et al., 2007). Thus, amyloplast statoliths can be viewed as primary but replaceable part of a system that senses gravity by sedimentation and other means, as will be shown below.

The analysis of amyloplast movements has become a focus of interest (MacClerry and Kiss, 1999; Allen et al., 2003; Palmieri and Kiss 2005; Kumar et al., 2008, Leitz et al., 2009) but most investigations are based on fixed tissue and examine over a given period the average or individual sedimentation of amyloplasts. The recognized interaction of amyloplasts with the cytoskeleton (Psaras, 2004) is ‘regulated and not solely dependent on amyloplast size’ (Schwuchow et al., 2002). Traditionally, the function of amyloplasts is viewed as ‘converting the gravitational potential energy into a biochemical signal’ (Morita and Tasaka, 2004; Leitz et al., 2009). Thus, the mass of sedimenting statoliths generates a response upon interacting with some receptor. The receptor may be the plasma membrane, the endoplasmic reticulum, the tonoplast, ion channels, or the cytoskeleton (Perbal and Driss-Ecole, 2003; Allen et al., 2003; Yoder et al., 2001). Measurements estimated amyloplast sedimentation in the order of 0.154 μm per min (Perbal, 2009) but the cortical ER network is capable of responding to gravity-induced statolith movements within <1 s (Leitz et al., 2009). Subsequent sedimentation requires considerably longer and does not fit estimates of presentation time, the minimum time required to elicit gravitropism, which is typically estimated in the range of seconds (Perbal et al., 2002). This time frame is hardly enough to elicit a substantial sedimentation of amyloplasts, when the sedimentation path, presumably half the width of the statocyte, is in the order of several μm. In addition, disrupting the actin cytoskeleton reduced the sedimentation rate to about 1/10 of the control (Driss-Ecole et al., 2000) but did not inhibit gravitropism (Blancaflor and Hasenstein, 1997; Staves et al., 1997). Instead, the curvature exceeds the ‘set-point angle’ achieved in controls with intact F-actin in roots (Hou et al., 2003) and shoots (Yamamoto and Kiss, 2002). These observations indicate that the concept of simple amyloplast sedimentation and subsequent force transduction through cytoskeleton or membrane systems is too simplistic to account for the sensitivity and speed of the graviresponse.

An alternative concept relies on the functioning of cells as dynamic systems. This concept emphasizes that cellular systems operate in persistent motion and integrates cytoplasmic streaming (Kato et al., 2002; Morita et al., 2002), cellular activities including cytoskeletal tread milling, and thermodynamic noise (kB×T). Instead of sedimentation and resting of statoliths at a gravity-defined site, which produces one stimulus per settled statolith, dynamic sensing stimulates the system continuously. A dynamic system integrates changes in the density of statoliths, metabolic activity, viscosity, and temperature and does not rely exclusively on a single organelle or mass as gravisensor. However, it does not rule out sedimenting masses as gravity sensors. Experimental evidence in support of this concept is the (actin-based) lifting of statolith in Chara rhizoids (Braun et al., 2002), saltatory movements of amyloplasts in corn coleoptiles (Sack et al., 1984), and the movement of amyloplasts in the stem endodermis (Toyota, 2009) and arabidopsis root caps (unpublished data). Cellular ‘agility’ as sensory principle is supported by the onset of gravisensitivity as early as 8 hours after imbibition, long before actual emergence of the radical (Ma and Hasenstein, 2006). If dynamic sensing depends on intracellular movements, then all parameters that affect cytoplasmic motility should affect the gravity sensing mechanism. Most noteworthy among these are physical parameters that contribute to the
distribution and relocation of cellular particles such as viscosity, cytoskeletal ‘stiffness’ and distribution. Viscosity in Chara rhizoids showed a remarkable anisotropy in the tip region, where gravity sensing and response take place (Scherp and Hasenstein, 2007) and is likely to vary in other systems as well. Moreover, the viscosity decreased with the depolymerization of the actin cytoskeleton and to a lesser degree after the depolymerization of microtubules. The variable nature of viscosity is part of the cellular properties that dampen, focus, and distribute forces and statolith movements. This concept was modeled to estimate the force transduction capabilities of the cytoskeleton (Shafrir and Forgacs, 2002; Hu et al., 2003, Sultan et al., 2004). These studies showed that the interconnected filamentous structure could act as a mechano- and signal transducer for mechanical perturbations. The cytoskeleton behaves as a tunable band filter, i.e., the energy transmission is optimal for a narrow range of stimulation frequencies. The efficiency (tuning) of mechano-transduction depends on the ratios and properties of the cytoskeletal elements, viscoelastic characteristics, and suitable frequency range. Interestingly, the estimated optimal frequency for a modeled cell was close to 10 Hz. The validity of this concept for gravising sensing is supported by experimental evidence that thermodynamic and mechanical noise amplified plant graviresponse at similar frequency range (5 Hz, Ma and Hasenstein, 2007). The exponential decay (half-life of about 20 minutes) of this amplification further suggests that short-lived perturbations can affect the sensitivity to mechanical stimuli. Further, preliminary analyses of amyloplast movements in Arabidopsis statocytes by Fourier transformation indicated a peak at about 0.06 Hz (~16 s, unpublished data). This periodicity was observed in vertically growing and horizontally placed Arabidopsis roots and indicates a frequency spectrum of that is susceptible to mechanical perturbations and changes in kBT.

How can these data contribute to a flexible, robust, and possibly universal gravising sensing system? The gravising system must respond to mechanical and thermodynamic noise and be compatible with the undisputed function of statoliths but must also be able to function in the absence of dense or heavy particles, as in starchless mutants. These conditions are met by “stochastic resonance”, which lowers the threshold of mechano-stimulation (Fig. 1). This process for mechano-perception may be universal and was demonstrated for crayfish (Douglass et al., 1993).

The model (Fig. 2) fits observed enhancement of gravitropic sensitivity in the absence of gravitational load (Perbal et al., 2004); it does not require amyloplasts but extends the notion of statoliths to other movable particles and is independent of the intracellular distribution of amyloplasts. Stochastic events can affect any susceptible particle and provide immediate, gravity-depending stimulation. Heavier particles lead to more and/or more energetic interactions between statoliths and membranes, cytoskeletal elements, or other sensitive structures, including vacuoles (Kato et al., 2002). The signal-generating collisions will have to elicit a membrane-related signal, perhaps the opening of stretch-activated channels (Perbal et al., 2004) that remain open until closed by a correcting (cytoskeletal?) activity. This concept is supported by related investigations on mechano-transduction in human leukemia cells where F-actin disassembly resulted in a reduction of the amplitude of stretch-activated currents but did not affect the probability of channel opening (Staruschenko et al., 2005).

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**Figure 1:** Model of a noise-based amplification of a mechanical signal (after Moss, 2000). The established threshold (ΔE) cannot be reached by the sub-threshold signal (A). Added noise induces spikes that exceed the threshold (B) and transform the original, amplitude-dependent signal into a frequency-modulated signal (C). This model can produce an above threshold signal in the presence of statoliths. Their kinetic or potential energy exceeds the threshold. In the absence of statoliths, the number of detectable events depends on the metabolic activity that provides noise, e.g., cytoskeletal movement, the quantity of (dense) particles, and the direction of the gravity vector.
A critical aspect of noise amplification of graviposition is the ability to integrate various parameters such as temperature, gravitational load, angle of stimulation, cytoskeletal integrity, viscosity, and other stimuli such as thigmotropism (Massa and Gilroy, 2003a, b; Monsenhausen and Gilroy, 2009), circumnutations (Kitazawa et al., 2005; Tanimoto et al., 2008; Johnsson et al., 2009), and sedimenting of protein crystals (Schimek et al., 1999). Proteins have a lower density ($\rho \sim 1.2$ g/cm$^3$; Andersson and Hovmöller, 2000) than starch ($\rho \sim 1.55$ g/cm$^3$ for potato starch (Iseib, 1958) and $\sim 1.38$ for soybean starch (Kuznetsov et al., 2001)) and therefore are weaker sensors (P particles in Fig. 2). It is possible to ascribe a tentative mass, about 1/5 of an amyloplast, to these particles considering that starchless mutants achieve wild-type volume. The density and size of these particles can vary and they do not have to be uniform in shape or volume.

Importantly, this model can account for the puzzling observation that disrupting f-actin does not prevent sensing or curvature but fails to stop the reorientation signal (Yamamoto and Kiss, 2002; Hou et al., 2003), possibly because the actomyosin system is less able to agitate amyloplasts. Stochastic events or noise amplification is also in line with the effect of high-gradient magnetic fields (HGMF) that induce curvature similar to gravistimulation (Kuznetsov and Hasenstein, 1996, 1997; Kuznetsov et al., 1999; Weise et al., 2000). Because HGMFs work only on particles with sufficient (density-dependent) magnetic susceptibility, the effective force is restricted to dense statoliths (starch-filled amyloplasts), the onset of curvature in response to HGMF is delayed, and the overall response weaker than reorientation in the gravity field despite stronger magnetic forces than unit $g$. The evidence for graviperception outside of the root cap in the distal elongation zone of corn roots where no amyloplasts are found (Wolverton et al., 2002a, b), further supports the concept of noise-amplified graviposition. This view of graviposition may sound heretic, but following Einstein’s logic “If at first, the idea is not absurd, then there is no hope for it”, it should provoke new investigations.

The Cytoskeleton: Sensor and Transducer

The distinction between perception and transduction is arbitrary (the scenario depicted in Fig. 2 already describes a speculative type of transduction by invoking channel activity). However, the well-documented involvement of the cytoskeleton in transport, organization, and growth makes it an attractive candidate for both perception and downstream events of mechanotransduction. The distribution of load-bearing rods (microtubules) and tension-providing actin filaments is the basis of the tensegrity model of cell mechanics (Ingber, 1993, 2003; Hu et al., 2003; Sultan et al., 2004). This concept renders the entire stress-strain behavior of cells during growth and mechanical perturbation (i.e., sedimenting or moving statoliths) susceptible to mechanical forces and constitutes a generic sensor. The connection of the cytoskeletal network to the plasma membrane, organelles, and the endomembrane system enables the transmission of forces to a discrete receiver (Fig. 2) and can affect metabolic changes that translate mechanostimulation into biochemical events. F-actin-based graviposition was linked to the disruption of actin filaments by sedimenting statoliths (Yoder et al., 2001); this model proposes that the perturbation of the actin mesh results in ion gradients but it is not compatible with the documented ability to perceive gravity signals after f-actin has been depolymerized (Blancaflor and Hasenstein, 1997; Hou et al., 2003). Because F-actin is not essential for the perception and response to gravity, it may not function as receptor but could serve as force transducer. However, since it is possible that a subset of the various isoforms remains intact after drug-induced depolymerization, relevant, vegetative actins (Meagher et al., 1999, Kandasamy et al., 2007) may have to be eliminated before relevant actin isoforms and function can be identified. Differential susceptibility of actin isoforms have been shown for Snapdragon shoots (Friedman et al., 2003) and Chara internodal cells (Foissner and Wasteneys, 2007).

![Figure 2: Model of gravisensing in statocytes that uses stochastic events that affects particles (P) with a mass that because of stochastic noise exceeds the minimum energy level. Conventional statoliths (S) are rarer but their mass provides kinetic energy sufficient to activate channels without stochastic assistance. Gravity affects the distribution of the combined statoliths and detectable events (see Fig. 1) increase in the direction of the gravity vector. Successful interaction with the membrane opens/activates mechanosensitive channels or efflux carriers (PIN3 proteins). The (F-actin) cytoskeleton is necessary to close the channels. As long as gravistimulation occurs, basal channels either on the ER or plasma membrane will open and provide discrete but frequent signals that indicate ‘down’. Disruption of the actin filaments prevents closure and causes persistent channel conductivity.](image-url)
Despite these complications, F-actin is a likely signal transducer because it has been implicated in cell-to-cell connectivity through plasmodesmata (Baluška et al., 2004) and endocytosis (Šamaj et al., 2004) and is linked to calcium channel activity in cells (Wang et al., 2004; Gu et al., 2005; Braun and Limbach, 2005) and in stems (Toyota et al., 2008). These data are interesting because of calcium’s well-established role as secondary messenger. An increasingly better understanding of the role of calcium as a mediator of gravitropism started with no evidence of calcium in response to gravistimulation (Legué et al., 1997). Subsequent data indicated a weak, but longer lasting increase in cytoplasmic calcium (Pleith and Trewavas, 2002). Recent studies documented a biphasic calcium wave that is sensitive to the speed and extent of reorientation (Toyota et al., 2008). A transient increase in calcium was also shown to precede the production of reactive oxygen species and alkalinization (Monshaufen et al., 2009), a phenomenon that was proposed as primary event in gravisensitive cells (Hou et al., 2004). Calcium also plays a role in the polarity of fern spores (Chatterjee et al., 2000; Salmi et al., 2007) and pH changes serve as generic secondary messenger (Felle, 2001), but also directly affects F-actin organization (Lovy-Wheeler et al., 2006). The interconnectedness between graviresponse, mechanosensitive calcium channels, pH, auxin transport, and F-actin illustrates the complexity of the graviresponse system. In addition, the actin cytoskeleton is sensitive to many other factors ranging from nitric oxide (Kasprówicz et al., 2009), light and salt stress (Dunáeva and Adámska, 2001), mechanical bending (Ditengou et al., 2008), ions (Amenos et al., 2009), and growth regulators (Kleine-Vehn et al., 2008, Dhonukshe et al., 2008). Especially important is the connection with apoptosis (Franklin-Tong and Gourlay, 2008), because excessive mecanostimulation (clinorotation) induces apoptosis in root cap cells (Smith et al., 1997, Ma and Hasenstein, 2006). In light of its dynamic reorganization, which includes terminal dissolution and extension (tread milling) and large-scale severing (Staiger et al., 2009), F-actin is not only an essential integrator for many processes but also likely to participate in mechanotransduction, organelle and statolith movement, and subsequent regulatory steps. These F-actin sensitive processes include redistribution of auxin efflux carriers (Gao et al., 2008), auxin dependent patterning (Maisch and Nick, 2007), and the response to self-incompatibility reactions (Geitmann et al., 2004), and circummutations (Yoshihara and Iino, 2006; Tanimoto et al., 2008; Johnsson et al., 2009).

The Growth Response

Since the days of Cholodny (1924) and Went (1926), auxin and its uneven redistribution between the upper and lower flank of a curving structure has been viewed as essential for gravitropic curvature. The identifi cation of PIN proteins (Gälweiler et al., 1998), as auxin efflux carriers has explained on a molecular level the auxin transport pattern (AKA soda fountain, Hasenstein and Evans, 1988). Auxin moves through the stele to the meristem and root cap, where it is distributed symmetrically in vertical roots and preferentially along the lower flank in non-vertical roots. The impressive progress in understanding auxin redistribution as prerequisite for curvature, relies on an F-actin mediated reorganization of auxin efflux carriers in the root cap (Muday, 2000). The cooperative mode of action of different pin proteins in the root tip exemplifies the significance of auxin distribution for root growth and development (Friml, 2003; Santelia et al., 2008; Vanneste and Friml, 2009). The reorganization of the auxin transport and graviresponse is at least partially dependent on pinoid kinase activity but this kinase does not affect cellular polarity (Gao et al., 2008; Sukumar et al., 2009). However, the effectiveness of the PIN secretion system depends on kinase activation (Zourelidou et al., 2009). The 3-phosphoinositide-dependent protein kinase (PDK1) may be the link that activates several protein kinases of the AGC kinase family (Bögre et al., 2003). Despite the identification of the PIN efflux carriers and the network of interdependent kinases, the cytoplasmic auxin gradient itself may serve as polar signal (Kramer, 2009; Teale et al., 2008). This concept is appealing because it does not require additional transduction steps and in line with the integration of auxin transport and signaling (Leyser, 2006).

The response to gravity eventually integrates a host of different modulators [peroxide (Joo et al., 2001), nitrous oxide (Neill et al., 2008), light (Galland et al., 2007; Molas and Kiss, 2009), gravimorphogenesis (Fujii et al., 2007), and touch (Fasano et al., 2002)] that affect gene transcription (Kim brough et al., 2004) and ultimately affects protein expression. Proteome analyses of undifferentiated callus tissue have shown that the gravity changes significantly up- and down regulates more than 20 proteins. Interestingly, hyper-g and 2D-clinorotation had similar effects but random positioning halved the number of affected proteins (Barjaktarović et al., 2007). While these data indicate that the standard procedure for mimicking weightlessness in ground studies, clinorotation around a single axis, is inadequate, they illustrate a ‘gravitational continuum’ between unit g and hyper-g (Martzivanou and Hampp, 2003; Wang et al., 2006). The logarithmic dependency of growth responses between 1 to 300 g-equivalents (Soga et al., 2006) suggests that plants are capable of thriving in complete weightlessness as well as in worlds of many times earth’s gravity. It is worth investigating if exposure to altered acceleration affects the metabolism of relevant amyloplasts such that hypergravity reduces and microgravity enhances starch accumulation; this adaptive change is possible because the metabolism of amyloplasts is based on more than 280 proteins (Balmer et al., 2006). Such flexibility could increase the statolith mass to compensate for reduced gravity or reduce the mass at higher acceleration.

Many details must be studied to produce a comprehensive and robust understanding of the parameters that contribute to the different stages of gravitropism. Although several of these interactions rely on the mandate to remove
gravity, i.e., space flights, there is ample demand for ground-based research. For example, the variable auxin distribution based on the localization of auxin efflux carriers (Vieten et al., 2007) generates an intra- and intercellular auxin gradient across the root cap. If the root tip is maintained horizontally at a constant angle relative to the gravity vector (Wolverton et al., 2002b), the secretion of auxin is likely to be higher than in a root that curves and adjusts to the gravity stimulus. Consequently, the auxin gradient must remain stronger and secondary processes (biosynthesis, adaptation, sensitivity, efflux efficiency etc.) are likely to change. High-resolution analyses of IAA concentration gradients within the Arabidopsis thaliana root tip show a maximum in the quiescent center and demonstrate that local biosynthesis and polar transport produce auxin gradients (Petersson et al., 2009). Higher auxin concentrations are dispersed by transport, diffusion, or degradation but the enhanced concentration of auxin at the lower side of the root cap still represents a type of memory. Despite this postulate, root curvature in intact roots does not continue once the root is oriented back to the vertical (Wolverton, pers. communication; own, unpublished data), unlike in roots that were reoriented but whose F-actin was disrupted.

Another, vast area of research concerns the integration of information gleaned from experiments with mutants. The solution undoubtedly requires mathematical approaches (Palme, 2006, Teale et al., 2008) but also a thorough functional characterization of the many useful mutants. Does temperature-sensitivity (gravity persistence signal, Wyatt et al., 2002) relate to the Altered Response to Gravity (ARG and its paralog ARL, Harrison and Masson, 2008) via changes in auxin transport and/or altered sensitivity of efflux carriers (Boonsirichai et al., 2003; Shin et al., 2005)? Wavy Growth 2 protein interfaces gravitropism and touch signals but actually links a transmembrane moiety with hydrolase activity (Mochizuki et al., 2005). Reversing the growth direction and reducing root undulations are controlled by the Wave-Dampened2 gene (Yuen et al., 2003) but changes in root hair development are also related to general epidermal cell file rotation and expansion patterns (Yuen et al., 2005). Shoot gravitropism (sgr) mutants of Arabidopsis affect transcription factors (Morita et al., 2006), and amyloplast development (Morita et al., 2007). Interestingly, mutants of microtubule associated EN D BINDING1 (EB1) proteins affect the gravitropic set-point angle by inducing roots that deviate from the vertical, and exhibit delayed responses to touch and gravity (Bisgrove et al., 2008). Null mutations of MILDEW RESISTANCE LOCUS O 4 (MLO4) and MLO11, which encode plasma membrane–localized proteins predominantly expressed in the root tip, result in aberrant root thigmomorphogenesis and demonstrate that closely-related proteins integrate responses to light, gravity, nutrients, and auxin transport; these proteins link exaggerated root-curling phenotypes to auxin gradients and thigmotropism (Chen et al., 2009).

The list of such mutants is extensive but creating a unified picture of gene activity, control, and interdependence that correctly describes the plant graviresponse is still elusive.

In all likelihood, a web-like system of many input and output parameters will emerge that illustrates the complexity, robustness, and sensitivity of the response of ‘sessile organisms’ to gravity.

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